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Size variations of the vestibula of *Krithe gnoma* DO CARMO & SANGUINETTI, 1999 (Ostracoda): a new procedure for their analysis

Dermeval Aparecido DO CARMO^{1, 2}

Ricardo Piazza MEIRELES^{2, 3}

Paulo Anselmo Ziani SUAREZ^{2, 4}

Vinicius Moreira MELLO²

Abstract: The species *Krithe gnoma* was described from Holocene sediments on the continental margin of Brazil, where it occurs on both shelf and slope. The shelf distribution of this species is restricted to those areas influenced by the Malvinas current between 32°11' and 22°31'S. *K. gnoma* was selected due to the excellent resolution of images of the anterior vestibule. So the range in size of the vestibula of this species was used to determine whether or not the dimensions of the anterior vestibule were to some degree related to amount of dissolved oxygen in the water at the sampling site. Female valves of the 7th and 8th instars were measured and their sizes and those of the anterior vestibule were compared. These valves and the reference carapace were collected at six localities in the southern shelf area. The anterior vestibule of right and left valves of the 7th instar and one of the 8th instar from discrete localities were measured. In the reference carapace, the larger left valve also has the larger vestibule. A gerontic 8th instar has valves larger than those of the previous instars, but its vestibula are smaller than those of the 7th instar. The vestibula of the left valves of the 7th instar collected at discrete localities showed consistent differences in size related to the oxygen content of the sampling site. The relationship between vestibule size and oxygen content is inversely proportional. However, the poor correlation factor ($R^2 < 1$) of these results are not precise enough to support PEYPOUQUET's hypothesis. But the size of the vestibula of *K. gnoma* does show some degree of relationship to oxygen content. So it is important to measure the vestibula of species of *Krithe* using the procedure described here. Rigorous application of this procedure will eliminate the possibility of discrimination based on variations in size due to ontogeny and dimorphism leaving only those related to actual valve size. In any case, variations in the size of vestibula may have a phenotypic origin.

Key Words: Ostracoda; *Krithe gnoma*; size variation of vestibula; PEYPOUQUET's hypothesis; Malvinas current.

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Resumo: *Variações de tamanho do vestibulo de Krithe gnoma DO CARMO & SANGUINETTI, 1999 (Ostracoda): novo procedimento para análise.*- A espécie *Krithe gnoma* foi descrita a partir de sedimentos do Holoceno da margem continental do Brasil onde a mesma ocorre da plataforma ao talude. Nesta margem continental, a distribuição desta espécie é restrita a áreas de influência da corrente das Malvinas entre latitudes de 32°11'/22°31'S. *K. gnoma* foi selecionada para ser utilizada no presente estudo devido a excelente resolução alcançada no imageamento do vestibulo anterior. Desta forma, *K. gnoma* foi utilizada para medir as diferenças de tamanho do vestibulo e para avaliar a relação entre o tamanho do vestibulo e a quantidade de oxigênio dissolvido na água do mar nas áreas de coleta. Valvas de fêmeas adultas foram comparadas e analisadas através das medições dos tamanhos do vestibulo anterior. Os resultados mostram que o vestibulo das valvas direita e esquerda de uma mesma carapaça são distintos. Neste caso, a valva maior apresenta também o maior vestibulo. Um estágio gerontico do 8°. Instar e, por isso com tamanho de valva maior do que aqueles das outras valvas do 7°. Instar, apresenta o menor tamanho do vestibulo. Com a análise das valvas esquerdas do 7°. Instar, coletadas em distintas localidades, tornou-se aparente que existiam diferenças consistente no tamanho do vestibulo. Neste caso, foi possível observar uma relação inversamente proporcional entre o tamanho do vestibulo o conteúdo de oxigênio. No entanto, considerando a pobreza do fator de correlação ($R^2 < 1$), estes resultados não são válidos para se avaliar a hipótese de PEYPOUQUET. Mesmo

¹ * Corresponding author

derme@unb.br

² UnB - Universidade de Brasília, Instituto de Geociências, Brasília - DF, CEP 70919-970 (Brazil)

³ meireles@unb.br

⁴ psuarez@unb.br

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assim, está claramente mostrado que há variações do vestibulo de *K. gnoma*. Neste sentido, vale salientar que é importante avaliar as variações do vestibulo em espécies de *Krithe* seguindo o procedimento aqui sugerido. Pois, desta forma pode-se evitar variações de tamanho devido a ontogenia, dimorfismo e aqueles relacionados a tamanhos de valvas distintos. Estes resultados mostram que variações do vestibulo são potencialmente de natureza fenotípica.

Palavra-Chaves: Ostracoda; *Krithe gnoma*; variações do tamanho de vestibulo; hipótese de PEYPOUQUET; corrente das Malvinas.

Résumé : *Nouvelle procédure pour analyser les variations des tailles de vestibules chez Krithe gnoma DO CARMO & SANGUINETTI, 1999 (Ostracoda).* - L'espèce *Krithe gnoma* a été décrite dans des sédiments de l'Holocène de la marge continentale du Brésil, où elle est présente de la plate-forme au talus. Le long de cette marge continentale, la distribution de cette espèce sur la plate-forme est restreinte aux régions influencées par le courant des Malouines à des latitudes comprises entre 32°11' et 22°31'S. *K. gnoma* a été choisie pour cette étude en raison des excellents résultats apportés par la forme du vestibule antérieur. On a mesuré les différentes tailles de vestibule et évalué la relation entre la taille de celui-ci et la concentration en oxygène des eaux océaniques sur les sites d'échantillonnage. Les valves des femelles adultes ont été analysées en mesurant et comparant la taille de leur vestibule antérieur. Les résultats sont basés sur l'observation du vestibule des 2 valves de carapaces d'individus appartenant tous au stade ontogénétique 7 dans des sites différents. Le vestibule le plus grand se trouvant sur la valve gauche, la plus grande. Un stade ontogénétique 8, de taille supérieure, a été observé montrant un vestibule plus petit que chez le stade 7. Après avoir analysé les vestibules des valves gauches des stades 7 recoltés dans des sites différents, il est apparu que des différences de tailles notables existaient. Dans ce cas, il a été possible d'observer une relation inversement proportionnelle entre la taille du vestibule et la concentration en oxygène. Compte tenu du faible facteur de corrélation ($R^2 < 1$), ces résultats ne permettent pas d'évaluer l'hypothèse de PEYPOUQUET. Néanmoins, des variations de taille du vestibules de *K. gnoma* ont été clairement observées. Il est important d'analyser les vestibules des espèces de *Krithe* en utilisant la procédure présentée dans ce travail. En suivant ce protocole, on évite l'effet des variations de taille due à l'ontogénie, le dimorphisme ou d'autres facteurs. Les résultats de cette étude montrent que les variations de la taille du vestibule sont potentiellement d'origine phénotypique.

Mots-Clefs : Ostracodes ; *Krithe gnoma* ; variation de la taille des vestibules ; hypothèse de PEYPOUQUET ; courant des Malouines.

1. Introduction

The continental shelf of Brazil includes three associations of ostracodes: Southern, Transitional and Northern/Eastern (COIMBRA & ORNELLAS, 1989). On this huge shelf, *Krithe gnoma* DO CARMO & SANGUINETTI, 1999, is restricted to that portion of the Southern association under the influence of the Malvinas current (DO CARMO & SANGUINETTI, 1999).

In order to evaluate size differences in the size of the anterior vestibule specimens of *K. gnoma* were sampled from localities where information was available about bathymetry and the level of dissolved oxygen in ambient water. These factors restrict the area studied to the shelf and slope of a tract bounded by 28°23'S and 23°28'S, and 47°34'W and 43°17'W (Fig. 1). The physical-chemical parameters of the areas are based on oceanographic cruises performed by the Brazilian Navy (Anonymous, 1969, 1970, 1972; CASTELLO & MÜLLER, 1977). Here we present a procedure for the analysis of size variation of vestibula presumed to have been caused by phenotypic plasticity. We also discuss the relationship between the quantity of oxygen dissolved in sea water and the size of the vestibula of *K. gnoma*.

K. gnoma was selected for analysis of size variations in vestibula after a detailed taxonomic study of this species' structure. Female and male instars are easily recognized based on valve and carapace morphology. *K. gnoma*

occurs in the southern shelf areas of Brazil in different latitudes and bathymetries, dependent to a large degree on the influence of the Malvinas current on temperature and salinity (DO CARMO & SANGUINETTI, 1995, 1999). *K. gnoma* ranges from Late Eocene to the Miocene - Holocene (MILLER *et alii*, 2002). Understanding the relationship between the ecology and morphology of this species and basic environmental variables, like dissolved oxygen, is important for these features are fundamental to palaeoenvironmental reconstructions.

PEYPOUQUET (1975) recognized variations in the size of the vestibula of *Krithe* and *Parakrithe*, and was the first to note an inverse proportional relationship between the size of the vestibule and the oxygen content of ambient sea water. This relationship was later named PEYPOUQUET's hypothesis and was tested by MCKENZIE *et alii* (1989), KEYSER (1990) and WHATLEY *et alii* (1993).

MCKENZIE *et alii* (1989), using quantitative methods based on multivariate analysis, tested this hypothesis for the first time. Based on digital images, valves of *Krithe praetexta praetexta* (SARS, 1866) were measured in order to estimate the areas of the vestibula. Through canonical analyses, a total of four groups of valves were identified, two for each sex. The vestibular area of each group remained unchanged, although oxygen content differed significantly with locality. KEYSER (1990), after analysing soft tissues of other genera, failed to find a

cellular or histological mechanism for the storage of oxygen in vestibula. WHATLEY *et alii* (1993) discussed PEYPOUQUET's hypothesis, suggesting that it should be rejected based on studies of the ecology, morphology and distribution of many species of *Krithe*. Supporting

their position, no respiratory function for the vestibule has been identified and no difference in morphology has been observed between cells that comprise the vestibule and those making up other portions of the carapace.

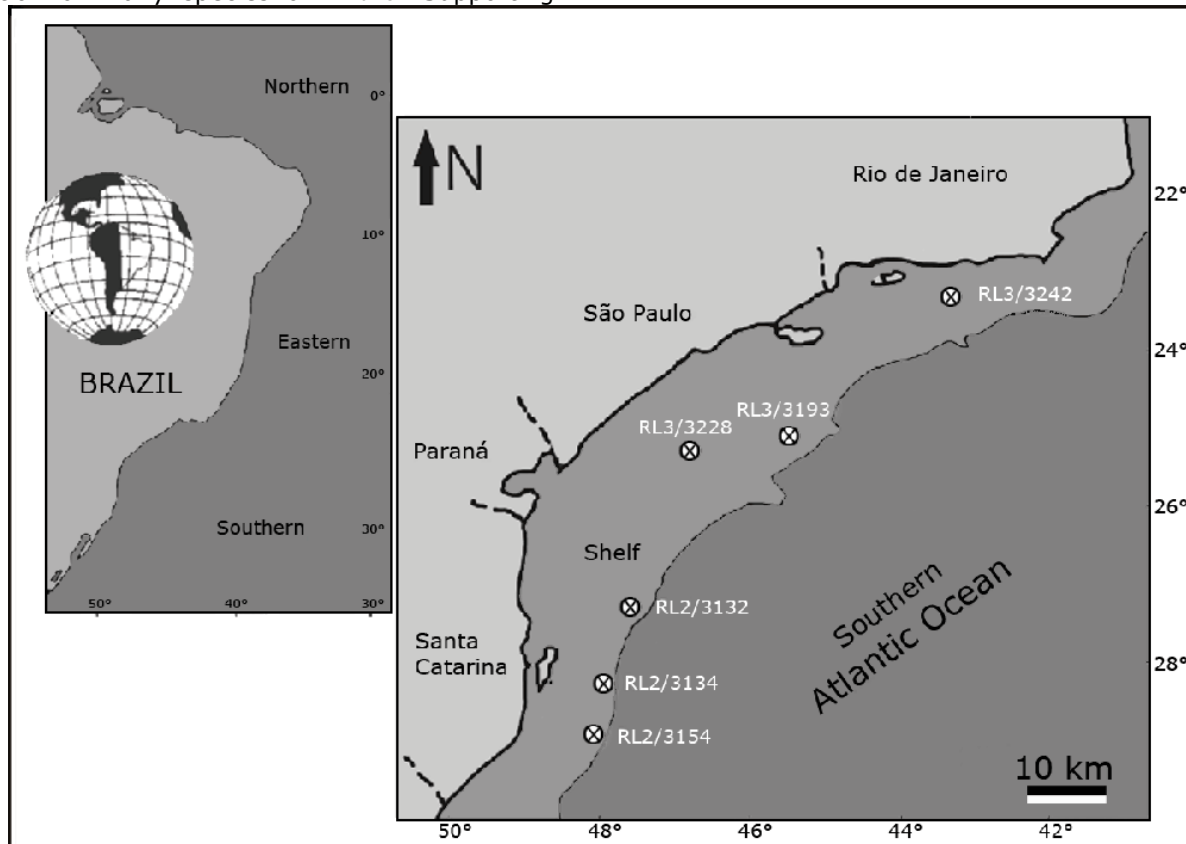


Figure 1: Map of sampling locations (adapted from CHAVES, 1983; COIMBRA & ORNELLAS, 1989).

Mapa de localização das amostras (adaptado de CHAVES, 1983; COIMBRA & ORNELLAS, 1989).

Carte des sites d'échantillonnage (adaptée de CHAVES, 1983 ; COIMBRA & ORNELLAS, 1989).

Taxonomic data on the genus *Krithe* and morphology of their vestibula were considered useful for distinguish species (COLES *et alii*, 1994). Considering the influence of temperature on relative numbers, CRONIN *et alii* (1996) present the ratios of Mg/Ca and Sr/Ca in *Krithe* from upper Quaternary strata in the Arctic Ocean. Their development had been markedly increased by a lower water temperature. For bottom water shallower than 900m, low Mg/Ca ratios in their carapaces correlate with periods of relative cold, when the genus *Krithe* is dominant among the ostracodes. CRONIN *et alii* (1999) studied Mg/Ca ratios and the dominance of *Krithe* in strata of the upper Quaternary in the deep sea portion of the North Atlantic Chain 82-24. They recognized that the dominance of the genus *Krithe* is clearly related to the glacial maximum and the corresponding low Mg/Ca ratios.

RODRIGUES-LAZARO & CRONIN (1999) present remarkable data on the diversity of species of

the genus *Krithe* recovered from the Florida-Hatteras slope of the North Atlantic. A brief history concerning the vestibula of *Krithe* is included. Note that only ZHOU & IKEYA (1992) give data corroborating PEYPOUQUET's hypothesis, along with an evaluation of the vestibula of the species of *Krithe*. Vestibule shape and size in a range of bathymetries were analyzed by RODRIGUES-LAZARO & CRONIN (*op.cit.*). Their study does not support PEYPOUQUET's hypothesis. Three major points militate against it. First, species with both large and small vestibula were recovered from all sites when the hypothesis postulates a zonation in size depending on the depth of the sea-floor. Second, occurrences of *Krithe pernoides* with a relatively small vestibule are found when the opposite would be expected if PEYPOUQUET's hypothesis were correct in the OMZ (Oxygen Minimum Zone). Finally, large vestibula were found in specimens from the glacial interval, when if PEYPOUQUET's hypothesis were well-founded they should be smaller.

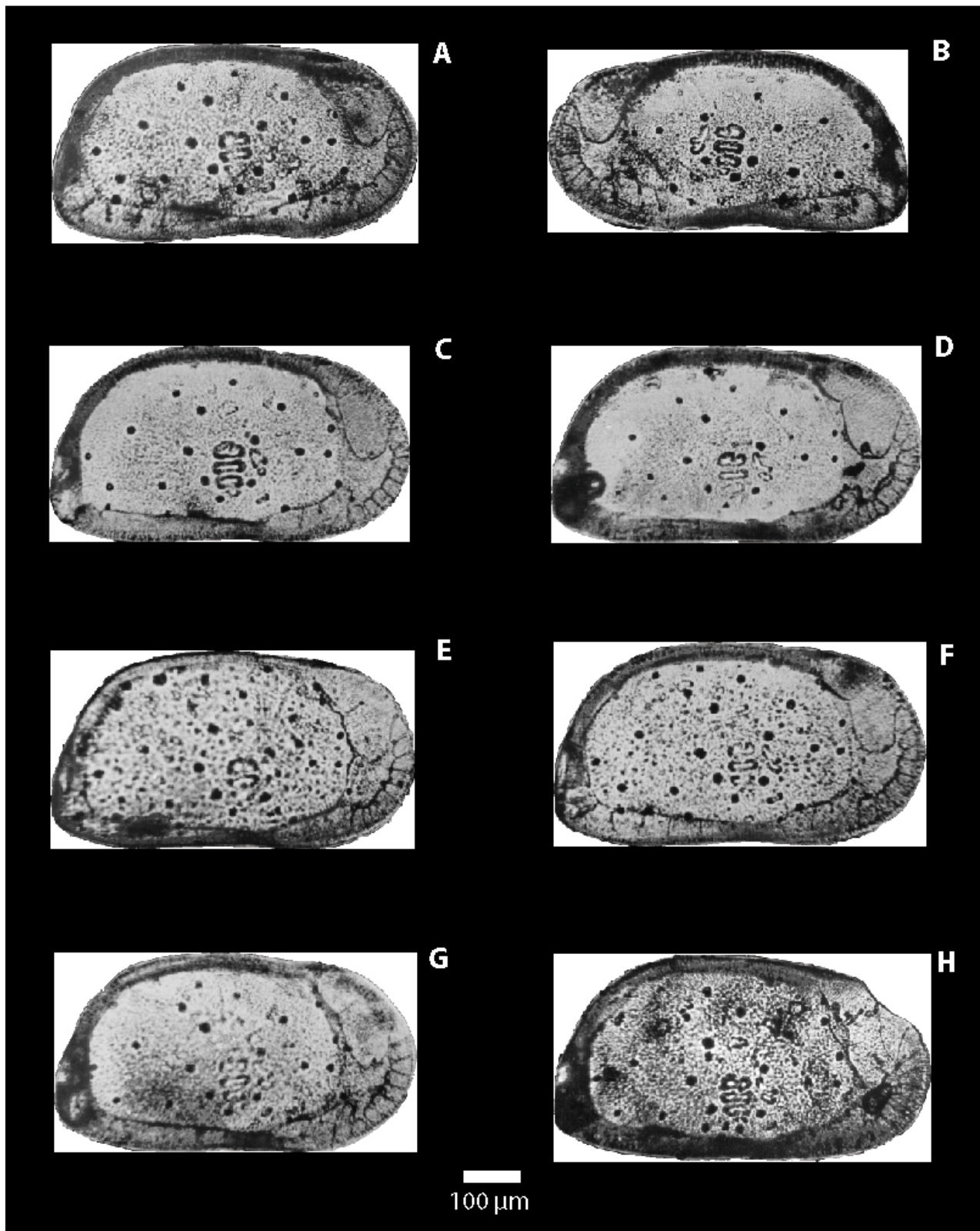


Figure 2: Specimens of *Krithe gnoma*. Valves used for measurement of the area of the vestibule. A-B: carapace base (R.T.2/3134), 7th instar; A: Left valve, B: Right valve; C-G: Left valve, 7th instar; C: (R.T.3/3193), D: (R.T.2/3132), E-F: (R.T.3/3228), G: (R.T.3/3242), H: (R.T.2/3154) 8th instar, male.

Espécimes de *Krithe gnoma*. Valvas utilizadas para medir a área do vestibulo. A-B: carapace de referência (R.T.2/3134), 7º estágio ontogenético; A: valva esquerda, B: valva direita; C-G: valvas esquerdas, 7º estágio ontogenético; C: (R.T.3/3193), D: (R.T.2/3132), E-F: (R.T.3/3228), G: (R.T.3/3242), H: (R.T.2/3154) macho adulto.
 Spécimens de *Krithe gnoma*. Valves utilisées pour la mesure de la superficie du vestibule. A-B : Carapace de référence (R.T.2/3134), 7ème stade ; A : Valve gauche, B : Valve droite; C-G : Valve gauche, 7ème stade ; C : (R.T.3/3193), D : (R.T.2/3132), E-F : (R.T.3/3228), G : (R.T.3/3242), H : (R.T.2/3154) 8ème stade, mâle adulte.



Figure 3: Bounds used to define and delimit the area of the anterior vestibule (sample R.L.2 /3134).

Área utilizada como o limite do vestibulo (amostra R.L.2/3134).

Surface utilisée pour délimiter le vestibule (échantillon R.L.2/3134).

MAJORAN *et alii* (2000) present intriguing results based on thermocultures evaluating the effect of temperature on the growth rate of *Kriethe praetexta praetexta*. They show that at lower temperatures (5° C), the average size of a specimen is greater than that of those reared at higher temperatures (14° C).

After studying recent adult specimens of *Leptocythere lacertosa*, YAMADA & KEISER (2009) gave an oral presentation during the 16th International Symposium on Ostracoda - ISO - held in Brasília (Brazil). They reported that vestibula are not formed in the first 30 hours after ecydisis but were completely formed 60 hours after ecydisis. In conclusion, the vestibular origin and stages of development took place in steps, even in adults. On the other hand, the shapes of vestibula and their pore canals were found to be valid criteria for taxonomic purposes.

2. Studied material

In *K. gnoma*, the left valve is the larger of the two, as is common in other members of this genus. To analyze and quantify the variability of vestibula in *K. gnoma*, the reference selected was an adult carapace, 7th instar (sample 3184). It is important to note that both valves were considered in the analysis. The remaining five left valves of 7th instar (samples 3193, 3132, 3228, 3242, and 3279) and one from the 8th instar (sample 3154) were used for comparisons of the size of vestibula. This one left valve of 8th instar, probably gerontic, was used to determine whether or not an older and

larger instar would have a comparatively larger vestibule (Fig. 2).

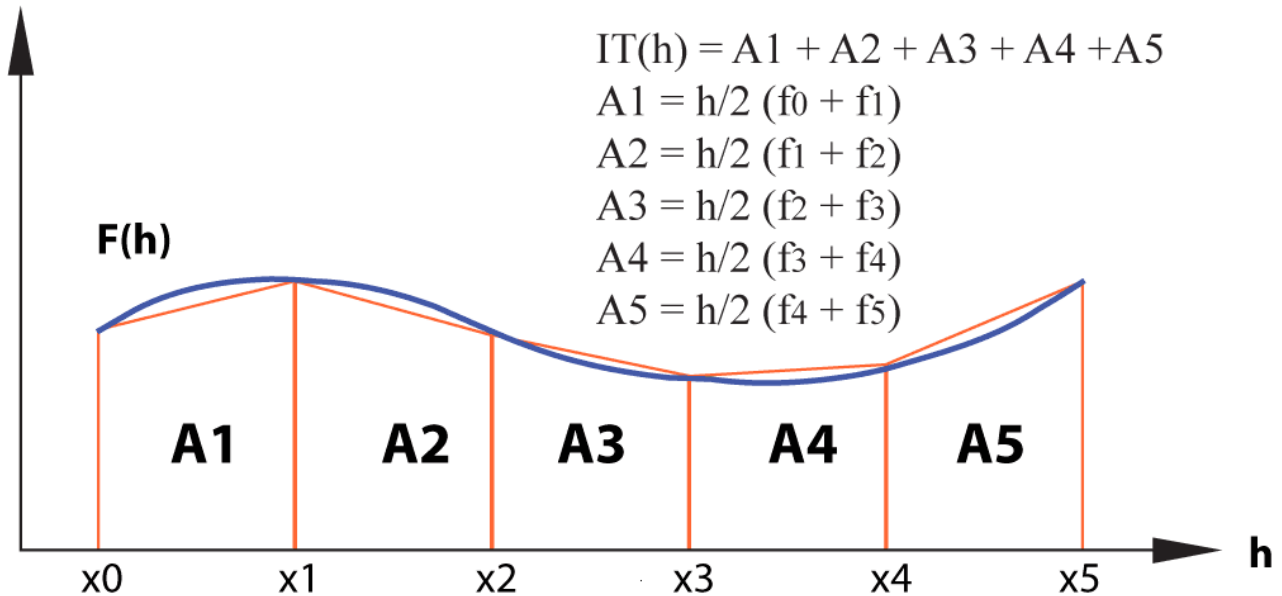
Vestibule areas of left and right valves were measured using digital images. Image distortions were avoided by imaging each valve following exactly the same procedure, internal view, magnification, illumination, *etc.* (Fig. 2). The anterior vestibule was chosen for study due its excellent resolution in imaging. To delimit and standardize the area of the vestibule of each sample, two tangent lines in the neck of the vestibular area were used (Fig. 3). Before measuring the area of a vestibule, it was necessary to select an adult female's instars and valve (right or left) to be used to avoid size variations due to ontogeny, differences of right and left valves, or dimorphism.

3. Quantitative method

The ROMBERG method was used to measure the areas of vestibula. Usually, this method is used to calculate irregular areas. It consists of iterating the results calculated for an integral through the trapezium method for different "h". These "h" must belong to a geometric progression divided by two. For the trapezium method, the inferior area is divided in a series of trapeziums, whose base is "h" and height is the value of a function in a given point, f(h) (Fig. 4). Today, there is sophisticated software to measure areas of carapace as well as to calculate the areas of vestibula using digital images.

$$IT(h) = h[f_0/2 + f_1 + f_2 + \dots + f_{n-1} + f_n/2]$$

F(n) is a value of function in the point "n"



$$IT(h) = h/2 [f_0 + 2 (f_1 + f_2 + f_3 + f_4 + f_5 + f_{n-1}) + f_n]$$

Figure 4: Trapezium method for calculating area.

Método para o cálculo do trapézio.

Méthode du trapèze.

4. Size variations in the vestibula of *Kriathe gnoma*

The size of the vestibule is different in the right and left valves of the carapace used as a reference. However, the left (and larger) valve had the bigger vestibule (Table 1). The area of the vestibula measured in several left valves averaged 87.37 μm^2 , with a standard deviation of 10.64 μm^2 , thus representing a variation of 12.77 %.

The left valve of gerontic 8th instar (sample 3154), the largest carapace studied, had the smallest vestibule; it is 38.35 % smaller than the average of the left valves of 7th instars (Table 1). The two left valves of the 7th instar (sample 3228) differ in size; one is 9.58 % larger than the other. The left and right valves of the reference carapace (sample 3134) have a proportional relationship between the area of the vestibula and the size of the valves. Consequently, the larger left valve has the bigger vestibule.

REMAC	Samples	Co-ordinate	Depth (m)	Temp. (°C)	Salinity (‰)	Oxygen (ml)	Size (μm^2)	Instar
LEG2	3134 (LV)	28°23'S/47°34'W	154	13	35.3	4.6	77.87	7
LEG2	3134 (RV)	28°23'S/47°34'W	154	13	35.3	4.6	65.37	7
LEG2	3132 (LV)	27°23'S/47°44'W	121	14.55	35.45	4.3	90.8	7
LEG2	3154 (LV)	28°53'S/48°19'W	114	14	35.45	4.2	60.26	8
LEG2	3193 (LV)	24°58'S/45°30'W	98	14.55	35.4	4	101.23	7
LEG3	3228 (LV1)	25°03'S/46°39'W	51	14.55	35.8	3.9	74.07	7
LEG3	3228 (LV2)	25°03'S/46°39'W	51	14.55	35.8	3.9	81.37	7
LEG3	3242 (LV)	23°28'S/43°17'W	106	14.55	35.4	4.1	74.9	7

Table 1: *Kriathe gnoma* DO CARMO & SANGUINETTI, 1999. Oceanographic data [Depth (m), Temperature (°C), Salinity (‰), Oxygen (ml), Size of Vestibule (μm^2) and Instar] (Anonymous, 1972).

Kriathe gnoma DO CARMO & SANGUINETTI, 1999. Dados oceanográficos [Profundidade (m), Temperatura (°C), Salinidade (‰), Oxigênio (ml), tamanho do vestíbulo (μm^2) e estágio] (Anônimo, 1972).

Kriathe gnoma DO CARMO & SANGUINETTI, 1999: Données océanographiques [Profondeur (m), Température (°C), Salinité (‰), Oxygène (ml), Taille du vestibule (μm^2) et stade ontogénétique] (Anonyme, 1972).

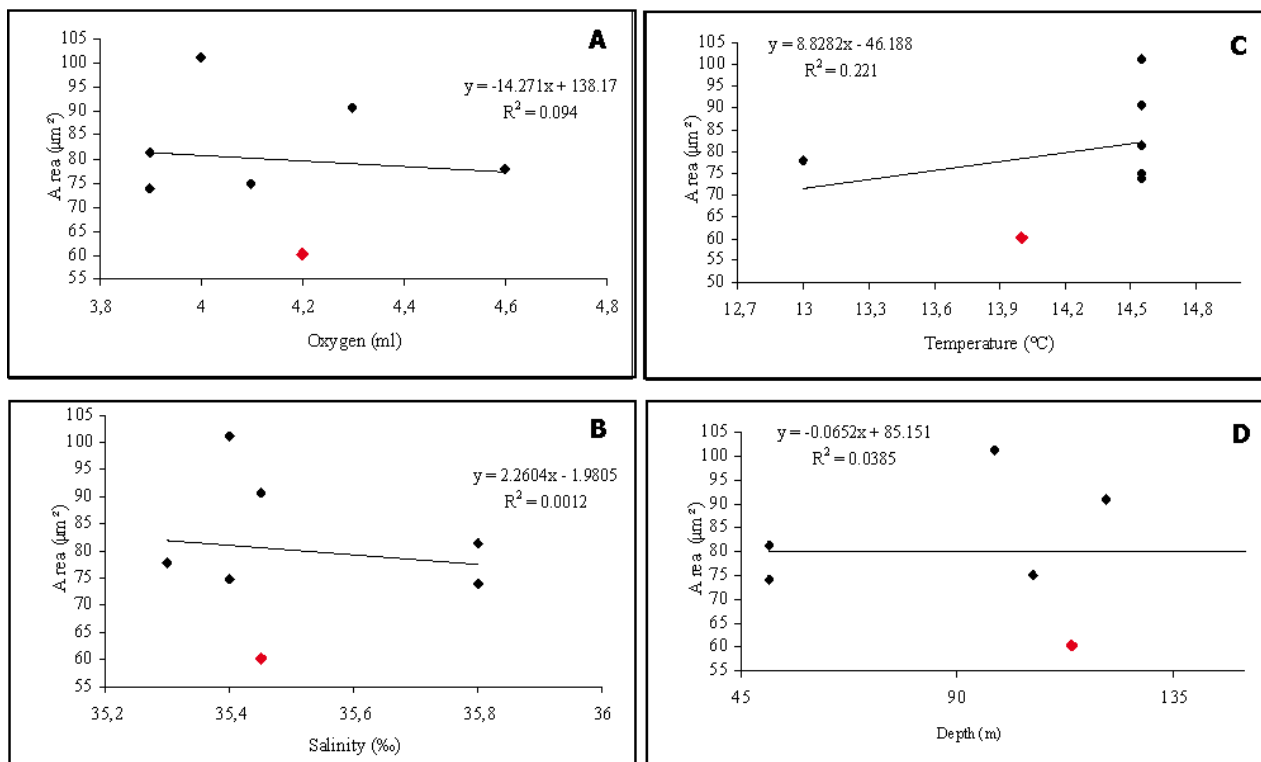


Figure 5: Areas of the vestibule in *Krithe gnoma* DO CARMO & SANGUINETTI, 1999. In black diamonds the measurements of six left valves of 7th instar [A: Oxygenation (ml) B: Salinity (‰) C: Temperature (°C) D: Depth (m)] (Anonymous, 1969, 1970, 1972).

Tamanho do vestibulo de *Krithe gnoma* DO CARMO & SANGUINETTI, 1999. Os pontos pretos indicam as seis valvas esquerdas adultas [A: Oxigênio (ml) B: Salinidade (‰) C: Temperatura (°C) D: Profundidade (m)] (Anônimo, 1969, 1970, 1972).

Taille du vestibule de *Krithe gnoma* DO CARMO & SANGUINETTI, 1999. Points noirs : six valves du 7ème stade [A: Oxygène (ml) B: Salinité (‰) C: Température(°C) D: Profondeur (m)] (Anonyme, 1969, 1970, 1972).

To evaluate the vestibule area in relation to oxygen content, salinity and depth, several curves and lines were examined to determine the procedure that presented the data best (straight line, exponential and logarithm curves). Using the least square method, a straight line was found to be the most appropriate to portray the relationship between vestibular size and oxygen content, temperature, salinity and other factors.

The results presented here show that variations in size of the vestibula have no clear relationship to oxygen content ($R^2=0.06047$), temperature ($R^2=0.02814$), depth ($R^2=0.04932$) and salinity ($R^2=0.01735$). On the other hand the data show that the vestibula range considerably in size even when several intrinsic biologic factors are taken into consideration: dimorphism, ontogeny and differences in the dimensions of left and right valves.

So, as regards the influence of oxygen content on vestibule size these findings do not corroborate this theory, but do not refute it either. Therefore, additional studies should be made to determine whether or not the size of the vestibula in *K. gnoma* and other species of *Krithe* is controlled to any degree by oxygen content, temperature, salinity or any other factor.

5. Remarks

Variation in vestibular size merits further discussion. The 7th instar reference carapace has the largest vestibule in the largest valve. This suggests a proportional relationship between carapace and vestibule size. On the other hand, the left valve of the 8th instar is even larger but has the smallest vestibule of all the reference specimens. Nevertheless, one may conclude that in any one carapace the vestibula are always larger in the left valve.

When considering a vestibular analysis of *Krithe*, several steps are required: 1. Selection of the species to analysed, 2. Choice of an instar and the valve (left or right), and the gender to be examined in order to avoid size variations caused by ontogeny and dimorphism and 3. Selection and standardization of the portion of the vestibule to be analyzed.

In summary, the vestibule-oxygen relationship proposed by PEYPOUQUET is not clearly verified here ($R^2 < 0.1$). The result providing the most support was obtained using a cross-plot of vestibular surface versus water temperature. Because *K. gnoma* has a broad distribution stratigraphically (Late Eocene/Miocene in the Pelotas and Santos basins), these sup-

portive results suggest that evaluating such relationships may be found useful in paleoceanographic studies as indicators - "proxies" - of temperate or cold water inferences regarding temperature (temperate or cold, Fig. 5). However, in view of the polemic nature of the subject, future studies should involve a larger number of specimens and include other species of *Krithe* while carrying out the procedures presented here.

If it is true that the development size of species of *Krithe* is affected by the temperature of oceanic waters (CRONIN *et alii*, 1996, 1999; RODRIGUEZ-LAZARO *et alii*, 1999), it would be interesting to conduct experiments to evaluate how and why the size of the vestibule varies in the several species attributed to this genus.

Thanks to YAMADA & KEISER (2009), a methodology to study the origin and development of vestibula has been introduced. It would be interesting to combine the experiment conducted by MAJORAN *et alii* (2000) with the methodology introduced by YAMADA & KEISER (*op.cit.*). This experimental might make it possible to determine whether or not the pattern recognized for *L. lacertosa* holds for *Krithe praetexta praetexta*. Also in thermocultures of *Krithe praetexta praetexta*, study of vestibular sizes and isotope ratios would be very useful.

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