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Leading with morphometric data in fossil vertebrates: a case-study of the intra-specific variation and allometry of the skull of Late Cretaceous side-necked turtle *Bauruemys elegans* (Pleurodira, Podocnemididae)

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Background. Previous quantitative studies about *Bauruemys elegans* (Suárez, 1969) shell variation, as well as the taphonomy interpretation of its type locality, have suggested that all specimens collected in this locality may have belonged to the same population. We rely on this hypothesis in a morphometric study of the skull. Also, we tried to assess the eating preference habits differentiation that might be explained as due to ontogenetic changes. **Methods.** We carried out an ANOVA comparing 29 linear measurements from 21 skulls of *B. elegans* using both caliper and ImageJ. A Principal Components Analysis (PCA) was performed using 27 measurements (excluding total length and width characters) in order to visualize patterns of scattering based on the form variance. Then, a PCA was carried out using ratios of length and width of each original measurement to assess shape variation among individuals. Finally, original measurements were log-transformed to describe allometries along ontogeny. **Results.** No statistical differences were found between caliper and ImageJ measurements. The first three PCs of the first analysis comprising 70.2% of the variance. PC1 was related to size variation and all others related to shape variation. Two specimens ~~have been~~ plotted outside the 95% ellipse in PC1xPC2 axes. The first three PCs of the second PCA comprised 64% of the variance. When considering PC1~~x~~PC2, all specimens ~~have been~~ plotted inside the 95% ellipse. In the third analysis, five measurements were positively allometric, 18 were negatively allometric and four represent truly negatively allometry. All bones of the posterior and the lateral emarginations, as well as the squamosal, lengthen due to size increasing, different from the jugal and the quadratojugal which decrease in width. **Discussion.** ImageJ is useful in replacing caliper since there was no statistical differences. Yet, iterative imputation is more appropriate to deal with missing data in PCA. Some specimens show small differences in form and shape. Form differences were interpreted as due to ontogeny, whereas shape differences are related to feeding changes ~~along~~ growth. Moreover, all

outlier specimens are crushed and/or distorted, thus the form/shape differences might be partially due to taphonomy. The allometric ~~lengthen~~ of parietal, quadrate, squamosal, maxilla, associated with the narrowing of jugal and quadratojugal may be related to changes in feeding habit between different stages of development. This change in shape might represent a progressive skull stretching and enlargement of posterior and lateral emargination during ontogeny, and consequently, the increment of the feeding-*apparatus* musculature. Smaller individuals may have fed ~~of~~ softer diet whereas ~~bigger~~ ones probably have had a harder diet, as seen in some living species of *Podocnemis*. We conclude that the skull variation is higher than expected and might be related to differences in feeding habits ~~along the~~ ontogeny ~~of~~ *B. elegans*.

Leading with morphometric data in fossil vertebrates: a case-study of the intra-specific variation and allometry of the skull of Late Cretaceous side-necked turtle *Bauruemys elegans* (Pleurodira, Podocnemididae)

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1. Introduction

1.1. Principal Component Analysis and fossil sampling bias

Paleontological data are intrinsic scarce (Strauss, Atanassov & Oliveira, 2003; Hammer, 2006), leading to incomplete data sampling. This limitation impact several approaches ~~on~~ paleontological studies, especially inter-specific variation analyses. Although there are some approaches proposed to deal with missing entries in fossil datasets (e.g.: Norell & Wheeler, 2003; Strauss, Atanassov & Oliveira, 2003), sometimes the study relies on a statistic exploratory evaluation of general structure in the data and Principal Component Analysis (PCA) is commonly used ~~to~~ this purpose.

PCA is a multivariate and exploratory analysis. Its aim is to identify the variables that account for the majority of the variance within a multivariate matrix, by means of linear combinations of all variables, which are converted into components that are independent of each other. Hence, PCA ~~technique~~ summarizes a large amount of the variance contained in the data (Krzanowski,1979; Hammer, Harper & Ryan, 2001). It thus reduces a multidimensional space into fewer components which retain the majority of the variance of the sample (Jolicoeur & Mosimann, 1960; Peres-Neto, Jackson & Somers, 2003), ~~becoming easier to make~~ interpretations on large data sets.

This approach has been largely applied to both extant and fossils vertebrates (e.g. Jolicoeur & Mosimann, 1960; Claude et al., 2004; Depecker et al., 2005, 2006; Astua, 2009; Burnell, Collins

& Young, 2012; Costa, Moura & Feio, 2013; Bhullar et al., 2012; Fabre et al., 2014; Werneburg et al., 2014; Ferreira et al., 2015), as well as a matter of discussion on 70's and 80's years (e.g.Krzanowski, 1979, 1982; Corruccini, 1983; Somers, 1986, 1989; Sundberg, 1989) under the light of allometric interpretations.

1.2. Case-study

1.2.1. Skull variation

The skull is one of the most variable structures in vertebrates because it concentrates several sensory organs, the brain, and the beginning of the respiratory and digestory systems, including chewing muscles (Smith, 1993). Consequently, the skull is the body portion with more phenotypes used in vertebrate cladistic analysis (Rieppel, 1993), as seen in turtles, in which most cladistic analysis rely mainly on cranial characters (Gaffney, 1975; Gaffney et al., 1991; Meylan, 1996; Hirayama, 1994; Hirayama, 1998; Hirayama, Brinkman & Danilov, 2000; de la Fuente, 2003; Takahashi, Otsuka & Hirayama, 2003; Gaffney et al., 2006, 2011; Joyce, 2007; Joyce & Lyson, 2010; Lyson & Joyce, 2009, 2010; Sterli et al., 2010; Sterli & de la Fuente, 2011a, b; Gaffney & Krause, 2011; Anquetin, 2012; Rabi et al., 2013; Havlik, Joyce & Böhme, 2014; Romano et al., 2014; Brinkman et al., 2015; Ferreira et al., 2015; Sterli, de la Fuente & Krause, 2015). Despite that, most of skull materials found in paleontological record of turtles are unique and/or damaged due to the fossilization process bias, not allowing intraspecific studies or ontogenetic inferences on most fossil turtle species known.

1.2.2. *Bauruemys* taxonomy

Bauruemys elegans (Suárez, 1969) is a Late Cretaceous freshwater side-necked turtle found at the Pirapozinho site (Suárez, 2002). This species was originally described as *Podocnemis* in three different communications by Suárez (1969a, b, c) and identification was based on the overall similarities of skull and shell to this living genus, a common practice at that time. Other South American Cretaceous side-necked turtles were initially identified as *Podocnemis* as well, such as the *nomina dubia “Roxochelys” harrisi* (Pacheco, 1913) and *“Bauruemys” brasiliensis* (Staeche, 1937) and the *incertae sedis “Podocnemis” argentinensis* (Cattoi & Freiberg, 1958) (see Romano et al., 2013 for a revision on Bauru Group species and Fig. 1). ~~On~~ a revision of *Bauruemys elegans*, Kischlat (1994) was the first to point out that all *Podocnemis* reported to the Cretaceous were doubtful and proposed a new genus to include *B. elegans* and, tentatively, *B. brasiliensis.* His approach was based on similarities of the plastron of both species. Kischlat (1994) and Kischlat et al. (1994) also pointed that *B. elegans* could belong to Podocnemididae, but they did not test~~ed~~ their hypothesis. Romano & Azevedo (2006) were the first to carry out a cladistic analysis to access the phylogenetic position of *Bauruemys*, placing it as a stem-Podocnemididae, i.e.: the sister group of all other Podocnemididae, which ~~were~~ confirmed by subsequent analysis including more podocnemidid species as terminals (França & Langer, 2006; Gaffney et al., 2011; Oliveira, 2011; Cadena, Bloch & Jaramillo, 2012).

1.2.3. Geological settings and taphonomic context of the Tartaruguito site

The Pirapozinho site, long ago known as “Tartaruguito” and formally assigned as such by Romano & Azevedo (2007) and Gaffney et al. (2011), is an Upper Cretaceous outcrop from the Presidente Prudente Formation, Bauru Basin (*sensu* Fernandes & Coimbra, 2000). It is located in Pirapozinho municipality, São Paulo State, Brazil (Fig. 1). The “Tartaruguito” name, which means “turtle in rock” (*tartaruga*, from Portuguese, turtle; *ito*, from Greek, rock), is due to the great amount of turtle specimens found at that place. It is comparable to other rich fossil turtle localities, such as (1) the recently found Middle Jurassic Qigu Formation of the Turpan Basin in

China (Wings et al., 2012; Rabi et al., 2013); (2) the Middle-Upper Paleocene Cerrejón Formation in Colombia (Jaramillo et al., 2007; Cadena et al., 2010; Cadena, Bloch & Jaramillo, 2012; Cadena et al., 2012); (3) and the Upper Miocene Urumaco Formation ('Capa de tortugas') in Venezuela (Aguilera, 2004; Sánchez-Villagra & Aguilera, 2006; Sánchez-Villagra & Winkler, 2006; Riff et al., 2010; de la Fuente, Sterli & Maniel, 2014). The two latter localities are near-shore marine coastal deposits with influence of freshwater rivers (Jaramillo et al, 2007; Gaffney et al., 2008), whereas the former and the Tartaruguito site correspond to rocks that had been deposited in a riverine system with seasonal droughts in which turtles gathered in retreating, ephemeral water pools and died when habitat dried up completely (Soares et al., 1980; Fulfaro and Perinotto, 1996; Fernandes & Coimbra, 2000; Henriques et al., 2002, 2005; Suárez, 2002; Bertini et al., 2006; Henriques, 2006; Wings et al., 2012). The Tartaruguito is also the type-locality of the Peirosauridae crocodile *Pepesuchus deiseae* Campos, Oliveira, Figueiredo, Riff, Azevedo, Carvalho & Kellner (2011).

The general lithology of the Tartaruguito site is composed of cyclic alternations of sandstones and mudstones deposited in a meandering fluvial system with crevasse splays (Fernandes & Coimbra, 2000; Henriques et al., 2005). Many articulated and complete fossils are found in these sequences, which indicate seasonal low energy floods (mudstones) followed by droughts (sandstones) in the region during Late Cretaceous (Henriques et al., 2002, 2005; Henriques, 2006). Because only medium- to b~~ig~~-sized fossil specimens are found at the locality, we believe that the Tartaruguito site was a foraging area for turtles (D. Henriques, pers. comm.). Thus, the fossil assemblage probably represents several episodes of floods and droughts. The flood periods might have allowed foraging areas expansion for turtles and crocodiles, while during the dry seasons turtles gathered on the remnants of water pools and some died when pools dried up completely (Henriques et al., 2002, 2005; Henriques, 2006).

That being said, we consider that all turtle specimens found at the Tartaruguito site might correspond to subadults to adult ages, and that is reasonable to assume all *B. elegans* individuals collected in the Tartaruguito site might have belong to a single population (agreeing with Henriques et al., 2002, 2005; Henriques, 2006). Indeed, as pointed by Romano & Azevedo (2007), this single population would consist on different generations of turtles' corpses grouped in the same locality. One might consider that size differences might be due to sexual dimorphism (R. Hirayama and S. Thomson, pers. comm.), on which the females would be bigger and have more posteriorly extended carapaces than the males. However, sexual dimorphism on podocnemidid turtles can be accessed only on shell shape and our data is based mostly on isolated skulls (see Material and Methods). As consequence, although it is possible to have some sexual dimorphism size effect on our data, we do not considered it, given the lack of evidence to assume such outcome. Moreover, Romano & Azevedo (2007) were not able to reject the single population hypothesis using shell measurements (from both plastron and carapace) in a morphometric approach neither describe sexual dimorphism in the data, concluding that the differences were due to ontogeny variation among individuals from different generations. Therefore, we highlight that we are assuming the population definition of Futuyma (1993), as taken on by Romano & Azevedo (2007), that a population is a conjunct of semaforontes temporally connected, i.e., a sequence of individuals from different generations, and limited in a restrict space, in this case, the Tartaruguito site.

1.3. Objectives

Many fossil materials are housed in foreign collections and are not easily accessible by researchers. It can narrow and even preclude their studies. In addition, given the missing data problem inherent to fossil record, the way one lead with the missing entries in morphometric studies can affect the results and conclusions. Here we test a novel approach to take linear measurements for morphometric studies based on photographs of fossil materials. We also evaluate how different approaches desinged to deal with missing data can impact results of exploratory statistical procedures and data interpretation by comparing two different substitution algorithms of missing entries. These procedures are exemplified using a real paleontological data set and with a paleobiological inferences.

We carried out the same approach of Romano and Azevedo (2007) using cranial characters in order to explore the variation among individuals from different ages and generations – then, assuming Henning's (1966) semaphoront concept to the specimens of our sample. Also, we described the differences in skull morphology along the ontogeny of *B. elegans* and the probably consequences of such variation to the diet preferences changes along the growth.

2. Material and Methods

2.1. Sample and characters

Twenty one skulls of *Bauruemys elegans* were examined in this study: AMNH-7888, LPRP0200, LPRP0369, LPRP0370, MCT 1492-R (holotype), MCT 1753-R (paratype), MCZ 4123, MN 4322-V, MN 4324-V, MN 6750-V, MN 6783-V, MN 6786-V, MN 6787-V, MN 6808-V, MN 7017-V, MN 7071-V, MZSP-PV29, MZSP-PV30, MZSP-PV32, MZSP-PV34, and MZSP-PV35. We established 39 landmarks (Fig. 2) that decompose the overall shape of the skull in order to take measurements between two landmarks. Moreover, since most of the specimens have deformation and breakage, we could not perform a geometric morphometric analysis using the landmarks because the taphonomical bias would incorporate error to the analysis of form and shape. Thus, we used the landmarks to set up 29 traditional morphometric characters that correspond to a linear measurement between two landmarks (all characters are described ~~on~~ table 1). Also, the use of landmarks to set up the measurements is useful to maintain the same anatomic references for all characters in each specimen, since the landmarks enable a better description of morphological variation and establishment of quantitative characters, as exemplified by Romano & Azevedo (2007). All measurements were taken by ~~TFM in~~ the same side of the skull (right side) unless the characters could not be ~~measurable~~ due to deformation or breakage. We used ImageJ version 1.47 (Rasband, 1997) to take the measurements after comparing its accuracy with the caliper (Mariani & Romano, 2014). This procedure was necessary because ~~PSRR~~ obtained photos of skulls housed in foreign collections and did not perform measurements by caliper. The error test between measurements taken using caliper and ImageJ are described bellow. We followed the bone nomenclature of Parsons & Williams (1961) and extended by Gaffney (1972, 1979) (see all abbreviations after Conclusion topic).

2.2. Statistical Analysis

Before carrying out the statistical analysis, we compared the same characters data set (Data S1) of the same sample ~~by~~ using two different approaches (= treatments): measurements taken using caliper and measurements taken using photographs via ImageJ. This comparison was necessary in order to evaluate whether or not the two measurements methods are significantly different. Then, we performed an One-way Analysis of Variance (ANOVA) comparing the 29 measurements in 12 specimens (LPRP0200, LPRP0369, LPRP0370, MN4322-V MN4324-V, MN6750-V, MN6783-V, MN6786-V, MN6787-V, MN6808-V, MN7017-V, and MN7071-V).

Two groups of variables were established: measurements taken directly from specimens using caliper (preliminary data set 1) and the same characters taken from photographs of the same specimens using ImageJ (preliminary data set 2). All characters taken using photographs/ImageJ that did not show significant differences to their correspondents taken by caliper were used on the subsequent statistical analyses of form and shape differences among the sample of *Bauruemys elegans*. By doing that, the sample was increased without including error and incomparable characters (i.e.: by using different measurement techniques).

Three analyses using the complete sample were carried out: (1) a descriptive statistics (mean, standard deviation, median, variance, maximum and minimum values) of all characters (Data S2), (2) an allometric analysis of length and width characters correlating them to total length and width measurements (Data S3), and (3) a multivariate non-parametric exploratory statistics via Principal Component Analysis (PCA). The ~~later~~ was divided into two different PCA: (3.1) using 27 characters from the raw data matrix (total lenght and width characters were excluded in this analysis; Data S4), and (3.2) using 27 charactes that represent proportions of each length and width characters in relation ~~with~~ total length and width characters, respectively (Data S5). All statistical analysis were performed using the software PAST version 3.05 (Hammer et al., 2001).

In the first PCA approach (3.1) we excluded total length and width characters because of its high influence ~~in~~ the PCA result, since higher values compose the majority of the summarized variance in PC's (Mingoti, 2013), and because of the redundance between these measurements and the others. We also assessed differences by applying two different substitution algorithms for missing data in PAST, using the default "mean value imputation" option (i.e. missing data are replaced by the column average), and the alternative "iterative imputation" option, which computes a regression upon an initial PCA until it converges to missing data estimations, replacing missing data by such estimations (Ilin & Raiko, 2010). The latter is recommended and, after comparing both results, we selected it (see supplemental material 3 to visualize PCA results computed using PAST’s default option approach). The second PCA (3.2) was conducted to remove effect of [illegible] and perform an exploratory analysis of the shape alone. Six specimens were removed from this second analysis because were broken and the total length or width measures were not measurable.

The first analysis was made in order to quantify and describe the variation of the characters set in *Bauruemys elegans* skull, using the assumption of the sample be representative of a single population. The second analysis allowed us to make inferences about osteological shape change related to size change, i.e., related to growth, by assuming that bigger specimens are older than smaller ones. This approach is, therefore, a study of allometry (Huxley & Teissier, 1936; Huxley, 1950; Gould, 1966; Gould, 1979; Somers, 1989; Futuyma, 1993) and the assumption of correlation between size and aging is based on continuous growth to be common on extant turtles (Klinger & Musick, 1995; Shine & Iverson, 1995; Congdon et al., 2003). ~~The PCA analyses were carried out in order to evaluate if there are some structuring in the data through the reduction of the variation into orthogonal axes which retains most of the variance~~. Since the use of a parametric statistic was infeasible due to the nature of the sample (i.e.: a small matrix that do not show homoscedasticity and normality in data set), the PCAs were used to search for a structure of the data that matches to that illustrated by Romano & Azevedo (2007) using postcranial characters. If the pattern observed is similar to previous morphometric and taphonomic inferences, then it is interpreted as not enough existing evidence to assume the sample represents different populations of *Bauruemys elegans*. In other words, since a parametric test is not feasible with statistical confidence, the lack of structure in the ~~PCAs projections~~ were herein interpreted as a fail to the attempt of falsifying the single population hypothesis.

3. Results

3.1. Does caliper differ from images?

The results of ANOVA are summarized in table 1. We found most of measurements do not differ statistically (p>0.05) between the two treatments (caliper and ImageJ). However, one measurement, length of maxilla (LMX), had statistical difference (p=0.017) between the treatments (see discussion). Because of this result, we increased our sample from 12 to 21 specimens.

3.2. Descriptive Analysis

The results of the descriptive statistics are summarized in table 2. As expected values of total length and width (TLS and WLS) were the most variable in comparison with others, because the variation scale in these characters is greater than in others. Characters of the bones forming the upper temporal fossa (i.e. PA, QJ, SQ, QU and OP) had great variation, being parietal the most variable in lenght (SD=6.45) and the ~~smallest in~~ width (SD=2.94), whereas quadratojugal obtained the smallest variation in lenght (SD=2.38) and the greatest in width (SD=4.03). Among the characters of the bones forming the lower temporal fossa (i.e. JU, MX, PO, PT and PAL), the variation in lenght was in general greater than in width. Postorbital and maxilla had almost the same variation in lenght (SD=4.12 and SD=4.11, respectively); WPO had the smallest variation within the group of bones forming the lower temporal fossa (SD=1.83); and the ~~streeth~~ of the maxilla had the greatest variation (SD=7.63) of all characters measured. Characters of the other bones had smaller values than the aforementioned bones, with the exception of WPO which was smaller than LFR (SD=2.08), LVO (SD=1.95), LBO (SD=2.12),WFR (SD=1.88) and WBS (SD=2.19).

3.3. Allometric Analysis

Among all comprised measurements, three were truly negatively allometric (LPF, WJU and WQJ); five were positively allometric (LPAL, LPT, LPO, WPF and WPO); and the others were negatively allometric. It is also worth to note that two were virtually isometric [WPF (a=1,0074) and WOP (a=0.98159)]. All regressions are shown on figures 3, 4 and 5.

3.4. Principal Component Analysis (PCA)

3.4.1. Raw data

3.4.1.1. Replacing missing data with mean values

By using the “mean value imputation” approach, a total of 70.32% of the variance was comprised by the first three principal components (PC1=42.15%; PC2=16.82%; PC3=11.35%), so that the others were less significant for the analysis and are not presented. We interpreted that PC1 variation is due to size change-over because an approach using all characters have shown a similar result. PC2 and PC3 seems to represent shape differences between individuals. In all PC individual projections (Fig. 6A and 6B) most of specimens were included inside the 95% ellipse. Two exceptions are MCZ4123 and MN7071-V, which have not been included in the ellipse when PC1 vs. PC2 were considered (Fig. 6A); also the former was outside the ellipse in PC2 vs. PC3 scatter plot (Fig. 6B), indicating shape differences of these specimens. However, both specimens have suffered different degrees of crushing due to taphonomic bias and that is likely the reason for this result.

In PC1' loadings (L; Table 3), only two characters were negatively related (LPF and WJU); SMX, LPA and LPO loadings were the highest related (L=0.69; L=0.27; L=0.36, respectively); and the rest of characters obtained intermediate values [e.g. LPT (L=0.17), LMX (L=0.18), WOP (L=0.21)]. PC2 has shown a high relation with character LPA (L=0.77), showing possible changes in shape in this region, and a negative loading for SMX (L= -0.38), whereas the others had no significant scores. The last considered principal component (=PC3), showed high correlations with bones in both lateral and posterior emarginations of the skull [LMX (L=0.68), WMX (L=0.25), LJU (L=0.30), WQJ (L=0.29) and LQU (L=0.32)] and, as the results in PC2, allows inferences in shape changes of these regions.

3.4.1.2. Replacing missing data with regression estimation

The alternative missing data approach (i.e. "iterative imputation"; Fig. 6C) generated two principal components which comprised 88.96% of the total variance (PC1=53.01%; PC2=35.95%). In contrast with the previous approach, PC1 was interpreted as shape, whereas PC2 as size. In addition, all specimens were included inside the 95% ellipse in PC1×PC2 scatter plot. The specimen MN7017-V, interestingly, was excluded from the ellipse when considering PC2 vs. PC3, but the percentage of variance represented by PC3 is too low (PC3=3.28%) to assume any difference from the others individuals. We agree with Ilin & Raiko (2010) and prefer to choose the iterative imputation approach for dealing with missing entries (see discussion on session 4.2. "The single population hypothesis"). Then, discussions concerning the form variation in our data are related to PCA analysis using iterative imputation.

In PC1 loadings (Table 3), LPA, WPA and LSQ were the highest positively related characters (L=0.89; L=0.22; L=0.16, respectively), whereas LMX, LJU, LQJ, WQJ and LQU were the highest negatively related characters (L= -0.18; L= -0.14; L= -0.16; L= -0.11; L= -0.11; L= -0.13, respectively). Only two characters were negative for PC2 (LPF and WJU), whereas the rest of the coefficients were positive. Among them, SMX was the highest (L=0.59); WPAL, WBS, LBO, LJU, LQU, LPO and WOP obtained intermediate scores (L=0.23; L=0.19; L=0.20; L=0.19; L=0.21; L=0.29; L=0.30, respectively); the others were less related [e.g. LPA (L=0.04), LPT (L=0.13) and WPO (L=0.10)]. In general, the values indicate that in *B. elegans* most changes occur in bones of both lateral and temporal emargination.

3.4.2. Shape characters (proportions)

3.4.2.1. Replacing missing data with mean values

When applying "mean value imputation", 53.99% of the variance were comprised by the first two principal components (PC1=35.29%; PC2=18.70%), both corresponding to shape, as all units of measurements were removed through the ratio of characters before carrying out the analysis. All specimens were comprised into the 95% ellipse (Fig. 7A).

The first PC was positively related to the loadings values of LPA/TLS (L=0.28), LMX/TLS (L=0.38), LQU/TLS (L=0.27), WPA/TWS (L=0.23), SMX/TWS (L=0.38), WMX/WTS (L=0.35), WQJ/TWS (L=0.48); the most negative values were LPO/TLS (L= -0.16) and WOP/TWS (L= -0.13). The second PC was positively related to LPA/TLS (L=0.66), WPA/TWS (L=0.32)WOP/TWS (L=0.27), and negatively to LMX/TLS (L= -0.50) (see Table 4 for all loading values). It is interesting to note that most of highly-related proportions were in reference to bones associated either with feeding *apparatus* (squamosal, parietal, quadratojugal and jugal) or catching food and trituration surface (maxilla).

3.4.2.2. Replacing missing data with regression estimation

The “iterative imputation” substitution model of missing data resulted in 77.35% of the variance comprised by two principal components (PC1=45.49%; PC2=31.86), both representing shape. All specimens were included in the ellipse (Fig. 7B), thus shape differences do not indicate possible different populations or species.

PC1 was highly related to LMX/TLS (L=0.48), LJU/TLS (L=0.16), LQJ/TLS (L=0.21), LQU/TLS (L=0.28), LSQ/TLS (L=0.20), SMX/TWS (L=0.33), WMX/TWS (L=0.30), WJU/TWS (L=0.26) and WQJ/TWS (L=0.41), which represent the highest values as well as bones constituting both lateral and posterior emargination. Conversely, PC2 was mostly represented by LPA/TLS (L=0.67), LSQ/TLS (L=0.34) and WPA/TWS (L=0.33) (see Table 4). These loadings represent shape changes in regions of the skull that are associated with muscles’ attachment as well as trituration surfaces (see below).

4. Discussion

4.1. Replacing the caliper by ImageJ

Almost all measurements did not differ between the two treatments, and only one measurement (= length of maxilla, LMX) had the opposite result. This indicates that ImageJ is a~~n~~ useful tool in replacing the use of caliper (see table 1). Although we found no statistical differences for many of the measurements, we had difficulties in taking some of them and we must discuss it herein. First, because of taphonomical processess, many cracks appears in the photos and can be confused with sutures between bones. Thus, a previous anatomical knowledge of the material is very helpful. Second, we had difficulties in identifying some landmarks due to overlapping structures or badly focused region. The first problem cannot be solved for one cannot break a piece of the material, and taking pictures from a different angle will lead to a measure different from the reality. The second is easily solved by a good accuracy in focusing the image, and by taking pictures in different focus.

Another problem is related to the result we found for LMX. Such a result is due to the optical processes that occurs in the camera. Photos are two dimensioned images and, for that reason, deeper points are not captured in their real positions because they are farther from the camera. Because of the anatomically curved shape of the maxilla, the rostralmost landmark (LM 24) established to take this measurement is deeper in relation to the caudalmost landmark (LM 11), which is also the plane the picture was taken. As a consequence, the straight line between landmarks 11 and 24 (used to take LMX) is smaller than the real line and this measurement is underestimated. This is also the case for steep structures. Therefore, one should be careful when establishing the landmarks and measurements in specimens with many curvatures and steep ~~e~~structures.

Despite this, the study *in situ* of the material is preferable, although pictures are an economic alternative in cases one are not able to handle the material. We must aware that one have to choose one of the two treatments to construct a morphometric matrix, otherwise it will be composed of values obtained by two diffent methods.

4.2. The single population hypothesis

In this section, we discuss our results by tackling in two fronts, one underlied on the taphonomy of the Tartaruguito locality, and another on the taxonomy of the valid fossil turtle species of the Bauru Group. The former will be taken briefly, since it is well stablished ~~on~~ the literature, the latter is more carefully considered because it is still a matter of debate among paleontologists.

4.2.1. The depositional context at the "Tartaruguito" site

The depositional environment at the Pirapozinho site is well-known from previous studies, which point out to seasonal floods in which turtles might have gathered in water bodies for foraging, followed by droughts that caused their death (Soares et al., 1980; Fulfaro and Perinotto, 1996; Fernandes & Coimbra, 2000; Henriques et al., 2002, 2005; Suárez, 2002; Bertini et al., 2006; Henriques, 2006). This is, consequently, a case of several seasonal non-selective death events, with individuals representing semaforonts connected temporally (between generations), thus comprising a single population (agreeing with Futuyma, 1993 population definition and used by Romano & Azevedo, 2007). We failed to disprove the null hypothesis that all individuals belong to a same population of *Bauruemys elegans*, agreeing with Romano & Azevedo (2007) conclusion using post-cranium data.

4.2.2. Taxonomic considerations between B. elegans *and other species of Bauru Basin*

Many skulls sampled have taphonomic effects, such as cracks and crushes. For instance, MN7071-V is notably the ~~biggest~~ specimen of the sample and is represented in the uppermost positive side of the size-related PC2 axis (Fig. 6C). Although it is indeed a big specimen, it was clearly a taphonomic effect (crushing) that caused its ~~bigger~~ size. On the other hand, Bertini et al. (2006) indicated that turtle bodies have suffered little transportation or crushing in Tartaruguito site. We agree with this taphonomical interpretation of the site but, although most specimens do not show huge breaks, these distortions might ~~mask~~ morphometric interpretation (the case of MN7071-V).

Another aspect is the presence of polymorphism in *B. elegans*. Romano (2008) presented an unusual carapace for the specimen MN7017-V, as having a seventh neural bone, differing from the diagnostic number of six neurals for this species, and with the diagnostic four-squared second neural bone not contacting first costals (Suarez, 1969; Kischlat, 1994; Gaffney et al., 2011). The morphometric analysis performed by Romano (2008) did not revealed significant statistical differences between MN 7017-V and other *B. elegans* specimens. We have also included the MN7017-V skull in our analysis, and there was no variation to state anything apart from Romano's (2008) conclusion that it is probably a polymorphic *B. elegans* specimen (Fig. 6C). Still, we reevaluated this skull and found the diagnosis characters for *B. elegans*. Therefore, all skulls included in our study belong to the same species (i.e. *B. elegans*).

Among the five valid fossil turtle species found throughout the Bauru Basin, only two have been collected at the Pirapozinho site so far (Romano et al., 2013). The first is *B. elegans*, which is recognized by both skull and shell materials; the second is *Roxochelys wanderleyi* Price, 1953, based only on shell material (de Broin, 1991; Oliveira & Romano, 2007; Romano & Azevedo, 2007; Gaffney et al., 2011; Romano et al., 2013). So far, none *R. wanderleyi* with skull-shell associated body parts were collected. It is possible that the chelonian fauna of the Bauru Basin might be overdimensioned (Romano et al., 2009, 2013). Then, the two new skull-only species from the Caiera Quarry recently described, *Peiropemys mezzalirai* and *Pricemys caiera* (Gaffney et al., 2011), might be a representative skull material of *R. wanderleyi*. However, we cannot claim that until a skull-shell *R. wanderleyi* specimen be found.

4.3. Ontogenetic changes in *B. elegans* skull

Once we have assessed that all specimens belong to the same species and population, we are able to discuss the skull variation in the sample assuming as due to inter-populational variety. For the sake of organization, we divided the discussion into two parts, based on the anatomical regions of the turtle skull: upper temporal fossa and lower temporal fossa, following Schumacher (1973), Gaffney (1979) and Gaffney et al. (2006). We have chosen this organization because the bones we found most association with the principal components in the two PCA analyses compose these two regions and are generally involved in aspects of the feeding mechanisms of turtles, either as muscles attachments or forming triturating surfaces.

4.3.1. Bones of the upper temporal fossa and skull roofing

The temporal emargination of podocnemidid turtles is formed by the dorsal, horizontal plate of the parietal, the quadratojugal and the squamosal, with no contribution of the postorbital (Gaffney, 1979; Gaffney et al., 2011). This region (and bones) is associated to the origin of the adductor muscle fibers (m. adductor complex; Fig. 9A and 9B) (Schumacher, 1973; Werneburg, 2011; Werneburg, 2012; Jones et al., 2012; Werneburg, 2013), which run through *cartilago transiliens* of the *processus trochlearis pterygoidei* of the pterygoid and insert at the coronoid process of the lower jaw (Schumacher, 1973; Gaffney, 1975; Gaffney, 1979; Lemell et al., 2000; Werneburg, 2011). These muscles promote the closure of the mouth, thus it is reasonable to associate the attachment surface to bite force and the latter to the prey hardness. Yet, on the ventral flange of the squamosal origins the muscle *depressor mandibulae* (Schumacher, 1973; Gaffney et al., 2006; Werneburg, 2011; Fig. 9B), which cause the abduction (=opening) of the mandible.

The variation in this area of the skull in turtles was a matter of some studies (e.g. Dalrymple, 1977; Claude et al., 2004; Pfaller et al., 2011), which indicated allometric ontogenetic growing patterns of the bones in these regions. Such authors were able to identify a high correlation with the increasing of muscle mass and shift in feeding features (Dalrymple, 1977; Pfaller et al., 2010; Pfaller et al., 2011). Moreover, there are changes in skull shape associated to the aquatic environment and foraging strategies, as suggested for emydids and testudinoids turtles by Claude et al. (2004). Although these studies focused on hide-necked turtles, the same morphoecological patterns can be applied to side-necked turtles, since there are habitat occupation similarities between side-necked and hide-necked turtles with implications to the skull morphology due to morphofunctional constraints (Schumacher, 1973; Lemell et al., 2000), besides the adaptive selection regarding fresh water feeding strategies (see Lauder & Prendergast, 1992, Aerts et al., 2001 and Van Damme & Aerts, 2001 for feeding strategies in freshwater turtles).

The high variance and positive allometric growth of the parietal (LPA: a=0.38; WPA: a=0.32), quadratojugal (LQJ: a=0.16; WQJ: a= -0.06) and squamosal (LSQ: a=0.30) lead to an increasing in temporal emargination and, consequently, a greater area for attachment of the external adductor muscle. The consequence of this would be the generation of large forces and high velocities during the fast closing phase of an aquatic feeder, as seen in *Pelusios castaneus* (Lemell et al., 2000), and even a more powerful bite for crushing harder prey, as seen in *Sternotherus minor* (Pfaller et al., 2011). In addition, the lenghthen of the squamosal would allow a greater insertion area of the m. *depressor mandibulae* and muscles of the hyobranchial apparatus (e.g. m. constrictor colli) (Schumacher, 1973; Gaffney, 1979; Claude et al., 2004; Gaffney et al., 2011; Werneburg, 2011). The m. *depressor mandibulae* is useful for an increased gape opening speed and the hyobranchial apparatus musculature is involved in backwards water flow generation by the lowering of the hyoid apparatus, two characteristics well reported for other pleurodire turtles (e.g.Van Damme & Aerts, 1997; Aerts et al., 2001; Lemell et al., 2000; Lemell et al., 2002). Moreover, Claude et al. (2004) demonstrated that aquatic turtles with suction feeding mode possess longer skulls than terrestrial turtles, being squamosal the most proeminent bone involved in this elongation and functionally related to the style of prey capture (= suction) as a support for mandible and hyoid muscles.

Also, Gaffney et al. (2011), in a comparison with other podocnemidid turtles, indicated *B. elegans* as having a "skull relatively wide and flat" (p. 12), which could be observed by the increasing of some bones, specially the postorbital (Figs. 3G and 4H), parietal (Fig. 3A and 3J), quadratojugal (Figs.3I and 4F) and jugal (Figs. 3C and 5B). Comparing the postorbital allometry (better discussed below) with those of the bones in contact with it in the skull roof (frontal, parietal, jugal and quadratojugal; Gaffney et al., 2011), we observe an influence of the positive growth of the former into the others, leading to flattening and widening of the skull.

In a study assessing the bite performance in turtles, Herrel et al. (2002) suggested that a higher skull is efficient in promoting stronger bite forces, specially in species which feed on hard prey, but they also pointed out that additions in bite forces may be achieved by "getting longer and larger" skull with no increasing in skull height. Thus, in addition to provide gains in muscle attachment area, by the growing of parietal, quadratojugal and squamosal, leading to a longer skull, a stronger bite and possibly a change in diet along the ontogeny. Also, the allometric growths of most of skull bones, particularly the positive allometry of the postorbital, indicate a more roofed skull in *B. elegans* adults. Given the allometric patterns aforementioned, *B. elegans* might have had a wide and flat but a long skull, which would have compensate the loss of muscle volume and attachment area caused by widening and flattening the skull (Herrel et al., 2002). Correlations between a more emarginated skull and increases in the volume of the adductor muscle were also explored in a cranial evolutionary framework of stem-turtles by Sterli and de la Fuente (2010).

At last, Gaffney et al. (2006, 2011) scored a character based upon the contact between quadratojugal and parietal bones (char. 13 of Gaffney et al., 2006; char. 5 of Gaffney et al., 2011). They also state that this contact is present in *Hamadachelys* + Podocnemididae clade, with a large quadratojugal (state 1), in contrast to most of other Pelomedusoides (state 0: contact absent in Pelomedusidae, Araripemydidae and many bothremydids (e.g. Kurmademydini, Cearachelyini and Bothremydini); state 2: contact present with small quadratojugal in some Taphrosphyini, Bothremydidae). Indeed *B. elegans* possess a large quadratojugal, which means that the reduction of postorbital evolved after *Bauruemys* node of divergence. However, we found a greater increasing (positive allometry) of the two measurements of the postorbital and this might have influenced the growth of parietal and quadratojugal, as well as the jugal (see below), so that the state 1 seen in *B. elegans* is possibly a consequence of allometric changes. This is easily seen if the truly negative allometry of the width of the quadratojugal (WQJ: a=-0.06) and the slight increasing in the length of this bone (LQJ: a=0.16) are compared with the postorbital measurements. It also could have influenced the growth of the parietal, but ~~in a less degree~~, as seen in the allometries of this bone (LPA: a=0.38; WPA: a=0.32).

When comparing the stem-Podocnemidinura species (i.e. *Brasilemys*, *Hamadachelys*) and stem-Podocnemididae (e.g. *Bauruemys*, *Peiropemys*, *Pricemys* and *Lapparentemys*), with the Podocnemidodda (i.e. Podocnemidand + Erymnochelydand) (Gaffney et al., 2011; Fig. 8), it is clear that an increasing in the parietal-quadratojugal contact has occurred along the podocnemidid lineage, and consequently led to a more roofed skull and to a less emarginated skull. We suggest that in *B. elegans* the small contact is due to the positive growth of the postorbital resulting in a more emarginated skull than other podocnemidids, as described by Gaffney et al. (2011). Yet, within Podocnemidand this bone suffered the opposite effect (i.e.

small growth), showing variations in size and even being absent in some species (e.g. *Podocnemis sextuberculata*; Ruckes, 1937; Gaffney, 1979; Gaffney et al., 2011), though the emargination is still great. On the other hand, in Erymnochelydand the postorbitals are large but the quadratojugal and parietal are large as well, leading to a greater contact between these bones and a well-roofed but less emarginated skull, being a reversion in *Bairdemys venezuelensis* and *B. sanchezi* within Erymnochelydand (Gaffney et al., 2011). Therefore, the increasing or decreasing in the temporal emargination within Podocnemididae could be due to variation of allometric patterns in bones that form the skull roof, particularly the postorbital, quadratojugal and parietal, among different lineages.

4.3.2. Bones of the lower temporal fossa

The lower adductor chamber in Pelomedusoides is formed externally and laterally by the jugal and quadratojugal, with the addition of the maxilla in some cases (e.g.: *Podocnemis* spp. and *Bairdemys sanchezi*). The well developed cheek emargination, found in most but not all podocnemidid turtles (the exceptions are many species of Erymnochelydand, but not *Bairdemys* spp., *Cordichelys antiqua* and *Latentemys plowdeni*), is also part of the adductor chamber (Gaffney, 1979; Gaffney et al., 2006; Gaffney et al., 2011). Internally and medially, the postorbital, the jugal and the pterygoid compose the *septum orbitotemporale*, partially separating the *fossa orbitalis* from the *fossa temporalis*; along with the palatine, they aid to suport the *processus trochlearis pterygoidei* of the pterygoid (Gaffney, 1975; Gaffney 1979; Gaffney et al., 2006). There is a passage medially to the process of the pterygoid and the *septum orbitotemporale*, running from the *fossa orbitalis* to the *fossa temporalis*, the *sulcus palatinopterygoideus*. The palatine and pterygoid form the floor of its passage, while the parietal, postorbital and frontal limit its upper portion. In this region, the external adductor fibers run through the *processus trochlaris pterygoidei*, and the internal adductor muscle (i.e. pterygoideus muscle and pars pseudotemporalis; Fig. 9B) mostly origins throughout the pterygoid and parietal bones (Schumacher, 1973; Lemell et al., 2000; Lemell et al., 2002; Werneburg, 2011). The internal adductor fibers are involved in the jaw-closure system by generating counter forces (protraction) to the external adductor (retraction) (Schumacher, 1973; Lemell et al., 2000; Lemell et al., 2002; Fig. 9C and 9D).

Variation of the upper temporal fossa has been studied in different turtles, such as various trionychids (Dalrymple, 1977) and *Chelydra serpentina* (Herrel et al., 2002). However, few studies report on the variation of the lower adductor chamber, although both the temporal fossa as well as the latter are anatomically and functionally coupled (Schumacher, 1973). Dalrymple (1977) identified a positve allometry in the width of the "temporal passageway" in trionychids. This area is related to the cryptodire pulley system (i.e. a *processus trochlearis* formed by the quadrate and opisthotic) and is analogous to the pleurodire pterygoid process, and thus can be comparable functionally (Gaffney, 1979). Herrel et al. (2002) concluded that the increase of the bite force in turtles is due to either the increased height of the skull, leading to a more open angle of the *processus trochlearis* in relation to skull longitudinal axis, or to enlargement (in width and lenght) of the skull, because it allows more area for muscle attachment and volume. We observed the same pattern of growth change in *B. elegans*, as evidenced by the positive allometry of the bones parietal, postorbital, palatine and pterygoid. Other features were observed by Dalrymple (1977) in trionychids (e.g. height and width of the supraoccipital crest, lengthen of the squamosal crest and a development of a horizontal crest in the parietal) and were correlated to changes in skull shape with a shift in feeding habits, from softer to harder preys as individuals age. Again, it seems to be the case of *B. elegans*, as evidenced by the positive allometry of the bones squamosal and parietal.

The bones that mainly compose the skull rostrolaterally and the lateral emargination revealed a correlated allometric shape shift. Even so jugal and maxilla showed small allometric variation (Figs. 4B, 4C, 6A, and 6B). The reduction of the jugal (WJU: a= -0.23) and quadratojugal (WQJ: a= -0.06) along with the small growth of maxilla (WMX: a=0.19) demonstrate a decrease in height at the anterior portion of the skull. Because of the contact between jugal and quadratojugal with postorbital (and its increasing; see previous topic), we suggest that the latter would possibly has affected the growth of the formers. Moreover, the strong development of the postorbital would ultimately affect the width of the maxilla, which in turn would also affect the jugal. In contrast, the lenghthen of this bone would be less affected (LMX: a=0.39). In addition, there is a considerable increment in the stretch of maxilla (SMX: a=0.70) (Fig. 3H) leading to a broader rostrum. Yet, this could allow a greater area for crushing (Kischlat, 1994) during ontogenetic growth. All these allometric changes indicate that *B. elegans* owns a more flattened and wider skull (Gaffney et al., 2011), which could have allowed greater bite forces generation (Herrel et al., 2002).

There are other morphological implications in which the lower adductor chamber bones are involved and that worth discussion. As previously pointed, three bones compose the *septum orbitotemporale*: pterygoid, jugal and postorbital (Gaffney, 1979; Gaffney et al., 2006). Together with palatine, these three bones provide support for the *processus trochlearis pterygoidei*, where runs the tendon that connect the external adductor complex into the lower jaw (Schumacher, 1973; Gaffney, 1975; Gaffney 1979; Lemell et al., 2000; Gaffney et al., 2006; Werneburg, 2011). Nearby the process, many muscle fibers origin or cross towards their insertions points

(Schumacher, 1973; Werneburg, 2011). The temporal emargination at the upper adductor chamber becomes more emarginted during growth. As a consequence, the attachment area for external adductor muscles increase during aging, potentially generating stronger bite forces. The consequence of this temporal emargination indentation is that the trochlear process ~~would~~ must be more robust to support higher forces. We interpret that the positive allometries of pterygoid (LPT a=1.37), postorbital (LPO a=1.25 and WPO a=1.36), and palatine (LPAL a=1.11) could be a response to this robustness of the trochlerar process during growth. In other words, they would act together by giving more resistance to the area in which the high forces created by the external adductors are applied. Gaffney (1979) suggested this robustness occurs because muscle volume increase and, consequently, higher bite forces, so these three bones would reinforce the *septum orbitotemporale* to support and not to break when muscles are contracted. In addition to such reinforcement, the growth of palatine could be associated to a larger area for crushing preys such as mollusks and crustaceans, as pointed out by Kischlat (1994).

The internal and posterior adductor muscles (Fig. 9B), which origin at the quadrate, prootic, pterygoid, palatine, postorbital and the descending process of the parietal (Schumacher, 1973; Werneburg, 2011), are important during the jaw-closure phase. The importance of these muscles has been debated for early tetrapods with flat skull and aquatic lifestyle (e.g. Temnospondyli and Lepospondyli; Frazzetta, 1968), in which the internal muscle might have assumed the main function of closing the jaw (Werneburg, 2012). This also occurs in turtles with flat skulls and with poorly developed crista supraoccipitalis (e.g. Chelidae; Werneburg, 2011; Werneburg, 2012). However, *B. elegans* does not have a skull as flat as chelids, but has a long supraoccipital bone as well as a greater emargination (Gaffney et al., 2011), indicating more area and volume to external adductor muscles (Dalrymple, 1977; Sterli & de la Fuente, 2010). The mechanical effects of adductor muscles upon the lower jaw during food capture has been demostrated in some turtles (Schumacher, 1973; Lemell et al., 2000; Lemell et al., 2002; Pfaller et al., 2011). These studies agree that besides acting to close the mouth, internal adductors execute counter protraction forces to the external adductors retraction forces, while posterior adductors produce medial forces (Fig. 10C and 10D). The contraction of all these muscles together avoid displacements of the mandible and reduce stresses at the articulation (Schumacher, 1973; Lemell et al., 2000; Lemell et al., 2002). The positive allometries of the bones of the lower adductor chamber of *B. elegans*, therefore, may reflect greater resistance for a more robust musculature of internal and posterior adductors in response to higher forces created by external adductors. Besides, these muscles also play the main role in feeding, as proposed for aquatic feeders (Frazzetta, 1968; Werneburg, 2012), in addition to a larger area between the two tips of the maxilla (i.e. SMX a=0.70) and a flattened skull.

4.4. Feeding changes ~~along~~ ontogeny in *B. elegans*

Changes in skull shape may be due to habitat differences in which on-land turtles (e.g. testudinids) possess higher and shorter skulls while aquatic turltes (e.g. emydids) own flatter and longer skulls (Claude et al., 2004). The changes in skull shape of turtles along ontogeny have been assessed in living species (Dalrymple, 1977; Pfaller et al., 2011). Generally, it is supported that a diet shift occurs from small soft prey to bigger harder ones, in association with higher, larger and more robust skulls. These, in turn, are more suitable for crushing clams and/or to capture fishes by having a greater gape. The overall aquatic morphology comprises adaptations to suction feeding, which was also discussed by Herrel et al. (2002), and could be the case of *B. elegans*. Firstly because taphonomic studies at Pirapozinho site suggested a riverine ephemerous system (Soares et al., 1980; Fulfaro and Perinotto, 1996; Fernandes & Coimbra, 2000; Henriques et al., 2002, 2005; Suárez, 2002; Bertini et al., 2006; Henriques, 2006) and fossils with little transportion (Bertini et al., 2006), thus *B. elegans* must have been a semi-aquatic turtle, similar to the extant freshwater turtles. Secondly, the general pattern observed revealed form and shape changes in both temporal and lateral emargination (upper and lower adductor chamber, respectively): as a whole, *B. elegans* skull seems to become more emarginated, flattened and longer as it grows in, according to the skull shape for aquatic turtles found by Claude et al. (2004), and indicating greater area and volume for muscles attachment. In addition, the deeper temporal emargination of *B. elegans* indicates a greater increse in muscle volume (Kischlat, 1994), thus leading to a stronger bite force (Sterli & de la Fuente, 2010). This leads us to interpret such changes as related to shift in diet as individuals grow instead of shift in habitat.

Malvasio et al. (2003) described diet changes in *Podocnemis expansa*, *P. unifilis* and *P. sexturberculata* due to aging, concluding that the latter is a carnivore species whereas the two former are omnivorous. Whereas *P. expansa* changes its diet towards a more herbivorous, *P. unifilis* remains more balanced with similar ingestion of vegetables and meat (Malvasio et al., 2003). Although more work is necessary to elucidate this issue in *Podocnemis* spp, the allometric variation found in *B. elegans* suggests that it might has been accompanied by changes in diet along ontogeny.

Although we cannot have certainty of which food items the individuals of *B. elegans* might have eaten along their lives, we have evidences that point to a shift in diet along ontogeny. Besides the allometric patterns and loadings values indicating skull changes associated to adductor muscles, *B. elegans* lived in a riverine system (Soares et al., 1980; Fulfaro and Perinotto, 1996; Fernandes & Coimbra, 2000; Henriques et al., 2002, 2005; Suárez, 2002; Bertini et al., 2006; Henriques, 2006), then the skull changes and the aquatic habit of this species could be related to the diet changes, as found in other turtles (Dalrymple, 1977; Malvasio et al., 2003; Claude et al., 2004; Pfaller et al., 2011). Once the skull of *B. elegans* comprises all these features, it might probably has gone through changes in diet along ontogeny, from softer to harder aquatic preys. Kischlat (1994) suggested that *B. elegans* might have fed of hard preys and, given the several mollusk and crustacean species described for the Pirapozinho site (Dias-Brito et al., 2001), it might have composed the diet of *B. elegans*. In this context, we agree with Kischlat (1994) and suggest that smaller juveniles individuals might have fed on less hard and small food itens (e.g. snails and small fishes) whereas bigger old specimens fed on harder and larger preys, such as crustaceans and bigger mollusks.

5. Conclusions

As Romano & Azevedo (2007) (for shell material), our data did not show enough morphometric~~al~~ variation to suggest population differences among our sample. So, we did not have any evidence to disprove that the "Tartaruguito" site is composed by a single population of *B. elegans*. However, it is feasible to assume that different generations of individuals were crowded in this locality by the accumulation of corpses due to several drying events. Since none *B. elegans* hatchling were found in the “Tartaruguito” site until now, it might have been a freshwater foraging area.

As regards to the empirical data, the variation and allometric patterns in the bones of the skull, mainly the PA, QJ, SQ, QU, PO, JU, MX, PAL and PT, as well as the loadings of PCA analysis, reflect shape differences in both upper and lower adductor chamber. This could indicate more area attachment and resistance for stronger adductor muscles, which are accompanied by changes in diet during aging, from softer to harder prey, as seen in living turles species.

As regards to the use of images for carrying out morphometrics studies, we conclude that the use of calipers can be replaced by softwares that work on images. ImageJ is an useful tool for this matter. However, one needs to beware of some procedures when taking pictures, in order to avoid methodological flaws in images such as bad focused objects.

Regarding the approaches applied to our data to deal with missing entries in the matrix (i.e. mean value and iterative imputation), both were useful for answering the questions we raised (i.e. the single population hypothesis), though little different results were obtained (few specimens out of 95% ellipse in mean value approach in contrast with none specimen out of ellipse in iterative imputation approach). We recommend the iterative imputation as the most appropriate approach to deal with missing data in paleontological studies on the basis of the statistical assumptions it was developed (a sample-based regression for characters estimation) and the more conservative results, once we have no evidence to assume any specimen as a different species.

Institutional Abbreviations: AMNH – American Museum of Natural History, New York, NY, United States; **LPRP** – Laboratório de Paleontologia da Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, SP, Brazil; **MN** – Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, Brazil; **MCT** – Museu de Ciências da Terra, Departamento Nacional de Produção Mineral, Rio de Janeiro, RJ, Brazil; **MCZ** – Museum of Comparative Zoology, Harvard University, Cambridge, MA, United States; **MZSP -** Museu de Zoologia, Universidade de São Paulo, São Paulo, SP, Brazil.

Anatomical abbreviations: PF – prefrontal; **FR** – frontal; **PA** – parietal; **VO** – vomer; **PAL** – palatine; **PT** – pterygoid; **BS** – basisphenoid; **BO** – basioccipital; **MX** – maxilla; **JU** – jugal; **QJ**

– quadratojugal; **QU** – quadrate; **PO** – postorbital; **SQ** – squamosal; **OP** – opisthotic; **CO** – choanal.

Measurements abbreviations: TLS – Total length of skull; **LPF** – Length of prefrontal; **LFR** – Length of frontal; **LPA** – Length of parietal; **LVO** – Length of vomer; **LPAL** – Length of palatine; **LPT** – Length of pterygoid; **LBS** – Length of basisphenoid; **LBO** – Length of basioccipital; **LMX** – Length of maxilla; **LJU** – Length of jugal; **LQJ** – Length of quadratojugal; **LQU** – Length of quadrate; **LPO** – Length of postorbital; **LSQ** – Length of squamosal; **TWS** – Total width of skull; **WPF** – Width of prefrontal; **WFR** – Width of frontal; **WPA** – Width of parietal; **SMX** – Stretch of maxilla; **WVO** – Width of vomer; **WCO** – Width of choanal; **WPAL** – Width of palatine; **WBS** – Width of basisphenoid; **WMX** – Width of maxilla; **WJU** – Width of jugal; **WQJ** – Width of quadratojugal; **WPO** – Width of postorbital; **WOP** – Width of opisthotic.

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1

Fossil turtle localities in Bauru Basin

Lithostratigraphical map of the oriental part of the Bauru Basin showing the fossil turtle localities (municipalities). Turtle species are: **1.** *Cambaremys langertoni* (*incertae sedis*), *Pricemys caieira* and *Peiropemys mezzalirai*; **2.** *Roxochelys harrisi* (*nomem dubium*); **3.** *Bauruemys brasiliensis* (*nomem dubium*) and Testudines indet.; **4.** Testudines indet.; **5.** Testudines indet.; **6.** *B. brasiliensis* and *Roxochelys wanderleyi*; **7.** Testudines indet.; **8.** Testudines indet.; **9.** Podocnemididae indet.; **10.** *Roxochelys* sp. and *R. wanderleyi*; **11.** *B. elegans*. Abbreviations: **GO,** Goiás State; **MG,** Minas Gerais State; **MS,** Mato Grosso do Sul State; **PR,** Paraná State; **SP,** São Paulo State. Scale bar in Km. Map modified from Romano et al. (2009); geology following Fernandes (2004); taxonomy status of species following Romano et al. (2013).