

# How the number of hinge teeth may induce errors in the taxonomy of Nuculidae and Nuculanidae (Bivalvia)

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## ABSTRACT

The hinge figures as an important feature in the taxonomy of bivalves, especially when soft parts are not available. For the Protobranchia, in addition to other shell features, the number of hinge teeth is often used in taxonomic studies. However, despite the importance of the number of hinge teeth, this character is not informative when shell size measurements are not available, since the number of teeth can increase during ontogeny. In addition, intraspecific variation may be observed for the same shell-size class. Since this variation has been up to now only empirically observed, the present study provides a statistical approach to the problem by computing the linear regression between number of teeth and shell size in 310 valves from five protobranch species (family Nuculidae: *Pronucula benguelana*; *Nucula semiornata*; *Ennucula puelcha*; and family Nuculanidae: *Adrana electa*; *A. patagonica*.) All species showed a statistically significant relationship ( $P$  value  $< 0.0001$ ) between these characters.

**Additional Keywords:** Linear regression, shell morphology, Nuculoidea, Nuculanoidea, Protobranchia, taxonomy

## INTRODUCTION

The protobranchs are a dominant bivalve group at abyssal depths, encompassing a high percentage of the bivalve species found in the deep-sea (Sanders and Allen, 1973). The recent sampling of deep-sea benthic fauna and the efforts of many investigators (e.g. Allen and Sanders, 1973, 1996; Moore, 1977; Rhind and Allen, 1992; Kilburn, 1994, 1999; Gofas and Salas, 1996; Roy et al., 2000; Allen, 2008; La Perna, 2008) have increased the number of known species and enlarged the known ranges of many protobranchs, providing a source for different proposals of classification for the group (e.g. Poel, 1955; Purchon, 1959; Cox, 1960; McAlester, 1964; Newell, 1969; Verrill and Bush, 1897; Yonge, 1959; Sanders and Allen, 1973; Scarlato and Starobogatov, 1985; Allen and Hannah, 1986; Maxwell, 1988; Morton,

1996; Salvini-Plawen and Steiner, 1996; Coan, Scott, and Bernard, 2000; Schneider, 2001; Giribet and Wheeler, 2002; Giribet, 2008).

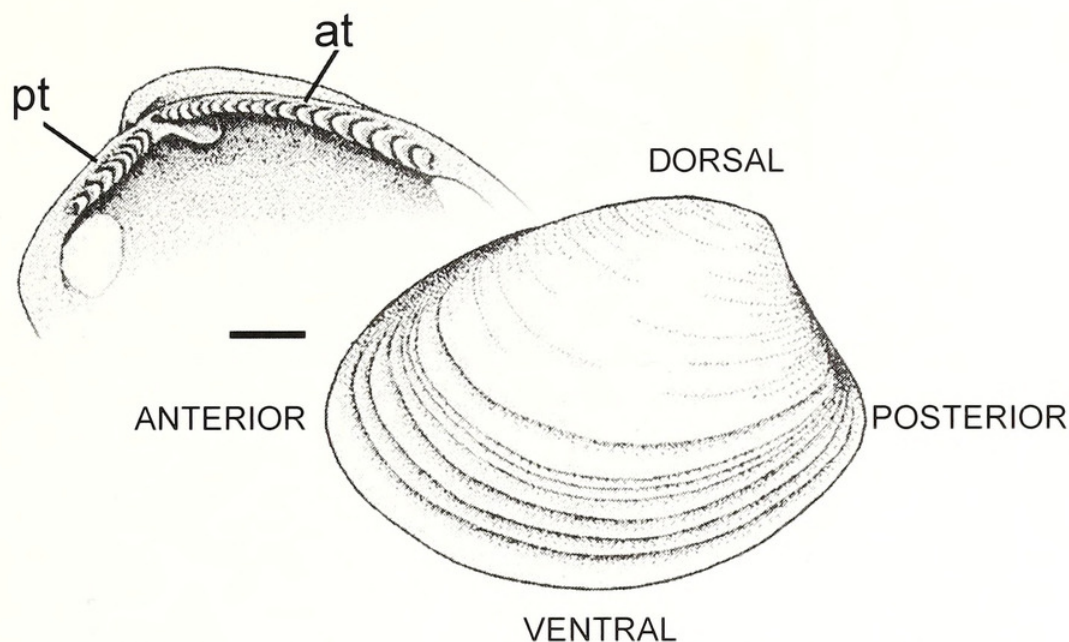
Among the protobranchs, the Nuculoidea Gray, 1824, and Nuculanoidea Adams and Adams, 1858, have had a problematic taxonomic history, often with obscure rearrangements of species and unclear changes in the higher-level taxonomy of many names (for more details see Schenck, 1934; Poel, 1955; Allen and Hannah, 1986; Maxwell, 1988; Rhind and Allen, 1992; Zardus, 2002). Most of the difficulties involved in the classification of the group arise from the conservative nature of the shell shape (Allen and Hannah, 1986) and from the morphological approach, which often considers only a single set of features (Sanders and Allen, 1973).

Although several characters have been taken into account (e.g., general outline, ornamentation and microstructure of the shell), in most taxonomic descriptions of protobranchs the hinge usually is an important taxonomic feature, especially when the studied specimens lack soft parts. The shape, number, position, and spacing of the teeth are often used in the diagnoses of species and even genera (Dall, 1886; Gofas and Salas, 1996). Moreover, the differences between the number of anterior and posterior teeth are used in identification, and even differences in the order of two or three teeth have been considered significant in descriptions or identification works (e.g. Esteves, 1984; Smith, 1885; Abbott, 1974; Kilburn, 1994; Rios, 1994; Espinosa and Ortea, 2001).

However, to consider the number of teeth without associating the character to measurements of shell size is not informative, and may cause taxonomic confusion. A morphometrical approach may improve on the traditional taxonomic methods and has been used with success by several authors (Bonfitto and Sabelli, 1995; Gofas and Salas, 1996; Fuiman et al., 1999).

This paper discusses the taxonomic importance of the size of the shell in proportion to the number of teeth on the hinge in three species of Nuculidae: *Pronucula benguelana* Clarke, 1961; *Nucula semiornata* d'Orbigny,





**Figure 1.** *Ennucula puelcha* d'Orbigny, 1842. Shell and the anterior and posterior hinge teeth. Abbreviations: at = anterior teeth; pt = posterior teeth. Scale bar = 2 mm. Adapted from Absalão & Pimenta (2005).

1846; *Ennucula puelcha* d'Orbigny, 1842; and two of Nuculanidae: *Adrana electa* (A. Adams, 1846); and *Adrana patagonica* (d'Orbigny, 1846).

## MATERIALS AND METHODS

The material examined includes samples taken during different cruises undertaken the South Atlantic Ocean.

The measurements used herein are commonly used in morphometric studies with bivalves (Sibaja and Vilalobos, 1986; Bonfitto and Sabelli, 1995; Gofas and Salas,

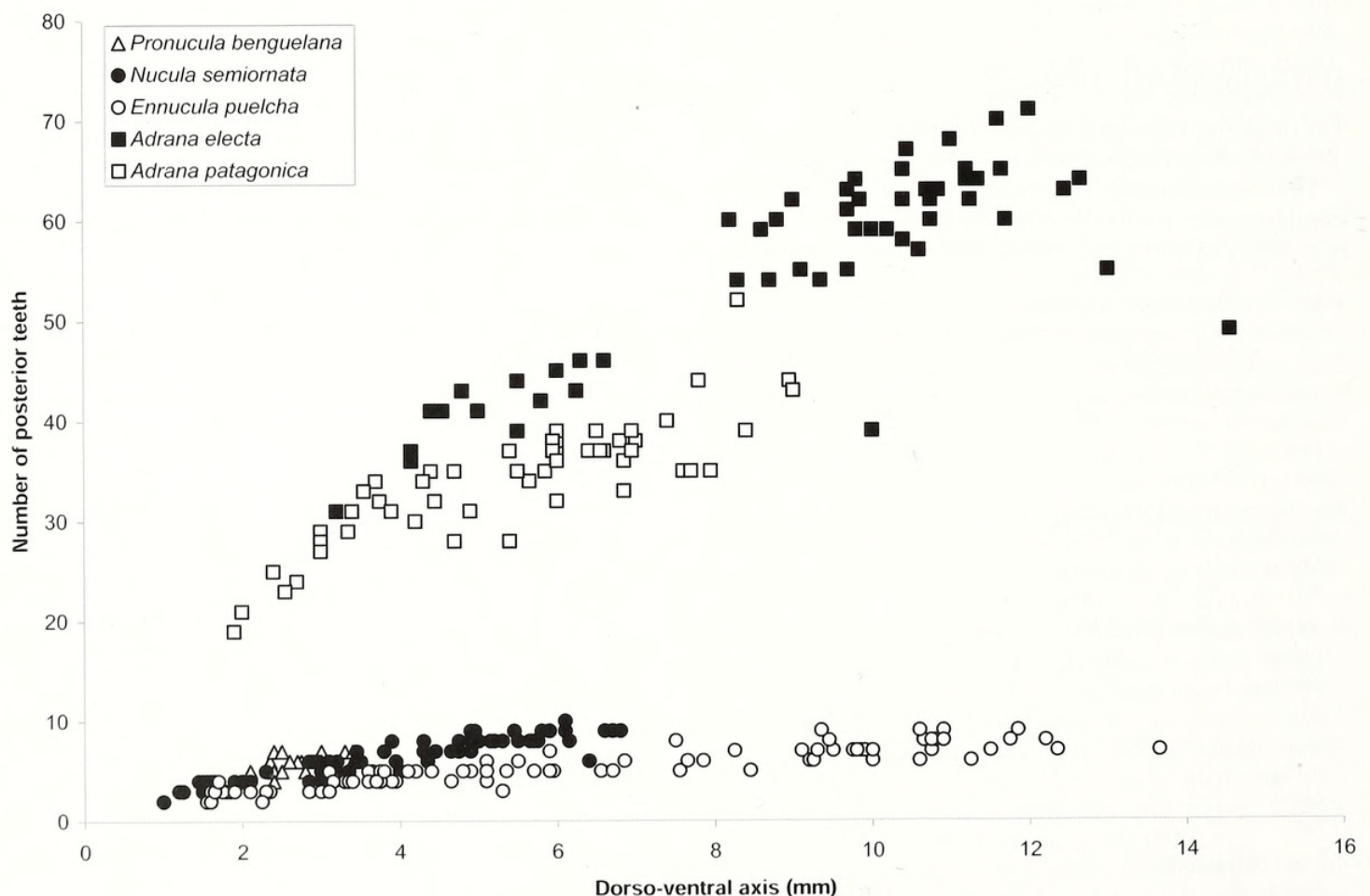
1996; Fuiman et al., 1999), and are represented in Figure 1. The numbers of anterior and posterior teeth were counted with the aid of a ZEISS SV-6 stereoscopic microscope. The antero-posterior and dorso-ventral axes of each valve were measured using a caliper of 0.05 mm accuracy. A total of 200 valves of nuculids and 110 valves of nuculanids were considered in this study (Table 1). The statistical approach consisted of linear regression analysis (Sokal and Rohlf, 1981). All material from this study is deposited in the Mollusca collection of the Departamento de Zoologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro (IBUFRJ).

**Table 1.** Descriptive statistics of the material analyzed. Abbreviation: sd = Standard deviation.

Species names	Antero-posterior axis	Dorso-ventral axis	Anterior teeth	Posterior teeth
<i>Pronucula benguelana</i> (N = 23)				
Range	1.7–3.8mm	1.6–3.45mm	5–10	3–7
Mean	2.81	2.62	7.65	5.52
sd	0.55	0.50	1.27	1.20
<i>Nucula semiornata</i> (N = 82)				
Range	0.85–6.85mm	1.0–6.8mm	6–23	2–10
Mean	3.60	3.43	13.93	5.76
Sd	1.72	1.71	4.70	2.09
<i>Ennucula puelcha</i> (N = 95)				
Range	1.65–15.25mm	1.55–13.65mm	4–22	2–9
Mean	6.71	6.20	13.24	5.25
sd	3.73	3.42	4.75	1.86
<i>Adrana electa</i> (N = 55)				
Range	12.45–56–60mm	3.20–14.55mm	32–64	31–71
Mean	35.68	9.15	50.76	55.47
Sd	9.20	2.66	7.11	10.02
<i>Adrana patagonica</i> (N = 55)				
Range	5–33.3mm	1.9–9mm	16–55	19–52
Mean	17.39	5.37	31.40	33.98
sd	6.22	1.88	6.68	5.91

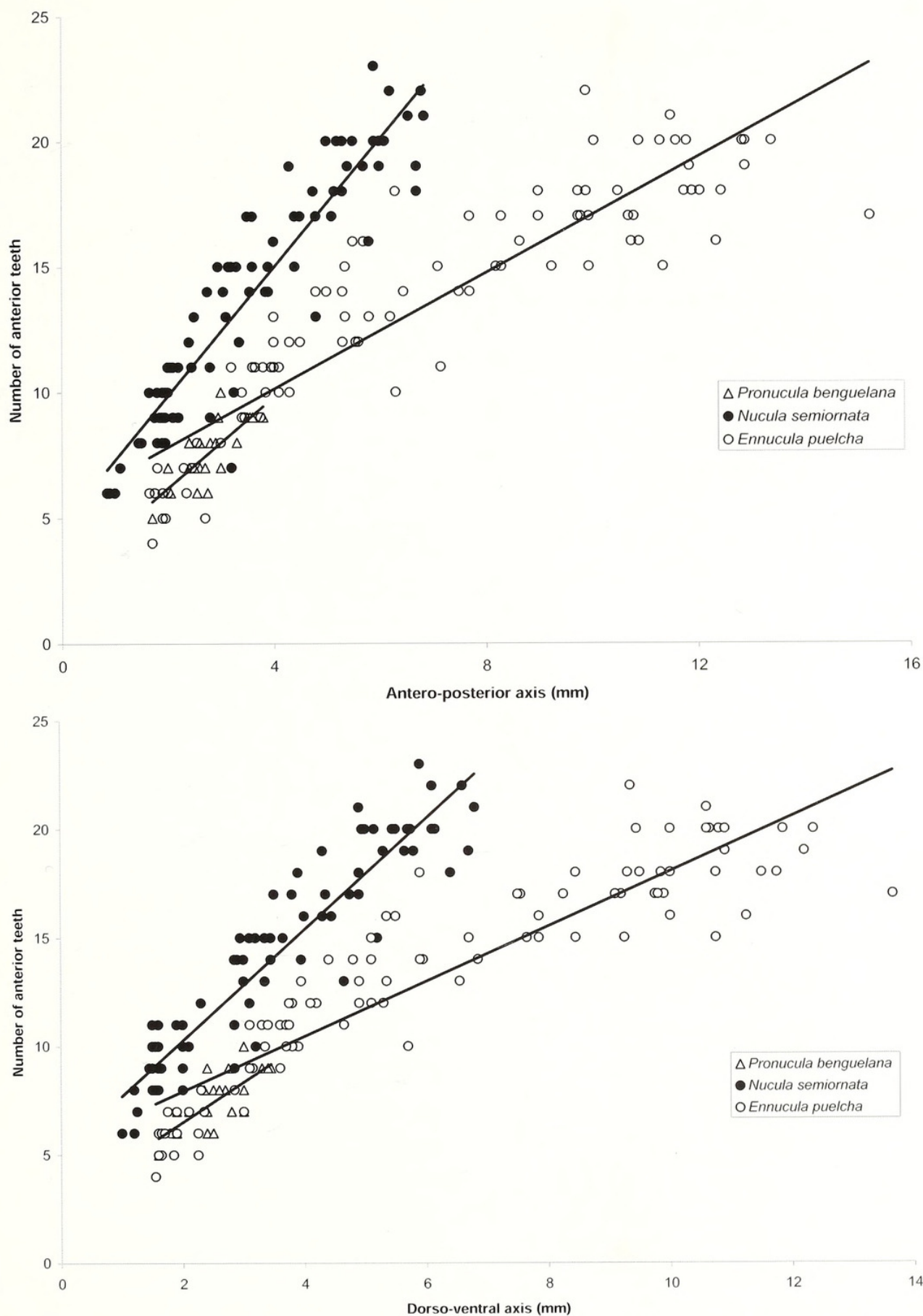
**Table 2.** Results of statistical analyses. Abbreviations: ap = antero-posterior axis; dv = dorso-ventral axis; at = anterior teeth; pt = posterior teeth.

Species names	x(ap) - y(at)	x(ap) - y(pt)	x(dv) - y(at)	x(dv) - y(pt)
<i>P. benguelana</i>	$y = 1.798x + 2.597$ $R^2 = 0.607$ $F = 32.44$ $P \text{ value} < 0.0001$	$Y = 1.68x + 0.793$ $R^2 = 0.589$ $F = 30.10$ $P \text{ value} < 0.0001$	$y = 1.848x + 2.810$ $R^2 = 0.538$ $F = 24.49$ $P \text{ value} < 0.0001$	$Y = 1.742x + 0.959$ $R^2 = 0.530$ $F = 23.72$ $P \text{ value} < 0.0001$
<i>N. semiornata</i>	$y = 2.550x + 4.757$ $R^2 = 0.8707$ $F = 538.9$ $P \text{ value} < 0.0001$	$Y = 1.139x + 1.659$ $R^2 = 0.8811$ $F = 592.7$ $P \text{ value} < 0.0001$	$y = 2.555x + 5.152$ $R^2 = 0.8635$ $F = 506.1$ $P \text{ value} < 0.0001$	$Y = 1.139x + 1.845$ $R^2 = 0.8693$ $F = 532.0$ $P \text{ value} < 0.0001$
<i>E. puelcha</i>	$y = 1.152x + 5.514$ $R^2 = 0.8183$ $F = 418.8$ $P \text{ value} < 0.0001$	$Y = 0.4425x + 2.284$ $R^2 = 0.7892$ $F = 348.1$ $P \text{ value} < 0.0001$	$y = 1.266x + 5.396$ $R^2 = 0.8338$ $F = 466.5$ $P \text{ value} < 0.0001$	$Y = 0.4858x + 2.241$ $R^2 = 0.8031$ $F = 379.3$ $P \text{ value} < 0.0001$
<i>A. electa</i>	$y = 0.6188x + 28.68$ $R^2 = 0.6412$ $F = 94.73$ $P \text{ value} < 0.0001$	$Y = 0.9373x + 22.03$ $R^2 = 0.7418$ $F = 152.3$ $P \text{ value} < 0.0001$	$y = 1.953x + 32.90$ $R^2 = 0.5324$ $F = 60.34$ $P \text{ value} < 0.0001$	$Y = 3.093x + 27.19$ $R^2 = 0.6732$ $F = 109.2$ $P \text{ value} < 0.0001$
<i>A. patagonica</i>	$y = 1.006x + 13.90$ $R^2 = 0.8776$ $F = 380.1$ $P \text{ value} < 0.0001$	$Y = 0.8626x + 18.98$ $R^2 = 0.8228$ $F = 246.1$ $P \text{ value} < 0.0001$	$y = 3.205x + 14.18$ $R^2 = 0.8115$ $F = 228.2$ $P \text{ value} < 0.0001$	$Y = 2.685x + 19.56$ $R^2 = 0.7261$ $F = 140.5$ $P \text{ value} < 0.0001$

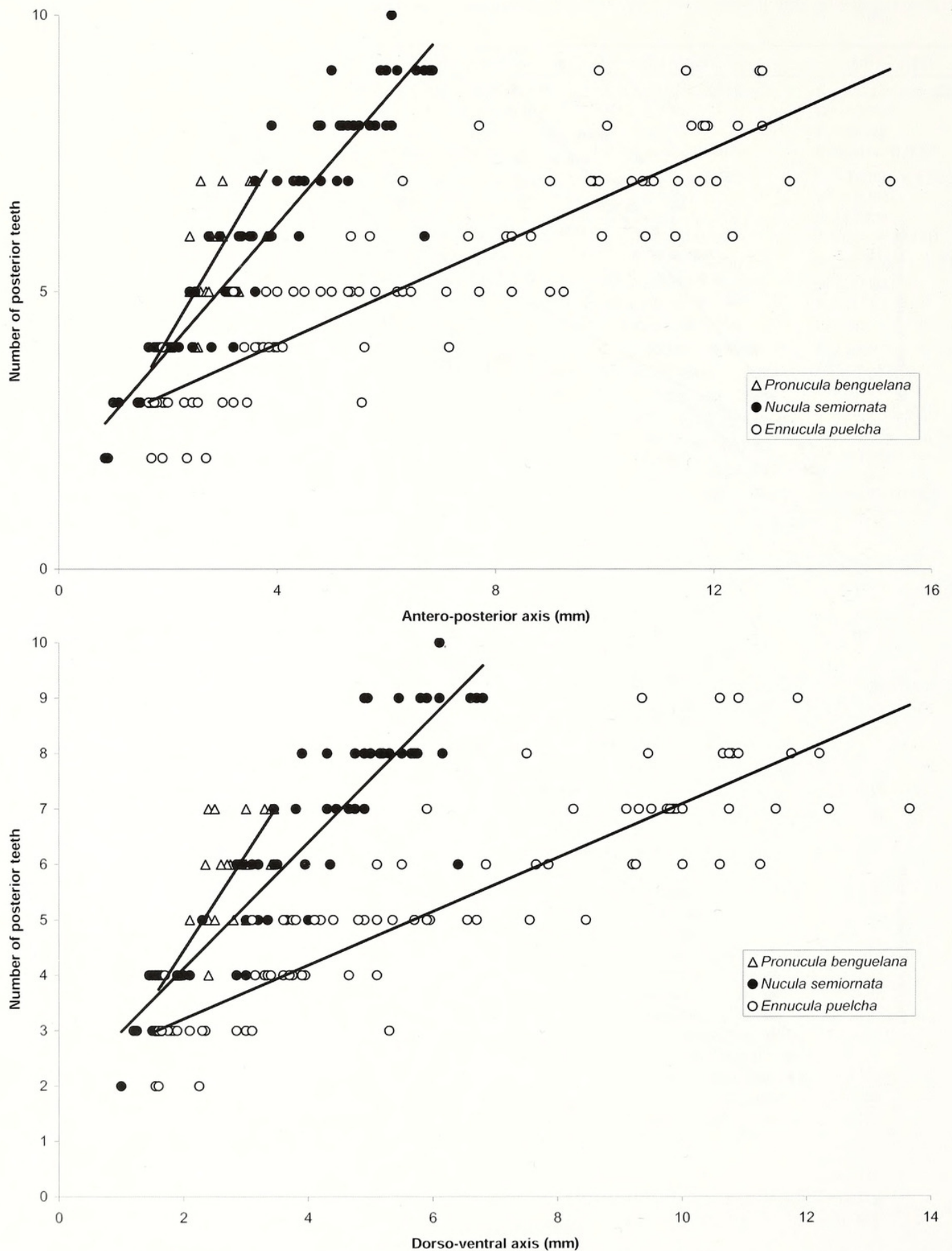


**Figure 2.** Relationship of dorso-ventral axis and number of posterior teeth in studied protobranch species. The two families analyzed occupy discrete morphospaces, reinforcing the importance of the number of teeth as a character at supra-specific levels.





**Figure 3.** Relationship between: **A.** antero-posterior and **B.** dorso-ventral axes with the number of anterior teeth, showing the morphospaces overlap between *Pronucula benguelana* and *Ennucula puelcha*.



**Figure 4.** Relationship between: **A.** antero-posterior and **B.** dorso-ventral axes with the number of posterior teeth, showing the overlap of the morphospaces of *Pronucula benguelana* and *Nucula semiornata*.



## RESULTS AND DISCUSSION

All the species studied exhibited a gradual increase of the number of anterior and posterior teeth during ontogeny. All results were statistically significant (Table 2), when we compared the importance of shell size with the number of anterior and posterior teeth. This statistical analysis confirmed the existence of a relationship between the two variables, size and number of teeth, and suggests that this relationship may be verified in other protobranch species. Furthermore, it confirmed the variation in the number of teeth for the same size class for each species studied. This attests to the inconsistency of this character when it is analyzed alone.

In addition, Figure 2 indicates a distinction among the genera *Adrana* and *Pronucula*, *Nucula*, and *Ennucula*, which becomes more evident when we compared the number of posterior teeth and the length of the dorso-ventral axis. This result matches most accepted classifications that consider several characters (not only number of teeth) and allocate these three genera into two distinct groups (e.g. Allen and Hannah, 1986; Maxwell, 1988; Giribet and Wheeler, 2002; Giribet, 2008).

On the other hand, considering the Nuculidae, the morphospace of *Pronucula benguelana* overlapped with *E. puelcha* in the number of anterior teeth regressed on antero-posterior axis (Figure 3a) and on dorso-ventral axis (Fig. 3b); and *P. benguelana* overlapped with *N. semiornata* in the number of posterior teeth regressed on antero-posterior axis (Figure 4a) and on dorso-ventral axis (Figure 4b). In both cases, these overlaps of the number of teeth (anterior or posterior) occurred up to about 4 mm in size, on each axis analyzed, for *P. benguelana*. Because this latter species is about 4 mm in size, this size limit in the overlap cannot be interpreted as a consequence of the number of specimens collected.

It is evident that the current taxonomy of Nuculidae presents confused generic definitions, not rare with a great correspondence of characters. Considering only the results presented herein, the overlaps of the morphospaces of *Pronucula* and *Nucula* are in agreement, and may reinforce the view of Bergmans (1978), who synonymized the two genera, or that of Allen and Hannah (1986), who proposed the allocation of *Pronucula*, at a subgeneric rank, to the genus *Nucula*. Along the same lines, the overlaps of the morphospaces of *Ennucula* and *Nucula* may reinforce the view of Schenck (1934) who placed *Ennucula* as a subgenus of *Nucula*. Nevertheless, because no other taxonomic features were analyzed in this study and, moreover, none of the species studied are type-species of *Pronucula*, *Nucula*, or *Ennucula*, this ratification of the opinions of above-mentioned authors may be premature.

## CONCLUSION

These statistical analyses confirmed empirical observations of the relation between shell size and number of

teeth in protobranch bivalves and attests to the inconsistency of the latter character when analyzed alone. For the taxa studied herein, the number of teeth on the hinge is an important taxonomic feature, but only when the size of the shell is also taken into account. Otherwise, taxonomic studies and descriptions based only on the number of teeth without providing any measures of the shell are not informative and might make it impossible to define whether one is dealing with several similar species or just one that shows intraspecific variation for the character number of hinge teeth.

The use of other characters in the taxonomy of the group is obviously important, but for the species studied here, at the family level, the distinction between *Adrana* (Nuculanidae) and *Pronucula*, *Nucula*, and *Ennucula* (Nuculidae) is in agreement with most accepted classifications. This attests the importance of number of teeth on the hinge related to the size of the shell for the distinction of these two families even when no other characters are considered. Nevertheless, for the nuculids, the differentiation of the distinct genera is unclear. The number of teeth on hinge and the size of the shell alone do not provided a good distinction among the three genera and the overlap of the morphospaces of these different taxa reinforces the demand for the use of more taxonomic characters and emphasizes the need for more comprehensive studies with these groups.

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## LITERATURE CITED

- Abbott, R.T. 1974. American Seashells. 2nd ed. Van Nostrand Reinhold Co., New York. 663 p., 24 pls.
- Absalão, R.S. and A.D. Pimenta, 2005. Moluscos Marinhos da APA do Arquipélago de Santana, Macaé, RJ. Chave Ilustrada para Identificação das Espécies do Substrato Inconsolidado. Editora Ciência Moderna, Rio de Janeiro. 84 p., 21 pls.
- Allen, J.A. 2008. Bivalvia of the deep Atlantic. *Malacologia* 50(1): 57–173.
- Allen, J.A. and F.J. Hannah, 1986. A reclassification of the Recent genera of the subclass Protobranchia (Mollusca: Bivalvia). *Journal of Conchology* 32: 225–249.
- Allen, J.A. and H.L. Sanders, 1973. Studies on deep-sea Protobranchia (Bivalvia): the families Siliculidae and Lametilidae. *Bulletin of the Museum of Comparative Zoology* 145: 263–310.
- Allen, J.A. and H.L. Sanders, 1996. Studies on the deep-sea Protobranchia (Bivalvia): the family Neilonellidae and the family Nuculanidae. *Bulletin-Natural History Museum Zoology Series* 62: 101–132.



- Bergmans, W. 1978. Taxonomic revision of Recent Australian Nuculidae (Mollusca: Bivalvia) except *Ennucula* Iredale, 1931. Records of the Australian Museum 31: 673–736.
- Bonfitto, A. and B. Sabelli. 1995. *Yoldiella seguenzae*, a new species of Nuculanidae (Bivalvia; Nuculoida) from the Mediterranean Sea. Journal of Molluscan Studies 61: 21–27.
- Coan, E.V., P.V. Scott, and F.R. Bernard. 2000. Bivalve seashells of western North America: marine bivalve mollusks from arctic Alaska to Baja California. Santa Barbara Museum of Natural History, Santa Barbara, 764 pp.
- Cox, L.R. 1960. Thoughts on the classification of the Bivalvia. Proceedings of the Malacological Society of London 34: 60–80.
- Dall, W.H. 1886. Report on the Mollusca. Part 1. Brachiopoda and Pelecypoda. Reports on the results of dredging by the US coast survey steamer 'Blake'. Bulletin of the Museum of Comparative Zoology 12: 171–318.
- Espinosa, J. and J. Ortea. 2001. Descripción de una nueva especie de *Adrana* Adams and Adams, 1858. Avicennia 4: 61–76.
- Esteves, I.R. 1984. Recent bivalves (Palaeotaxodonta and Pteriomorpha) from the Brazilian continental shelf. Pesquisas, Porto Alegre, 16: 190–226.
- Fuiman, L.A., J.D. Gage, and P.A. Lamont. 1999. Shell morphometry of the deep sea protobranch bivalve *Ledella pustulosa* in the Rockall Trough, Northeast Atlantic. Journal of the Marine Biological Association United Kingdom 79: 661–671.
- Giribet, G. 2008. Bivalvia. In: Ponder, W.F. and D.R. Lindberg (eds.) Phylogeny and Evolution of the Mollusca. University of California Press Berkeley, pp. 105–141.
- Giribet, G. and W. Wheeler. 2002. On Bivalve Phylogeny: A High-Level Analysis of the Bivalvia (Mollusca) Based on Combined Morphology and DNA Sequence Data. Invertebrate Biology: 271–324.
- Gofas, S. and C. Salas. 1996. Small Nuculidae (Bivalvia) with functional primary hinge in the adults. Journal of Conchology 35: 427–436.
- Kilburn, R.N. 1994. The protobranch genera *Jupiteria*, *Ledella*, *Yoldiella* and *Neilo* in South Africa, with the description of a new genus (Mollusca: Bivalvia: Nuculanoidea). Annals of the Natal Museum 35: 157–175.
- Kilburn, R.N. 1999. The family Nuculidae (Bivalvia: Protobranchia) in South Africa and Mozambique. Annals of the Natal Museum 40: 245–268.
- La Perna, R. 2008. Revision of the protobranch species described by Dautzenberg and Fischer (1897) with description of a new species and taxonomic comments on *Bathyspinula* (Bivalvia, Nuculanoidea). The Veliger 50: 149–162.
- Maxwell, P. 1988. Comments on "A reclassification of the Recent genera of the subclass Protobranchia (Mollusca: Bivalvia)" by J.A. Allen and F.J. Hannah (1986). Journal of Conchology 33: 85–96.
- Mcalester, A.L. 1964. Preliminary suggestions for a classification of nuculoid bivalves. Journal of Paleontology 38: 397–400.
- Moore, D.R. 1977. Small species of Nuculidae (Bivalvia) from the tropical western Atlantic. The Nautilus 91: 119–128.
- Morton, B. 1996. The evolutionary history of the Bivalvia. In: Origin and evolutionary radiation of the Mollusca (J.D. Taylor, ed.), pp. 337–359. Oxford: Oxford University Press.
- Newell, N.D. 1969. Classification of Bivalvia. In: Moore, R.C. (ed.) Treatise on Invertebrate Paleontology, Part N, Vol. 1, Mollusca 6, Bivalvia. Geological Society of America and the University of Kansas Press, Lawrence, N205–N224.
- Poel, L. 1955. Structure du test et classification des Nucules. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 11: 1–68.
- Purchon, R.D. 1959. Phylogenetic classification of the Lamellibranchia, with special reference to the Protobranchia. Proceedings of the Malacological Society of London 33: 224–230.
- Rhind, P.M. and J.A. Allen. 1992. Studies on the deep-sea Protobranchia (Bivalvia): the family Nuculidae. Bulletin of the British Museum, Natural History, Zoology 58: 61–93.
- Rios, E.C. 1994. Seashells of Brazil. 2nd ed. Museu Oceanográfico Prof. E.C. Rios da Fundação Universidade de Rio Grande, Rio Grande. 368 p., 113 pls.
- Roy, K., D. Jablonski, and J.W. Valentine. 2000. Dissecting latitudinal diversity gradients: functional groups and clades of marine bivalves. Proceedings of the Royal Society of London, Series B 267: 293–299.
- Salvini-Plawen, L. and G. Steiner. 1996. Synapomorphies and plesiomorphies in higher classification of Mollusca. In: J.D. Taylor (ed.) Origin and evolutionary radiation of the Mollusca. Oxford University Press, Oxford, pp. 29–51.
- Sanders, H.L. and J.A. Allen. 1973. Studies on deep-sea Protobranchia (Bivalvia); Prologue and the Pristiglomidae. Bulletin of the Museum of Comparative Zoology 145: 237–262.
- Scarlato, O.A. and Y.I. Starobogatov. 1985. General evolutionary patterns and the system of the class Bivalvia. Harvard University Department Special Occasional Publication, 67 pp. [English translation from the Russian original.]
- Schenck, H.G. 1934. Classification of nuculid pelecypods. Bulletin du Musée Royal d'Histoire Naturelle de Belgique 10: 1–70.
- Schneider, J.A. 2001. Bivalve Systematics during the 20th Century. Journal of Paleontology 75: 1119–1127.
- Sibaja, W.G. and C.R. Villalobos. 1986. Crecimiento del mejillón *Mytella guyanensis* L. (Bivalvia: Mytilidae), en el Golfo de Nicoya, Costa Rica. Revista de Biología Tropical 34: 231–236.
- Smith, E.A. 1885. Report on the Lamellibranchiata collected by HMS Challenger during the years 1873–1876. Challenger Reports, Zoology 13, 341 pp.
- Sokal, R.R. and F.J. Rohlf. 1981. Biometry. The principles and practice of statistics in biological research. Freeman and Company, New York, 859 pp.
- Verrill, A.E. and K.J. Bush. 1897. Revision of the genera of Ledidae and Nuculidae of the Atlantic coast of the United States. American Journal of Science 3: 51–63.
- Yonge, C.M. 1959. The status of the Protobranchia in the bivalve Mollusca. Proceedings of the Malacological Society of London 33: 210–214.
- Zardus, J.D. 2002. Protobranch bivalves. Advances in Marine Biology 42, 65 pp.



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