



Geometrical modeling of the internal profile of the muscle scar in limpet shells (*Patellogasteropoda*) suggests constraints on their morphological diversity

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Abstract

The phylogenetic relationships between the major families and genera within limpets (*Patellogasteropoda*) have proven challenging to resolve. One of the reasons is that shell morphology, despite being a salient character, shows nonetheless a large degree of intraspecific variation as well as convergent ecophenotypes in different species. Our work aims to contribute to the effort by developing a geometrical method to characterize the muscle scar shape. We applied a geometrical model of the muscle scar to 183 specimens from 117 species, 15 genera and 5 families. Our results show that the muscle scar shape has a very low variability in general, and what variability it has is not correlated with currently suggested phylogenetic relationships. Nevertheless, we consider geometrical modeling of the muscle scar a useful tool for the study of *Patellogasteropoda*. Among future uses could be testing if muscle scar shows ecophenotypic variation, and to perform large-scale studies on fossil shells.

Keywords: *Patellogasteropoda*, limpets, morphometry, geometrical model, biodiversity

1. Introduction

Limpets (Patellogasteropoda) are a major phylogenetic group of marine gastropods. Limpet shells are shaped as a flattened cone, and the majority of species are commonly found adhering strongly to rocks or other hard substrates (Nakano & Sasaki, 2011). The phylogeny of Patellogasteropoda has suffered several revisions, as species determination and reconstruction of evolutionary relationships has proven challenging within this group.

Two kinds of methodologies are generally used in the study of Patellogasteropoda: genetic and morphometric. Methodologies based on genetic analysis (Nakano & Ozawa, 2004, 2005, 2007; Nakano & Spencer 2007; Mauro *et al.*, 2003; Espinosa & Ozawa, 2006; Casu *et al.*, 2006, 2010; Faria *et al.*, 2017) are good for identification purposes, but give inconsistent results when reconstructing phylogenies (Nakano & Sasaki, 2011). In the case of methodologies based on the analysis of the morphological characters, several problems arise due to the inter- and intraspecific variability of Patellogasteropoda (Nakano & Sasaki, 2011; Sanna *et al.*, 2012).

On the one hand, there is considerable morphological convergence between species not closely related (Nakano & Sasaki, 2011), and several cases of cryptic species with similar morphologies have been found (Nakano & Spencer, 2007, Nakano & Ozawa, 2007, Sá-Pinto *et al.*, 2008). On the other hand, Patellogasteropoda also show large intraspecific variability and ecophenotypic plasticity, which leads to the development of superficially different phenotypes depending on the substrate and other environmental variables (Pagarete *et al.*, 2005, Teske *et al.*, 2007, Nakano *et al.*, 2009). Thus, the coloration and

morphology of the shell are not reliable characters, as they are strongly conditioned by the environment (Lindberg & Pearse, 1990; Tyler *et al.*, 2014) and vary between populations of the same species (Sanna *et al.*, 2012). This is true even for more detailed morphometric studies, be it of the ratios of individual shells (Christiaens, 1973) or of the general shapes of a population in statistical terms (Mauro *et al.*, 2003), which are unable to reliably separate species (Mauro *et al.*, 2003; Cabral & Natal Jorge, 2007).

Despite the ambiguity that originates from the high morphological variability of Patellogasteropoda, some morphological and morphometric studies have found limited success: The study of the mineral microstructure of the shell (MacClintock, 1963) in combination with other morphological characteristics has resulted in a robust morphological definition of different genera (Ridgway *et al.*, 1998). However, the determination of species is still problematic with this method, as is a clear reconstruction of phylogenetic relationships between genera (Ridgway *et al.*, 1998).

Lastly, Faria *et al.* (2017) had a degree of success in the use of landmark and distance-based morphometry to study phenotypic differentiation of a limpet species across the Azores, Madeira and Canaries archipelagos and integrating them with genetic data. Faria and colleagues found solid evidence for extensive differentiation between archipelagos. However, the differentiation patterns when using morphometric and genetic analyses did not agree. Shell morphology grouped Azores and Canaries in a close cluster, with Madeira separate, whilst genetic analyses clustered Canaries and Madeira, and left Azores separate. The main challenges they cite for morphometric analyses they cite are finding appropriate, homologous landmarks on a highly variable shell, as well as the information lost when reducing a three-dimensional conical shape to a two-dimensional surface.

The aim of the current work is to develop a new tool for the morphometric study of Patellogasteropoda. On the one hand, we focus on the interior line delimited by the impression of the muscles that attach the animal to the shell. The muscle impression is a homologous character in all *Patellogastropoda*, and has the advantage of allowing the study of preserved shells without soft tissues while circumventing the problems that come with the high variability of the shell, as the impression corresponds to the anatomical structures of the animal itself. On the other hand, our new method tries to minimize reliance in landmarks, and instead uses a geometrical model to characterize the overall shape of the muscle scar. We expect such an analysis to determine whether there is significant variation in the muscle scar across taxonomical groups, and whether such variation shows any discernible pattern.

2. Methods

2.1. Images of *Patellogastropoda*: we used pictures of samples stored online in the Mollusca collection database of the Natural History Museum of Rotterdam website (nmr-pics.nl). The actual shells sizes in the pictures refer to the longest axis of the specimen in mm. We studied a total of 183 individuals, 117 species from 15 genera and 5 families of *Patellogastropoda* (**Annex 1**).

2.2. Geometrical model: we used the GeoGebra software [1] to create a template of the muscle scar impression. Our model had the general shaped of an ovoid, and was constructed according to the geometric procedure described in Rodríguez and Álvarez (1990). The ovoid is defined using two circumferences $C1$ and $C2$ of radii $r1$ and $r2$, respectively, separated by a distance (d) between their centers ($O1$, $O2$). A tangency point (T) was defined in one of them (Figure 1A) given an angle alpha. In order to define the ovoid, a circumference (c) centered in $O1$ and with radius $r1$ minus $r2$ is drawn. T and $O1$ are connected with a line that cuts c at point t . Point t is connected with $O2$ with a line (m). A

pb bisector is traced perpendicular to m , which crosses the T-O1 line at point $O3$. From point $O3$ a line k is traced that passing through $O2$, which crosses $C2$ at $T1$. Finally, a circumference arc centered in $O3$ and touching T and $T1$ is drawn. (Figure 1B). A mirror image of this circumference arc completes the ovoid.

In this model, three sliders allow to assign different values to the main variables that define the ovoid: I) The angle (variable α) which determines the position of tangency point T ; II) the relationship (variable r) between the radii of circumferences $C1$ and $C2$; III) the relationship (variable p) between the radius of circumference $O1$ and the distance d between the centers of both circumferences (Figure 1C).

2.3 Data processing: We applied the geometrical model to each of the 183 shell pictures adjusted to the internal muscle scar. We used the variables obtained for each specimen to study the differences between super-families, families and genera. Levene and Fisher tests, along with hierarchic conglomerate analysis, were carried out using IBM SPSS Statistics 19.0 (SPSS, Inc., Chicago, IL).

3. Results

In the 117 studied species the first variable (r) had a very consistent value of two, which meant that the radius of the larger circumference doubled the radius of the smaller circumference. Likewise, angle α was always 45° . Therefore, the only variable that showed significant variation was p which varied between 0.10 and 1.00 with a mean of 0.51 (SD = 0.181). The geometrical model (Figure 1) was a good fit to the profile of the muscular scar (Figure 2A) of the shell of all 117 species in the study. The distribution of frequencies was leptokurtic (0.361) and presented a high level of concentration around the central values of the variable (Figure 2B).

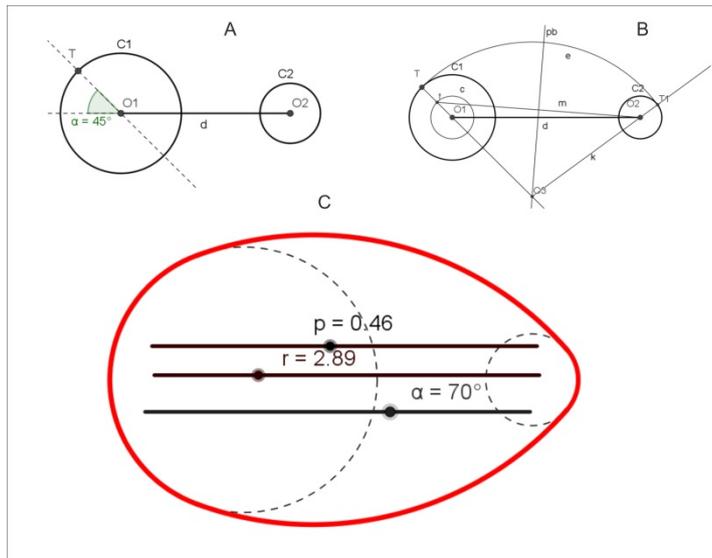


Figure 1. Three-step summary of the creation of an ovoid according to our model. **A)** The two base circumferences C1 and C2, with centers O1 and O1 separated by distance d. Also shown is tangency point T and angle α . **B)** displays circumference c (with radius r_1-r_2) and the associated line m and point t. Also shown is bisector pb, the associated point O3 and line k. Lastly, the circumference arc between T and T1 is shown. **C)** An example of an ovoid built with our model using the variable values $p=0.46$, $r=2.89$ and $\alpha=70^\circ$.

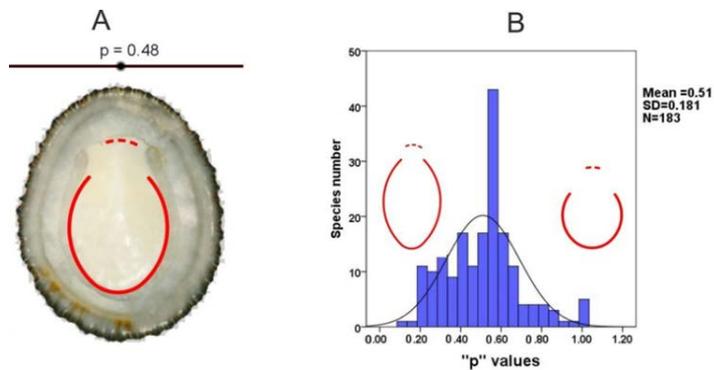


Figure 2. **A)** Model (in red) adjusted to a ventral image of a specimen of *Cymbula canescens*. **B)** Frequency plot for the p variable (blue bars), which shows the normal curve (black line) and the models (red ovoids) corresponding to the extremes of the normal curve.

There were not significant differences between the two super-families best represented with our data: *Patelloidea* with 87 individuals, mean of 0.522 (SD = 0.183) and *Lottioidea* with 94 individuals, mean of 0.495 (SD = 0.178). The variances were homogeneous and the means were not significantly different (Levene statistic = 0.221, Sig. = 0.639; and Fisher F test = 0.974, Sig. = 0.325).

There were not significant differences between the three families best represented with our data: *Patellidae* with 87 individuals, mean of 0.522 (SD = 0.183), *Nacellidae* with 44 individuals, mean of 0.519 (SD = 0.213) and *Lottiidae* with 49 individuals, mean 0.473 (SD = 0.141). The variances were homogeneous and the means were not significantly different (Levene statistic = 2.159, Sig. = 0.119; and Fisher F test = 1.261, Sig. = 0.286).

It was not the same case with genera. If we considered the best represented genera in our sample (with 5 or more species) like *Patella* (11 species), *Cellana* (24 species), *Lottia* (19 species), *Patelloidea* (11 species), *Cymbula* (6 species), *Scutellastra* (12 species) and *Nacella* (7 species) we observed that the variances differed, while the means were not significantly different (Levene statistic = 2.272, Sig. = 0.039; and Fisher F test = 5.815, Sig. = 0.00).

Finally, we performed a hierarchical conglomerates analysis on all the studied genera (see dendrogram in Figure 3) which used a mean link between groups and a squared Euclidean distance using p as variable. The analysis clustered the genera in three groups with a mean of 0.60 (SD = 0.04), 0.28 (SD = 0.02) and 0.43 (SD = 0.06) respectively. The variances were similar, while the means were significantly different (Levene statistic = 3.091, Sig. = 0.083; and Fisher F test = 42.759, Sig. < 0.00). These three groups showed no direct correspondence with families or superfamilies.

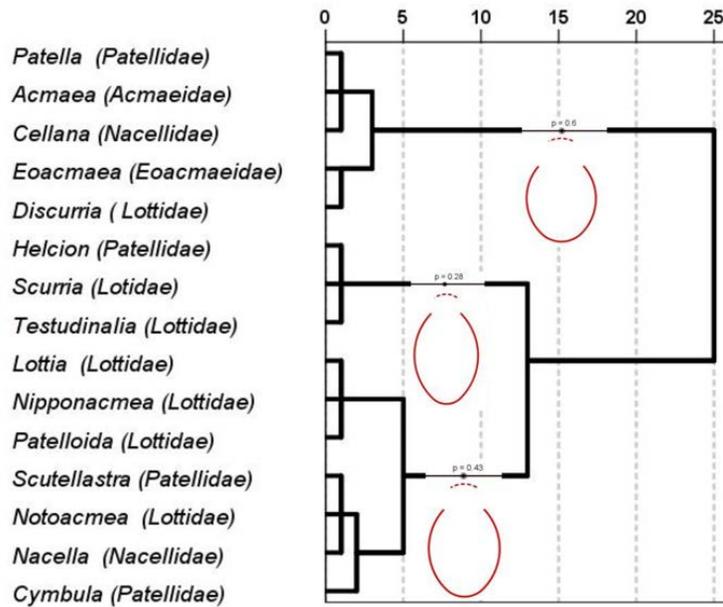


Figure 3. A dendrogram constructed using mean correlation (between groups) and a squared Euclidean distance using p as variable. p values are relative to the distance d with respect to the radius (r_1) of the larger circumference (see Figure 1). Ovoid outline (in red) corresponds to the mean of the genera included in each of the three groups generated by our analysis

4. Discussion

The different possible combinations of the three variables that build the ovoid in our model allow us to build a very large array of shapes (Supplemental figure S1). However, when we adjust this model to the muscle scar profile of different species of limpets, the variability is very limited. The values for r and α remain fixed at 2 and 45° , respectively. On the other hand, p , which essentially represents the distance between the two initial circumferences, fluctuates between 0.20 and 1 in our sample of 117 species. However, the distribution of values was highly leptokurtic with a mean at 0.51 ± 0.181 (Figure 2B). A principal component analysis was able to divide our samples into three groups with an average p of 0.5, 0.28 and 0.43, respectively and construct a dendrogram using the results. However, a comparison with the results of the Nakano and Sasaki (2011) did not find correlations with any of the phylogenies shown in the

review. In summary, variation of the muscle scar shape in our examined sample of *Patellogasteropoda* was small and randomly distributed across phylogenetic groups. This puts it in stark contrast to the large variation in shell morphology across and even within species, where shell variability can give rise to different ecophenotypes (Pagarete *et al.*, 2005, Teske *et al.*, 2007). It also suggests that, though associated with the shell, these muscles show independence in their variation (or lack thereof) and are influenced by their own set of constraints.

Patellogasteropoda are a clade with a very specific ecological niche. Although the type of biological innovation that leads to the occupation of a new niche is traditionally seen as an enabler of evolutionary radiation and diversification (Price *et al.*, 2010), in practice this is not always the case, and optimization for a new niche can lead to stabilizing selection in certain traits and, consequently, to limits on morphological variation (Ord *et al.*, 2020). Limpets are under substantial pressure to optimize the morphology of their mantle and their muscular foot alongside it in order to optimize adhesion to rocks and avoid being dislodged by waves and currents. In this sense, the shape of the muscle scar, as a reflection of the general shape of the body and foot may be a mostly invariant character related to the general *bauplan* that defines Patellogasteropoda as a group. In contrast, the morphology of the shell is free to vary in several dimensions independently of the overall body shape, and thus has a larger morphological space within which it can vary without drastically decreasing the animal's fitness.

Although the character we selected does not vary in a pattern that corresponds to phylogeny, our approach to the study of the morphology of limpets using geometrical modeling has value as a way to better characterize specific morphological traits. Moreover, although the muscle scar by itself and within the limitations of our sample is not informative regarding phylogeny, it can have

other uses. Future studies will explore larger samples from each species in order to better characterize intraspecific variation as well as variability between distinct ecophenotypes. Finally, it is worth noting that the muscle scar imprint may be present in fossils and could feasibly be used as a proxy to examine variation in general body shape during evolution.

Funding

This project was supported by the Animal Anatomy Laboratory Foundation (Project n° 2019_1). Nicolas Palanca-Castan is funded by a FONDECYT postdoctoral grant (3180149).

References:

- Cabral, J.C. and Natal Jorge, R.M. 2007. Compressibility and Shell failure in the European Atlantic *Patella* limpets. *Mar. Biol.*, **150**: 585–597.
- Casu, M., Casu, D., Piero Cossu, T.L., Curini-Galletti, M. 2006. Inter-simple sequence repeat markers reveal strong genetic differentiation among populations of the endangered mollusk *Patella ferruginea* (Gastropoda: Patellidae) from two Sardinian marine protected areas. *Mar. Biol.*, **149**: 1163-1174.
- Casu, M., Sanna, D., Cristo, B., Lai, T., Luca, G., Curini-Galletti, D., Curini-Galletti, M. 2010. COI sequencing as tool for the taxonomic attribution of *Patella* spp. (Gastropoda): the case of morphologically undistinguishable juveniles settled on a *Patella ferruginea* adult. *J. Mar. Biol. Assoc. U.K.*, **90**: 1449-1454.
- Christiaens, J. 1973. Révision du genre *Patella* (Mollusca, Gastropoda). *Bull. Mus. Natl. Hist. Nat.*, **182** : 1306-1392.

- Espinosa, F. and Ozawa, T. 2006. Population genetics of the endangered limpet *Patella ferruginea* (Gastropoda: Patellidae): taxonomic, conservation and evolutionary considerations. *J. Zool. Syst. Evol. Res.*, **44**: 8-16. doi:10.1111/j.1439-0469.2005.00348.x
- Faria, J., Martins, G.M., Pita, A., Ribeiro, P.A., Hawkins, S.J., Presa, P., Neto, A.I. 2017. Disentangling the genetic and morphological structure of *Patella candei* complex in Macaronesia (NE Atlantic). *Ecol. Evol.*, **7**: 6125-6140. <https://doi.org/10.1002/ece3.3121>.
- Lindberg, D.R. and Pearse, J.S. 1990. Experimental manipulation of shell color and morphology of the limpets *Lottia asmi* (Middendorff) and *Lottia digitalis* (Rathke) (Mollusca: Patellogastropoda). *J. Mar. Biol.*, **140**: 173-185. [https://doi.org/10.1016/0022-0981\(90\)90125-V](https://doi.org/10.1016/0022-0981(90)90125-V).
- MacClintock, C. 1963. Reclassification of gastropod *proscutum* fischer based on muscle scars and shell structure. *J. Paleontol.*, **37**: 141-156. <http://www.jstor.org/stable/1301416>.
- Mauro, A., Arculeo, M., Parrinello, N. 2003. Morphological and molecular tools in identifying the Mediterranean limpets *Patella caerulea*, *Patella aspera* and *Patella rustica*. *J. Exp. Mar. Biol. Ecol.*, **295**: 131-143. [https://doi.org/10.1016/S0022-0981\(03\)00291-0](https://doi.org/10.1016/S0022-0981(03)00291-0).
- Nakano, T. and Ozawa, T. 2004. Phylogeny and historical biogeography of limpets of the order *Patellogastropoda* based on mitochondrial DNA sequences. *J. Molluscan Stud.*, **70**: 31-41.
- Nakano, T. and Ozawa, T. 2005. Systematic revision of *Patelloida pygmaea* (Dunker, 1860) (Gastropoda: Lottiidae), with a description of a new species. *J. Molluscan Stud.*, **71**: 357-370. <https://doi.org/10.1093/mollus/eyi039>.

- Nakano, T. and Spencer, H.G. 2007. Simultaneous polyphenism and cryptic species in an intertidal limpet from New Zealand. *Mol. Phylogenet. Evol.*, **45**: 470-479.
- Nakano, T. and Ozawa, T. 2007. Worldwide phylogeography of limpets of the order Patellogastropoda: molecular, morphological and Palaeontological evidence. *J. Molluscan Stud.*, **73**: 79-99. doi:10.1093/mollus/eym001.
- Nakano, T., Marshall, B.A., Kennedy, M., Spencer, H.G. 2009. The phylogeny and taxonomy of New Zealand *Notoacmea* and *Patelloida* species (Mollusca: Patellogastropoda: Lottiidae) inferred from DNA sequences. *Molluscan Res.*, **29**: 33-59.
- Nakano, T. and Sasaki, T. 2011. Recent advances in molecular phylogeny, systematics and evolution of patellogastropoda limpets. *J. Molluscan Stud.*, **77**: 203-217.
- Ord, T. J., Garcia-Porta, J., Querejeta, M., & Collar, D. C. (2020). Gliding dragons and flying squirrels: diversifying versus stabilizing selection on morphology following the evolution of an innovation. *The American Naturalist*, 195(2)
- Pagarete, A. J. (2005). Genetic conspecificity in two habitat morphs of the limpet *Patella candei gomesii* Drouët (Mollusca: Gastropoda: Patellidae) reinforces limpet morphological plasticity. *Journal of Young Investigators*.
- Price, S. A., Wainwright, P. C., Bellwood, D. R., Kazancioglu, E., Collar, D. C., & Near, T. J. (2010). Functional innovations and morphological diversification in parrotfish. *Evolution: International Journal of Organic Evolution*, 64(10), 3057-3068.

- Ridgway, S.A., Reid, D.G., Taylor, J.D., Branch, G.M., Hodgson, A.N. 1998. A cladistic phylogeny of the family Patellidae (Mollusca: Gastropoda). *Philos. Trans. Royal Soc. B*, **353**: 1645-1671. doi: 10.1098/rstb.1998.0316.
- Rodriguez De Abajo, F. J., & Álvarez Bengoa, V. (1992). Curso de dibujo geométrico y de croquización. *San Sebastián*.
- Sá-Pinto, A., Branco, M., Sayanda, D., & Alexandrino, P. (2008). Patterns of colonization, evolution and gene flow in species of the genus *Patella* in the Macaronesian Islands. *Molecular ecology*, *17*(2), 519-532.
- Sanna, D., Dedola, G.L., Lai, T., Curini-Galletti, M., Casu, M. 2012. PCR-RFLP: A practical method for the identification of specimens of *Patella ulyssiponensis* s.l. (Gastropoda: Patellidae). *Ital. J. Zool.*, **79**: 50-59. doi: 10.1080/11250003.2011.620988.
- Teske, P. R., Barker, N. P., & McQuaid, C. D. (2007). Lack of genetic differentiation among four sympatric southeast African intertidal limpets (Siphonariidae): phenotypic plasticity in a single species?. *Journal of Molluscan Studies*, *73*(3), 223-228.
- Tyler, C.L., Leighton, L.R., Kowalewski, M. 2014. The effects of limpet morphology on predation by adult cancrid crabs. *J. Exp. Mar. Biol. Ecol.*, **451**: 9-15.

ANEXO 1

Superfamily	Family	Size (mm)	Genus	Species	Sub-species	Author and date	Variable "p"
Patelloidea	Patellidae	44	Cymbula	canescens		Gmelin, 1791	0.48
Patelloidea	Patellidae	70	Cymbula	granatina		Linnaeus, 1758	0.6
Patelloidea	Patellidae	98	Cymbula	miniata		Born, 1778	0.52
Patelloidea	Patellidae	60	Cymbula	miniata		Born, 1778	0.61
Patelloidea	Patellidae	85	Cymbula	oculus		Born, 1778	0.26
Patelloidea	Patellidae	90	Cymbula	safiana		Lamark, 1819	0.29
Patelloidea	Patellidae	90	Cymbula	safiana		Lamark, 1819	0.17
Patelloidea	Patellidae	90	Cymbula	safiana		Lamark, 1819	0.22
Patelloidea	Patellidae	90	Cymbula	safiana		Lamark, 1819	0.26
Patelloidea	Patellidae	60	Cymbula	sanguinans		Reeve, 1854	0.23
Patelloidea	Patellidae	72	Cymbula	sanguinans		Reeve, 1854	0.22
Patelloidea	Patellidae	40	Helcion	concolor		Krauss, 1848	0.27
Patelloidea	Patellidae	50	Patella	aspera		Röding, 1798	0.39
Patelloidea	Patellidae	50	Patella	aspera		Röding, 1798	0.39
Patelloidea	Patellidae	50	Patella	aspera	nicklesi	Röding, 1798	0.42
Patelloidea	Patellidae	50	Patella	aspera	teneriffae	Röding, 1798	0.56
Patelloidea	Patellidae	50	Patella	aspera	lowei	Röding, 1798	0.66
Patelloidea	Patellidae	53	Patella	aspera	lowei	Röding, 1798	0.58
Patelloidea	Patellidae	50	Patella	caerulea		d'Orbigny, 1839	0.81
Patelloidea	Patellidae	50	Patella	caerulea		d'Orbigny, 1839	0.63
Patelloidea	Patellidae	50	Patella	caerulea	adpersa	d'Orbigny, 1839	0.56
Patelloidea	Patellidae	50	Patella	caerulea	fragilis	d'Orbigny, 1839	0.85
Patelloidea	Patellidae	50	Patella	caerulea	stellata	d'Orbigny, 1839	0.54
Patelloidea	Patellidae	50	Patella	caerulea	subplana	d'Orbigny, 1839	0.57
Patelloidea	Patellidae	45	Patella	candei		Pennant, 1777	0.84
Patelloidea	Patellidae	45	Patella	candei		Pennant, 1777	0.55
Patelloidea	Patellidae	45	Patella	candei		Pennant, 1777	0.5
Patelloidea	Patellidae	45	Patella	candei		Pennant, 1777	0.87
Patelloidea	Patellidae	65	Patella	candei		Pennant, 1777	0.57
Patelloidea	Patellidae	50	Patella	candei		Pennant, 1777	0.47
Patelloidea	Patellidae	60	Patella	candei		Pennant, 1777	0.4
Patelloidea	Patellidae	45	Patella	candei	citrus	Pennant, 1777	0.63
Patelloidea	Patellidae	45	Patella	candei	citrus	Pennant, 1777	0.68
Patelloidea	Patellidae	45	Patella	candei	citrus	Pennant, 1777	0.47
Patelloidea	Patellidae	45	Patella	candei	gomesii	Pennant, 1777	0.57
Patelloidea	Patellidae	60	Patella	candei	ordinaria	Pennant, 1777	0.64
Patelloidea	Patellidae	60	Patella	candei	gomesii	Pennant, 1777	0.49
Patelloidea	Patellidae	60	Patella	candei	ordinaria	Pennant, 1777	0.57
Patelloidea	Patellidae	60	Patella	candei	ordinaria	Pennant, 1777	0.54
Patelloidea	Patellidae	60	Patella	candei	saxea	Pennant, 1777	0.56
Patelloidea	Patellidae	60	Patella	candei	saxea	Pennant, 1777	0.6
Patelloidea	Patellidae	76	Patella	candei	teneriffae	Pennant, 1777	0.55
Patelloidea	Patellidae	50	Patella	candei	tenuis	Pennant, 1777	0.43
Patelloidea	Patellidae	50	Patella	candei	tenuis	Pennant, 1777	0.33

<i>Patelloidea</i>	<i>Patellidae</i>	50	<i>Patella</i>	<i>depressa</i>		Pennant, 1777	0.67
<i>Patelloidea</i>	<i>Patellidae</i>	50	<i>Patella</i>	<i>depressa</i>		Pennant, 1777	0.9
<i>Patelloidea</i>	<i>Patellidae</i>	50	<i>Patella</i>	<i>depressa</i>		Pennant, 1777	0.75
<i>Patelloidea</i>	<i>Patellidae</i>	30	<i>Patella</i>	<i>depressa</i>	<i>vatheliti</i>	Pennant, 1777	0.23
<i>Patelloidea</i>	<i>Patellidae</i>	60	<i>Patella</i>	<i>ferruginea</i>		Gmelin, 1791	0.63
<i>Patelloidea</i>	<i>Patellidae</i>	60	<i>Patella</i>	<i>ferruginea</i>		Gmelin, 1791	0.54
<i>Patelloidea</i>	<i>Patellidae</i>	38	<i>Patella</i>	<i>ferruginea</i>		Gmelin, 1791	0.42
<i>Patelloidea</i>	<i>Patellidae</i>	50	<i>Patella</i>	<i>lugubris</i>		Gmelin, 1791	0.57
<i>Patelloidea</i>	<i>Patellidae</i>	50	<i>Patella</i>	<i>lugubris</i>		Gmelin, 1791	0.57
<i>Patelloidea</i>	<i>Patellidae</i>	50	<i>Patella</i>	<i>lugubris</i>		Gmelin, 1791	0.62
<i>Patelloidea</i>	<i>Patellidae</i>	16	<i>Patella</i>	<i>pellucida</i>	<i>laevis</i>	Pennant, 1777	0.64
<i>Patelloidea</i>	<i>Patellidae</i>	30	<i>Patella</i>	<i>piperata</i>		Gould, 1846	0.54
<i>Patelloidea</i>	<i>Patellidae</i>	30	<i>Patella</i>	<i>piperata</i>		Gould, 1846	0.33
<i>Patelloidea</i>	<i>Patellidae</i>	25	<i>Patella</i>	<i>rustica</i>		Linnaeus, 1758	1
<i>Patelloidea</i>	<i>Patellidae</i>	25	<i>Patella</i>	<i>rustica</i>		Linnaeus, 1758	0.57
<i>Patelloidea</i>	<i>Patellidae</i>	50	<i>Patella</i>	<i>rustica</i>		Linnaeus, 1758	0.38
<i>Patelloidea</i>	<i>Patellidae</i>	50	<i>Patella</i>	<i>ulyssiponensis</i>		Gmelin, 1791	0.64
<i>Patelloidea</i>	<i>Patellidae</i>	50	<i>Patella</i>	<i>ulyssiponensis</i>		Gmelin, 1791	0.57
<i>Patelloidea</i>	<i>Patellidae</i>	50	<i>Patella</i>	<i>ulyssiponensis</i>	<i>athletica</i>	Bean in Thorpe, 1844	0.68
<i>Patelloidea</i>	<i>Patellidae</i>	50	<i>Patella</i>	<i>ulyssiponensis</i>	<i>bonardii</i>	Payraudeau, 1826	0.69
<i>Patelloidea</i>	<i>Patellidae</i>	45	<i>Patella</i>	<i>ulyssiponensis</i>	<i>Pontica</i>	Valenciennes in Monterosato, 1888	0.54
<i>Patelloidea</i>	<i>Patellidae</i>	50	<i>Patella</i>	<i>vulgata</i>		Linnaeus, 1758	0.74
<i>Patelloidea</i>	<i>Patellidae</i>	60	<i>Patella</i>	<i>vulgata</i>		Linnaeus, 1758	0.48
<i>Patelloidea</i>	<i>Patellidae</i>	50	<i>Patella</i>	<i>vulgata</i>		Linnaeus, 1758	0.58
<i>Patelloidea</i>	<i>Patellidae</i>	50	<i>Patella</i>	<i>vulgata</i>		Linnaeus, 1758	0.73
<i>Patelloidea</i>	<i>Patellidae</i>	50	<i>Patella</i>	<i>vulgata</i>		Linnaeus, 1758	0.35
<i>Patelloidea</i>	<i>Patellidae</i>	46	<i>Patella</i>	<i>vulgata</i>		Linnaeus, 1758	0.5
<i>Patelloidea</i>	<i>Patellidae</i>	50	<i>Patella</i>	<i>vulgata</i>	<i>elevata</i>	jeffreys, 1865	0.54
<i>Patelloidea</i>	<i>Patellidae</i>	50	<i>Patella</i>	<i>vulgata</i>	<i>radiata</i>	Perry, 1811	0.67
<i>Patelloidea</i>	<i>Patellidae</i>	50	<i>Patella</i>	<i>vulgata</i>	<i>secernenda</i>	Dautzenberg, 1887	0.94
<i>Patelloidea</i>	<i>Patellidae</i>	80	<i>Scutellastra</i>	<i>argenvillei</i>		Krauss, 1848	0.28
<i>Patelloidea</i>	<i>Patellidae</i>	80	<i>Scutellastra</i>	<i>argenvillei</i>		Krauss, 1848	0.27
<i>Patelloidea</i>	<i>Patellidae</i>	25	<i>Scutellastra</i>	<i>chapmani</i>		Tenison-Woods, 1875	0.19
<i>Patelloidea</i>	<i>Patellidae</i>	40	<i>Scutellastra</i>	<i>cochlear</i>		Born, 1778	0.11
<i>Patelloidea</i>	<i>Patellidae</i>	25	<i>Scutellastra</i>	<i>flexuosa</i>		Quoy & Gaimard, 1835	0.71
<i>Patelloidea</i>	<i>Patellidae</i>	50	<i>Scutellastra</i>	<i>granularis</i>		Linnaeus, 1758	0.51
<i>Patelloidea</i>	<i>Patellidae</i>	95	<i>Scutellastra</i>	<i>laticostata</i>		Blainville, 1825	0.48
<i>Patelloidea</i>	<i>Patellidae</i>	75	<i>Scutellastra</i>	<i>longicosta</i>		Lamarck, 1819	0.36
<i>Patelloidea</i>	<i>Patellidae</i>	153	<i>Scutellastra</i>	<i>mexicana</i>		Broderip & G.B.Sowerby, 1829	0.59
<i>Patelloidea</i>	<i>Patellidae</i>	25	<i>Scutellastra</i>	<i>obtecta</i>		Krauss, 1848	0.41
<i>Patelloidea</i>	<i>Patellidae</i>	70	<i>Scutellastra</i>	<i>optima</i>		Pilsbry, 1927	0.36
<i>Patelloidea</i>	<i>Patellidae</i>	40	<i>Scutellastra</i>	<i>peronii</i>		Brainville, 1825	0.49
<i>Patelloidea</i>	<i>Patellidae</i>	130	<i>Scutellastra</i>	<i>tabularis</i>		Krauss, 1848	0.31
<i>Eoacmaeidea</i>	<i>Eoacmaeidae</i>	10	<i>Eoacmaea</i>	<i>calamus</i>		Crosse & P.Fischer, 1864	0.5

<i>Eoacmaeidea</i>	<i>Eoacmaeidae</i>	20	<i>Eoacmaea</i>	<i>conoidalis</i>		Pease, 1868	0.78
<i>lottioidea</i>	<i>Nacellidae</i>	63	<i>Cellana</i>	<i>ardosiaea</i>		Hombron & Jacquinot, 1841	0.24
<i>lottioidea</i>	<i>Nacellidae</i>	21	<i>Cellana</i>	<i>conciliata</i>		Iredale, 1940	0.79
<i>lottioidea</i>	<i>Nacellidae</i>	35	<i>Cellana</i>	<i>cylindrica</i>		Gmelin, 1791	0.6
<i>lottioidea</i>	<i>Nacellidae</i>	50	<i>Cellana</i>	<i>denticulata</i>		Martyn, 1784	0.33
<i>lottioidea</i>	<i>Nacellidae</i>	35	<i>Cellana</i>	<i>eucosmia</i>		Pilsbry, 1891	0.58
<i>lottioidea</i>	<i>Nacellidae</i>	40	<i>Cellana</i>	<i>exarata</i>		Reeve, 1854	1
<i>lottioidea</i>	<i>Nacellidae</i>	45	<i>Cellana</i>	<i>flava</i>		Hutton, 1873	0.83
<i>lottioidea</i>	<i>Nacellidae</i>	35	<i>Cellana</i>	<i>grata</i>		Gould, 1859	0.56
<i>lottioidea</i>	<i>Nacellidae</i>	35	<i>Cellana</i>	<i>karachiensis</i>		Winckworth, 1930	0.5
<i>lottioidea</i>	<i>Nacellidae</i>	30	<i>Cellana</i>	<i>karachiensis</i>		Winckworth, 1930	0.57
<i>lottioidea</i>	<i>Nacellidae</i>	37	<i>Cellana</i>	<i>livescens</i>		Reeve, 1855	0.29
<i>lottioidea</i>	<i>Nacellidae</i>	40	<i>Cellana</i>	<i>livescens</i>		Reeve, 1855	0.4
<i>lottioidea</i>	<i>Nacellidae</i>	40	<i>Cellana</i>	<i>livescens</i>		Reeve, 1855	1
<i>lottioidea</i>	<i>Nacellidae</i>	50	<i>Cellana</i>	<i>nigrolineata</i>		Reeve, 1854	0.3
<i>lottioidea</i>	<i>Nacellidae</i>	50	<i>Cellana</i>	<i>nigrolineata</i>		Reeve, 1855	0.4
<i>lottioidea</i>	<i>Nacellidae</i>	23	<i>Cellana</i>	<i>nigrolineata</i>	<i>divergens</i>	Pilsbry, 1891	0.19
<i>lottioidea</i>	<i>Nacellidae</i>	35	<i>Cellana</i>	<i>ornata</i>		Dillwyn, 1817	0.41
<i>lottioidea</i>	<i>Nacellidae</i>	35	<i>Cellana</i>	<i>radians</i>		Gmelin, 1791	0.25
<i>lottioidea</i>	<i>Nacellidae</i>	35	<i>Cellana</i>	<i>radiata</i>		Born, 1778	0.48
<i>lottioidea</i>	<i>Nacellidae</i>	33	<i>Cellana</i>	<i>radiata</i>	<i>orientalis</i>	Pilsbry, 1891	0.61
<i>lottioidea</i>	<i>Nacellidae</i>	30	<i>Cellana</i>	<i>radiata</i>	<i>capensis</i>	Gmelin, 1791	0.59
<i>lottioidea</i>	<i>Nacellidae</i>	30	<i>Cellana</i>	<i>radiata</i>	<i>capensis</i>	Gmelin, 1791	0.32
<i>lottioidea</i>	<i>Nacellidae</i>	17	<i>Cellana</i>	<i>radiata</i>	<i>capensis</i>	Gmelin, 1791	0.5
<i>lottioidea</i>	<i>Nacellidae</i>	17.5	<i>Cellana</i>	<i>radiata</i>	<i>capensis</i>	Gmelin, 1791	0.66
<i>lottioidea</i>	<i>Nacellidae</i>	30	<i>Cellana</i>	<i>rota</i>		Gmelin, 1791	0.58
<i>lottioidea</i>	<i>Nacellidae</i>	70	<i>Cellana</i>	<i>solida</i>		Brainville, 1825	1
<i>lottioidea</i>	<i>Nacellidae</i>	45	<i>Cellana</i>	<i>stellifera</i>		Gmelin, 1791	0.54
<i>lottioidea</i>	<i>Nacellidae</i>	45	<i>Cellana</i>	<i>strigilis</i>		Hombron & Jacquinot, 1841	0.4
<i>lottioidea</i>	<i>Nacellidae</i>	36	<i>Cellana</i>	<i>taitensis</i>		Röding, 1798	0.57
<i>lottioidea</i>	<i>Nacellidae</i>	44	<i>Cellana</i>	<i>talcosa</i>		Gould, 1846	0.59
<i>lottioidea</i>	<i>Nacellidae</i>	80	<i>Cellana</i>	<i>testudinaria</i>		Linnaeus, 1758	0.71
<i>lottioidea</i>	<i>Nacellidae</i>	35	<i>Cellana</i>	<i>toreuma</i>		Reeve, 1854	0.34
<i>lottioidea</i>	<i>Nacellidae</i>	50	<i>Cellana</i>	<i>tramoserica</i>		Holten, 1802	0.54
<i>lottioidea</i>	<i>Nacellidae</i>	10	<i>Cellana</i>	<i>turbator</i>		Iredale, 1940	1
<i>lottioidea</i>	<i>Nacellidae</i>	50	<i>Nacella</i>	<i>clypeater</i>		Lesson, 1831	0.56
<i>lottioidea</i>	<i>Nacellidae</i>	50	<i>Nacella</i>	<i>clypeater</i>		Lesson, 1831	0.43
<i>lottioidea</i>	<i>Nacellidae</i>	45	<i>Nacella</i>	<i>concinna</i>		Strebel, 1908	0.2
<i>lottioidea</i>	<i>Nacellidae</i>	45	<i>Nacella</i>	<i>concinna</i>		Strebel, 1908	0.56
<i>lottioidea</i>	<i>Nacellidae</i>	50	<i>Nacella</i>	<i>deareata</i>		Gmelin, 1791	0.43
<i>lottioidea</i>	<i>Nacellidae</i>	40	<i>Nacella</i>	<i>deareata</i>		Gmelin, 1791	0.37
<i>lottioidea</i>	<i>Nacellidae</i>	36	<i>Nacella</i>	<i>delicatissima</i>		Strebel, 1907	0.23
<i>lottioidea</i>	<i>Nacellidae</i>	40	<i>Nacella</i>	<i>flammea</i>		Gmelin, 1791	0.43
<i>lottioidea</i>	<i>Nacellidae</i>	50	<i>Nacella</i>	<i>magellanica</i>		Gmelin, 1791	0.43

<i>lottioidea</i>	<i>Nacellidae</i>	42	<i>Nacella</i>	<i>varicosa</i>		Reeve, 1854	0.52
<i>lottioidea</i>	<i>Lottiidae</i>	25	<i>Discurria</i>	<i>insessa</i>		Hinds, 1842	0.65
<i>lottioidea</i>	<i>Lottiidae</i>	16	<i>Lottia</i>	<i>albicosta</i>		C. B. Adams, 1845	0.59
<i>lottioidea</i>	<i>Lottiidae</i>	22	<i>Lottia</i>	<i>antillarum</i>		G. B. Sowerby, 1834	0.24
<i>lottioidea</i>	<i>Lottiidae</i>	24	<i>Lottia</i>	<i>antillarum</i>	<i>wottonae</i>	Christiaens, 1975	0.54
<i>lottioidea</i>	<i>Lottiidae</i>	12	<i>Lottia</i>	<i>asmi</i>		Middendorff, 1847	0.54
<i>lottioidea</i>	<i>Lottiidae</i>	22	<i>Lottia</i>	<i>digitalis</i>		Rathke, 1833	0.49
<i>lottioidea</i>	<i>Lottiidae</i>	30	<i>Lottia</i>	<i>dorsuosa</i>		Gould, 1859	0.52
<i>lottioidea</i>	<i>Lottiidae</i>		<i>Lottia</i>	<i>gigantea</i>		Gray in G. B. Sowerby, 1834	
<i>lottioidea</i>	<i>Lottiidae</i>	13	<i>Lottia</i>	<i>jamaicensis</i>		Gmelin, 1791	0.52
<i>lottioidea</i>	<i>Lottiidae</i>	15	<i>Lottia</i>	<i>leucopleura</i>		Gmelin, 1791	0.54
<i>lottioidea</i>	<i>Lottiidae</i>	35	<i>Lottia</i>	<i>limatula</i>		Carpenter, 1864	0.57
<i>lottioidea</i>	<i>Lottiidae</i>	25	<i>Lottia</i>	<i>mesoleuca</i>		Menke, 1851	0.45
<i>lottioidea</i>	<i>Lottiidae</i>	13	<i>Lottia</i>	<i>mixta</i>		Reeve, 1855	0.54
<i>lottioidea</i>	<i>Lottiidae</i>	18	<i>Lottia</i>	<i>onychitis</i>		Menke, 1843	0.57
<i>lottioidea</i>	<i>Lottiidae</i>	27	<i>Lottia</i>	<i>pelta</i>		Rathke, 1833	0.42
<i>lottioidea</i>	<i>Lottiidae</i>	40	<i>Lottia</i>	<i>persona</i>		Rathke, 1833	0.31
<i>lottioidea</i>	<i>Lottiidae</i>	30	<i>Lottia</i>	<i>scabra</i>		Gould, 1846	0.41
<i>lottioidea</i>	<i>Lottiidae</i>	30	<i>Lottia</i>	<i>scabra</i>		Gould, 1847	0.49
<i>lottioidea</i>	<i>Lottiidae</i>	50	<i>Lottia</i>	<i>scutum</i>		Rathke, 1833	0.54
<i>lottioidea</i>	<i>Lottiidae</i>	17	<i>Lottia</i>	<i>septiformis</i>		Quoy & Gaimard, 1834	0.52
<i>lottioidea</i>	<i>Lottiidae</i>	25	<i>Lottia</i>	<i>stanfordiana</i>		Berry, 1957	0.23
<i>lottioidea</i>	<i>Lottiidae</i>	24	<i>Lottia</i>	<i>subrugosa</i>		d'Orbigny, 1846	0.54
<i>lottioidea</i>	<i>Lottiidae</i>	32	<i>Lottia</i>	<i>tenuisculpta</i>		Sasaki & Okutani, 1994	0.59
<i>lottioidea</i>	<i>Lottiidae</i>	26	<i>Nipponacmea</i>	<i>concinna</i>		Lischke, 1870	0.33
<i>lottioidea</i>	<i>Lottiidae</i>	30	<i>Nipponacmea</i>	<i>fuscoviridis</i>		Teramachi, 1949	0.44
<i>lottioidea</i>	<i>Lottiidae</i>	18	<i>Nipponacmea</i>	<i>gloriosa</i>		Habe, 1944	0.45
<i>lottioidea</i>	<i>Lottiidae</i>	26	<i>Nipponacmea</i>	<i>nigrans</i>		Kira, 1961	0.83
<i>lottioidea</i>	<i>Lottiidae</i>	30	<i>Nipponacmea</i>	<i>schrenckii</i>		Lischke, 1868	0.23
<i>lottioidea</i>	<i>Lottiidae</i>	45	<i>Niveotectura</i>	<i>pallida</i>		Gould, 1859	0.59
<i>lottioidea</i>	<i>Lottiidae</i>	8	<i>Notoacmea</i>	<i>badia</i>		Oliver, 1926	0.29
<i>lottioidea</i>	<i>Lottiidae</i>	10.5	<i>Notoacmea</i>	<i>daedala</i>		Suter, 1907	0.21
<i>lottioidea</i>	<i>Lottiidae</i>	9	<i>Notoacmea</i>	<i>elongata</i>		Quoy & Gaimard, 1834	0.27
<i>lottioidea</i>	<i>Lottiidae</i>	10	<i>Notoacmea</i>	<i>parviconoidea</i>		Suter, 1907	0.62
<i>lottioidea</i>	<i>Lottiidae</i>	18	<i>Notoacmea</i>	<i>pileopsis</i>		Quoy & Gaimard, 1834	0.54
<i>lottioidea</i>	<i>Lottiidae</i>	16	<i>Notoacmea</i>	<i>scopulina</i>		Oliver, 1926	0.48
<i>lottioidea</i>	<i>Lottiidae</i>	6	<i>Notoacmea</i>	<i>subtilis</i>		Suter, 1907	0.36
<i>lottioidea</i>	<i>Lottiidae</i>	40	<i>Patelloida</i>	<i>alticostata</i>		Angas, 1865	0.54
<i>lottioidea</i>	<i>Lottiidae</i>	29	<i>Patelloida</i>	<i>corticata</i>		Hutton, 1880	0.54
<i>lottioidea</i>	<i>Lottiidae</i>	20	<i>Patelloida</i>	<i>heroldi</i>		Dunker, 1861	0.51
<i>lottioidea</i>	<i>Lottiidae</i>	30	<i>Patelloida</i>	<i>insignis</i>		Menke, 1843	0.3
<i>lottioidea</i>	<i>Lottiidae</i>	18	<i>Patelloida</i>	<i>latistrigata</i>		Angas, 1865	0.36
<i>lottioidea</i>	<i>Lottiidae</i>	7	<i>Patelloida</i>	<i>mimula</i>		Iredale, 1924	0.61
<i>lottioidea</i>	<i>Lottiidae</i>	15	<i>Patelloida</i>	<i>nigrosulcata</i>		Reeve, 1855	0.68

<i>lottioidea</i>	<i>Lottiidae</i>	23	<i>Patelloida</i>	<i>nigrosulcata</i>		Reeve, 1856	0.36
<i>lottioidea</i>	<i>Lottiidae</i>	14	<i>Patelloida</i>	<i>pygmaea</i>		Dunker, 1860	0.49
<i>lottioidea</i>	<i>Lottiidae</i>	40	<i>Patelloida</i>	<i>saccharina</i>		Linnaeus, 1758	0.54
<i>lottioidea</i>	<i>Lottiidae</i>	21	<i>Patelloida</i>	<i>saccharinoides</i>		Habe & Kosuge, 1966	0.76
<i>lottioidea</i>	<i>Lottiidae</i>	29	<i>Patelloida</i>	<i>striata</i>		Quoy & Gaimard, 1834	0.48
<i>lottioidea</i>	<i>Lottiidae</i>	25	<i>Scurria</i>	<i>araucana</i>		d'Orbigny, 1841	0.26
<i>lottioidea</i>	<i>Lottiidae</i>	15	<i>Testudinalia</i>	<i>testudinalis</i>		O. F. Müller, 1776	0.3
<i>lottioidea</i>	<i>Acmaeidae</i>	14	<i>Acmaea</i>	<i>mitra</i>		Rathke, 1833	0.58