

# VARIATION IN THE SHELLS OF THE ENDANGERED LIMPET *PATELLA FERRUGINEA* (GASTROPODA: PATELLIDAE) FROM THE SOUTH WESTERN MEDITERRANEAN: A GEOMETRIC MORPHOMETRIC APPROACH USING OUTLINE SHAPE ANALYSIS

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*PATELLA FERRUGINEA*  
PLASTICITY  
GEOMETRIC MORPHOMETRICS  
ELLIPTIC FOURIER TRANSFORM  
ALGERIAN BASIN

**ABSTRACT.** – *Patella ferruginea* (Gmelin, 1791) is a prosobranch gastropod endemic to the western Mediterranean and considered as an endangered species. This limpet has two ecotypes and morphologies [*Rouxii* (conical non-centric) and *Lamarckii* (depressed and concentric)]. Geometric morphometric techniques allow the analysis of variation in biological shape and have not been used before to study the morphological dissimilarities between the *Rouxii* and *Lamarckii* forms. Individuals of these two forms were collected from seven stations of the Algerian coast. Biometrical characters [the total length (L), the total width (W), height (H), the distance between the apex and the anterior edge of the shell (DA) and the distance between the apex and the posterior edge of the shell (DP)] were measured on each specimen. In order to analyze morphological dissimilarities between the *Rouxii* form and the *Lamarckii* form, a discriminative analysis was performed using morphometric variables [the ratios (H/L, H/W, L/W, DA/DP) and the geometrical mean (GM)] supported by an outline shape analysis of the shells. The results showed that *Rouxii* form is high and voluminous with an outline tending towards a circular shape; whereas, *Lamarckii* form is flattened and concentric with an outline tending towards an elliptic shape. The vertical migration and the environmental pressures could be the reasons explaining the dissimilarity between *Rouxii* and *Lamarckii* forms.

## INTRODUCTION

Generally limpets are subject to extreme environmental pressures affecting their habitat. Several physical factors may potentially be stressful under these conditions including desiccation, temperature and salinity variations (Branch 1981, Denny & Blanchette 2000). Limpets possess adaptive strategies to face important variations in ecological factors; morphological plasticity is the rule to face these extreme conditions (Vermeij 1973, Branch 1981, Sá-Pinto 2008, Bouzaza & Mezali 2013). For a long time, morphological criteria such as the color of podia, shell shape and radular teeth morphology were the base for limpets identification. However, these criteria show high morphological plasticity influenced by the adaptive capacity to different environmental conditions, leading to confusion between species (Branch 1981, Titselaar 1998, Sá-Pinto *et al.* 2008). It is the case for *Patella caerulea* (Linnaeus, 1758), *P. rustica* (Linnaeus, 1758) and *P. ulyssiponensis* (Gmelin, 1791) (Mauro *et al.* 2003). Denny & Blanchette (2000) mentioned, in their study on the influence of hydrodynamic factors on shell shape of *Lottia gigantea* (G. B. Sowerby I, 1834) that this species adopts hydrodynamic shell forms to avoid dislodgement against high water velocity affecting its habitat. Furthermore, Nuñez *et al.* (2018) reported that the extreme and unpredictable conditions

of the upper shore may impose strong selection pressure on *Siphonaria lessonii* (Blainville, 1827) individuals, leading to considerable morpho-physiological and genetic differentiation between upper and lower shore populations. Moreover, Bouzaza & Mezali (2018) noted that *Patella caerulea* could adopt two different ecotype shell shapes associated with two different biotopes. The “giant limpet” *Patella ferruginea* (Gmelin, 1791) is considered among the limpet species that commonly show high morphological plasticity. It is a prosobranch patellid grazer living generally on wave-swept rock surfaces of the intertidal zone and exhibits rigid homing behavior to a fixed scar (Espinosa *et al.* 2008a, Rivera-Ingraham 2010). This species is endemic to the western Mediterranean Sea and is probably the most endangered species in this area (Templado & Moreno 1997, Espinosa *et al.* 2008b, 2009). The taxonomic status of *P. ferruginea* has been extensively discussed in the literature. Currently, this species is known for possessing two ecomorphotypes: *Rouxii* and *Lamarckii* (Espinosa & Ozawa 2006, Mezali 2007, Bouzaza & Mezali 2013, Meinesz & Dominici 2015). But these two forms have not been admitted in the past. In fact, Payraudeau (1826) considered the two forms as separate species [*Patella rouxii* (having conical shell with a shifted apex and many regular ribs) and *P. lamarckii* (having depressed concentric shell and few irregular ribs)]. Thereafter, Philippi (1836) considered that *P. rouxii* and

*P. lamarckii* were two different forms of *P. ferruginea*. Later, Porcheddu & Milella (1991) suggested that morphological differences between the two morphotypes may correspond to two different species. Conversely, phylogenetic studies based on the Cytochrome Oxidase subunit I gene (COI) do not support that *Rouxii* and *Lamarckii* forms are two ecotypes of the same species (but beware that a single marker study cannot prove that they are the same species) (Espinosa & Ozawa 2006, Mezali 2007, Bouzaza & Mezali 2013). In order to investigate and better assess the morphological plasticity between the two forms of *P. ferruginea* (*Rouxii* and *Lamarckii*), a morphometric study based on biometrical measurements and an outline shape analysis was performed.

## MATERIALS AND METHODS

**Study Area:** The sampling was carried out during 2015 along a part of the Algerian seashore (Fig. 1) on wave-swept exposed rocky shore. Because *Patella ferruginea* is threatened with extinction and its reimplantation has not given relevant results (Laborel-Deguen & Laborel 1991, Espinosa *et al.* 2008b, 2009, Meinesz & Dominici 2015), a reduced number of individuals from each station were taken (Table I). Specimens were collected carefully using a sharp knife inserted under the slightly open edge of the shell, taking care to not damage it. Each shell form (*Rouxii* and *Lamarckii*) was identified using the following morphological criterions established by Payraudeau (1826) and Philippi (1836): the *Rouxii* form has a high shell with a shifted apex toward the anterior edge. Its ribs are of equal size, not prominent and do not extend beyond the shell edge (Fig. 2A); The *Lamarckii* form has a depressed shell with a sub-centric apex. Its ribs are close together with unequal size, exceeding the shell edge (Fig. 2B).

**Biometric analysis:** The following biometric variables [the total length (L), the total width (W), height (H), the distance between the apex and the anterior edge of the shell (DA) and the distance between the apex and the posterior edge of the

shell (DP)] were measured on each individuals using a caliper ( $\pm 0.01$  mm) (Fig. 2). The aforementioned variables were replicated twice in order to assess “measurement error”. A model II ANOVA was used to partition the total variance due to among replicate variations in order to quantify measurement error (see Bailey & Byrnes 1990, Yezzerinac *et al.* 1992). The ratios H/L, H/W and L/W were calculated (Jarne *et al.* 1988, Porcheddu & Milella 1991, Espinosa & Ozawa 2006). The geometric mean (GM) was also calculated according to the equation:  $GM = 3\sqrt{(L \times R \times H)}$  (Bouzaza & Mezali 2018). In order to estimate the centricity of the shell apex, the ratio DA/DP was determined. A one-way MANOVA (Multivariate Analysis of Variance) was performed on the aforementioned morphometric variables (GM and all ratios) to test the dissimilarity between *Rouxii* and *Lamarckii* forms using the software “PAST v 1.93” (Hammer *et al.* 2001). Thus, a Box’s M-test was performed, and then the Wilk’s Lambda parameter ( $\lambda$ -Wilk) was calculated with a Rao approximation. A one-dimensional test of class means was established in order to determine the most discriminative variables.

**Outline shape analysis:** The shells of *Rouxii* and *Lamarckii* forms were photographed from the oral and the lateral view using a scanner “Genx Rcf4601eu” and a camera “Samsung LCD 10 mega pixels”, respectively, to analyze their outline shape trends. A relative measurement error was assessed by taking all photos of each view (oral and lateral) twice. Measure-

Table I. – List of sampling stations and number of individuals collected for each *Patella ferruginea* form.

Stations	Coordinates	<i>Lamarckii</i>	<i>Rouxii</i>
Stidia (1)	35.49° N, 0° E	7	5
Salamandre (2)	35.55° N, 0.03° E	3	2
Kharouba (3)	35.58° N, 0° 6' E	4	7
Cap Ivi (4)	36.12° N, 0.23° E	4	3
Bérard (5)	36.6° N, 2.6° E	2	–
Figuier Plage (6)	36.78° N, 3.53° E	2	3
Rocher Noir (7)	36.78° N, 5.63° E	1	–

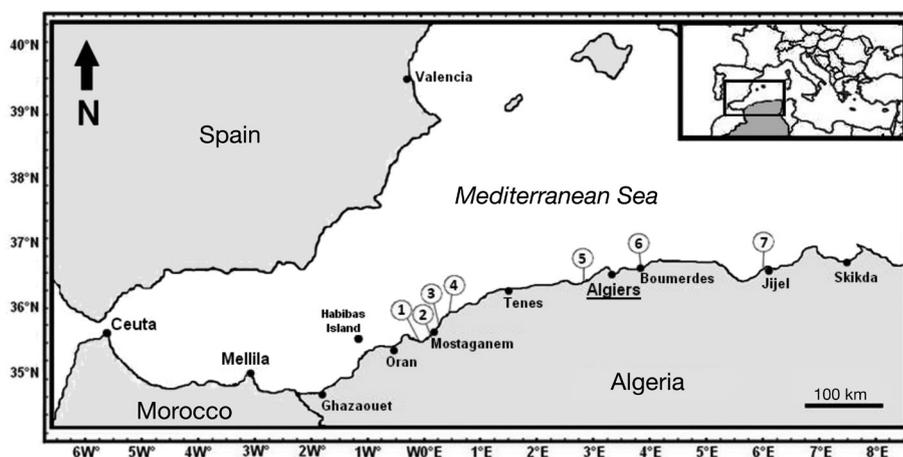


Fig. 1. – Sampling stations along the Algerian coast (see Table I for details).

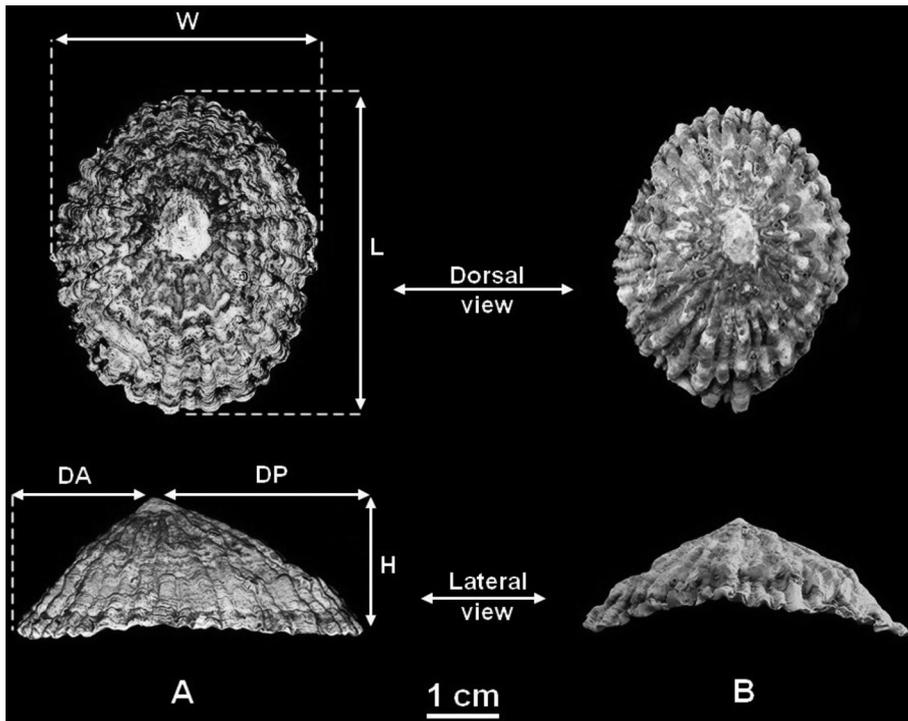


Fig. 2. – Dorsal and lateral views of two *Patella ferruginea* individuals collected from Kharouba (see Table I). A: *Rouxii* form; B: *Lamarckii* form (Photograph: Z Bouzaza).

ment error was calculated from Fourier coefficients of the ten first harmonics (Saucède *et al.* 2013) following the aforementioned model II ANOVA. Full color photographs were transformed into binary black and white images and outline shapes were analyzed and normalized using the software “SHAPE v 1.3” (Iwata & Ukai 2002) based on Elliptic Fourier Transform (EFT) (Bookstein 1997, Cucchi *et al.* 2015, Bouzaza 2018, Nuñez *et al.* 2018). However, a limited number of harmonics must be analyzed to minimize analytical error contribution estimated by the “Fourier power” (Crampton 1995, Renaud & Michaux 2003). The number of harmonics to retain for the analysis was determined by the inflexion point on the curve showing the cumulative Fourier power in terms of the harmonic order (Renaud & Millien 2001, Renaud & Michaux 2003, Saucède *et al.* 2013). In order to highlight main outline shape variations between *Rouxii* and *Lamarckii* shells, a Principal Component Analysis (PCA) was performed from the variance/covariance matrix of normalized Fourier coefficients ( $Fc_s$ ) of the oral and the lateral views using the software “SHAPE v 1.3” (Iwata & Ukai 2002). Outlines were reconstructed to visualize shape variation on each principal component. An ANOSIM (ANALYSIS OF SIMILARITIES) was performed from  $Fc_s$  to test for the significance of the outline shape differences between *Rouxii* and *Lamarckii* shells, using the Euclidean distance with 10,000 replicates permutations among groups using the software “Past v 1.93” (Hammer *et al.* 2001). In order to highlight the relation between outline shapes and morphometric variables, a regression was conducted between the component representing the most relevant outline shapes of the two views (oral and lateral) and the most discriminative morphometric variables from the aforementioned MANOVA, using Spearman’s correlation test. A combined projection of the most relevant principal components

of oral and lateral views was established in order to summarize *P. ferruginea* global shape trends of the two forms (*Rouxii* and *Lamarckii*) in a single plan.

## RESULTS

### Biometric analysis

Measurement errors of L, W, H, DA and DP were 0.08 %, 0.09 %, 1.53 %, 0.44 % and 0.21 %, respectively. To ascertain the homoscedasticity of the covariance matrix, a Box’s M-test was performed ( $M = 140.08$ ;  $P < 0.001$ ) and a one-way MANOVA was carried out giving a  $\lambda$ -Wilk value equal to 0.20 ( $P < 0.001$ ). This value indicates a significant dissimilarity between *Rouxii* and *Lamarckii* forms. The one-dimensional test of class means indicates that the morphometric variables (H/L, H/W, DA/DP and GM) are discriminative ( $P < 0.001$ ) except for the ratio L/W ( $P = 0.10$ ) (Table II). Moreover, the shells of *Rouxii* form are high and voluminous with an offset apex toward the anterior edge (highest values of H/L, H/W and GM; lowest value of DA/DP mean); in contrast *Lamarckii* form shells are flattened and concentric (Fig. 2; Table II).

### Outline shape analysis

The relative measurement errors of the ten first harmonics were 5.14 % and 11.83 % for the oral and lateral views, respectively. After normalizing Fourier coefficients ( $Fc_s$ ) of all shell shapes (oral and lateral views) by Elliptic Fourier Transform (EFT), the three and four first

Table II. – One-dimensional test of class means between *Rouxii* and *Lamarckii* forms.

Morphometric variables	Mean		$\lambda$ -Wilk	F	df1	df2	P
	<i>Rouxii</i>	<i>Lamarckii</i>					
L/W	1.24 ± 0.09	1.29 ± 0.08*	0.94	2.77	1	41	0.104
H/L	0.35 ± 0.03*	0.28 ± 0.02	0.36	72.93	1	41	< 0.0001
H/W	0.44 ± 0.04*	0.37 ± 0.02	0.51	39.07	1	41	< 0.0001
DA/DP	0.63 ± 0.07	0.80 ± 0.09*	0.49	42.63	1	41	< 0.0001
GM	3.35 ± 0.86*	2.12 ± 0.72	0.61	25.69	1	41	< 0.0001

harmonics were retained to establish the most reliable outlines of the oral and the lateral views, respectively. A PCA was performed from the most representative components of the oral view [PC1\_ORAL (50.12 %),  $P < 0.05$ ; PC2\_ORAL (16.93 %),  $P < 0.05$ ] and the lateral view [PC1\_LAT (56.50 %),  $P < 0.05$ ; PC2\_LAT (9.27 %),  $P < 0.05$ ] projecting 67.05 % and 65.77 % of the total variance, respectively (Fig. 3). The main outline shape variation of the oral view concerns both rotundity and ellipticity of the shell (PC1\_ORAL) (Fig. 3A). Whereas, the presence of a shape either wide with a pointed anterior edge, or stocky with smooth anterior edge, is secondary (PC2\_ORAL) (Fig. 3A). In the same way, the main outline shape variation of the lateral view concerns the height/conicity and the flatness/concavity of the shell (PC1\_LAT) (Fig. 3B). However, the trend of the apex to the anterior edge or to the center is secondary (PC2\_LAT) (Fig. 3B). The ANOSIM performed from  $F_c$  of the three and four first

harmonics of the oral and the lateral view (respectively) indicates a highly significant outline shape differences between *Rouxii* and *Lamarckii* shells (all  $P < 0.001$ , Bonferroni corrected); where *Rouxii* form tends to be circular, stocky and smooth outline shape with an apex tending to the anterior edge unlike *Lamarckii* form which tends to be elliptic, wide and concave shell with a centric apex (Fig. 3). The linear regressions between PC1\_ORAL and the parameters H/L, DA/DP and GM are significant (Spearman's values: 0.52, -0.40 and 0.57, respectively; all  $P < 0.05$ ) (Fig. 4A-C). However, the linear regressions between PC1\_LAT and the parameters H/L and GM are significant (Spearman's values: 0.50 and 0.62, respectively; all  $P < 0.05$ ) (Fig. 4D, F) except for the linear regression between PC1\_LAT and the parameter DA/DP (Spearman's value: -0.27;  $P = 0.07$ ) (Fig. 4E). This reveals that shell outline shape of *P. ferruginea* from the oral view is determined by the three morphometric variables H/L,

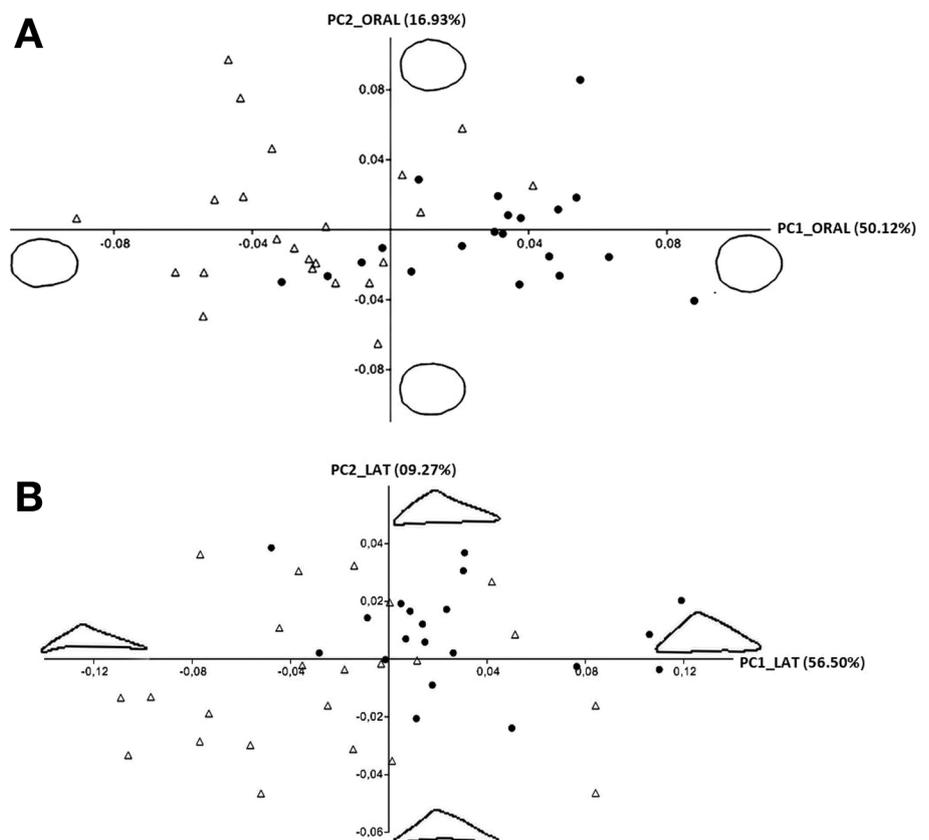


Fig. 3. – Principal component analysis of *Patella ferruginea* individuals. **A**: Oral view; **B**: Lateral view. Triangles represent *Lamarckii* form; filled circles represent *Rouxii* form.

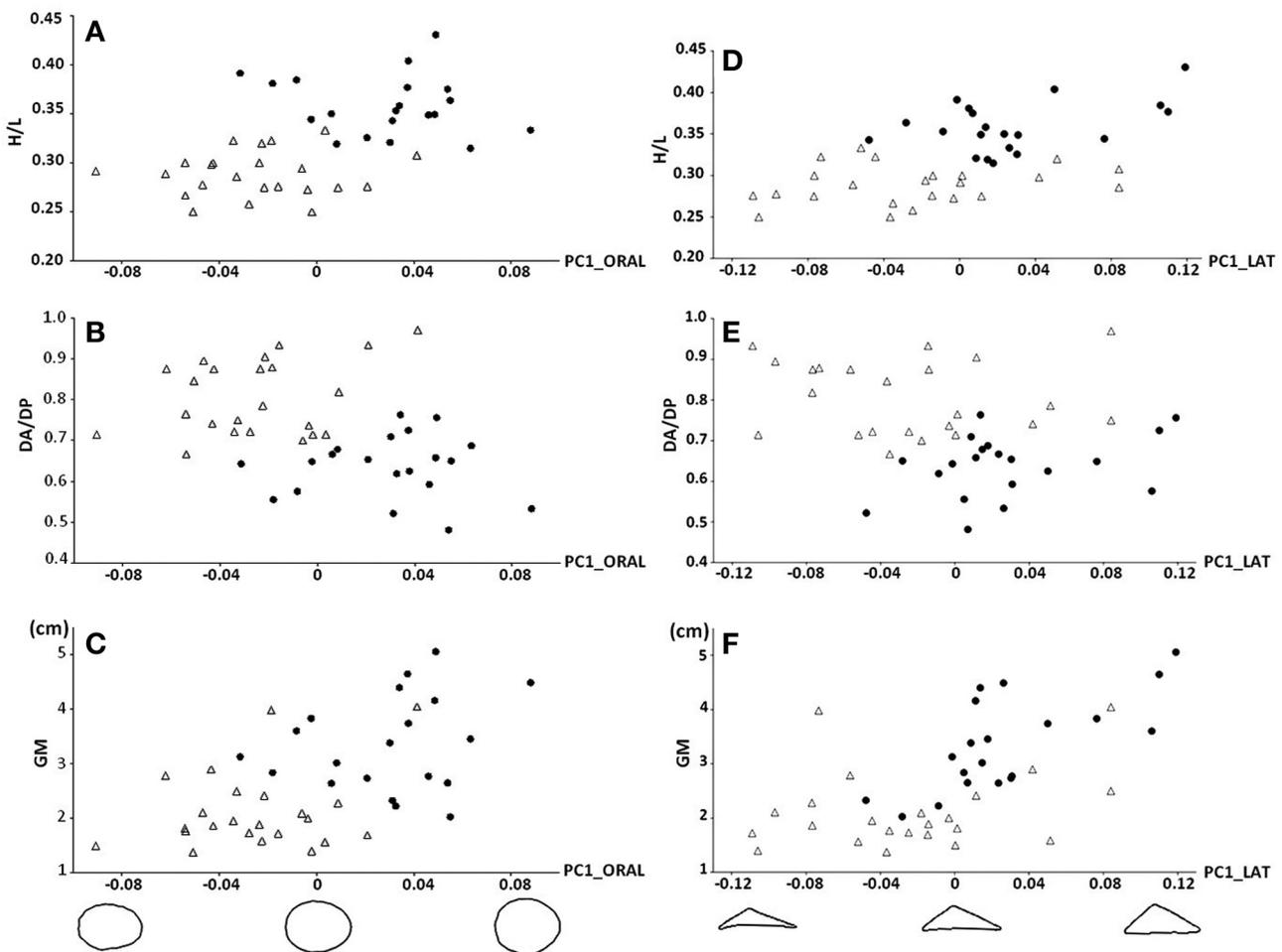


Fig. 4. – Linear regression between the most discriminative morphometric variables (H/L, DA/DP and GM) and the most representative principal components (PC1\_ORAL and PC1\_LAT) score values. Triangles represent *Lamarckii* form; filled circles represent *Rouxii* form.

DA/DP and GM, where circular outlines are associated to highest values of H/L (Fig. 4A), lowest values of DA/DP (Fig. 4B) and highest values of GM (Fig. 4C) corresponding to *Rouxii* form. Conversely, elliptic outlines are associated to the opposite values of the aforementioned morphometric variables and corresponding to *Lamarckii* form (Fig. 4A, B, C). Regarding the shell outline shape of the lateral view, it is determined by the two morphometric variables H/L and GM where conical outlines are associated to highest values of H/L and GM (Fig. 4D, F) corresponding to *Rouxii* form and a few individuals of *Lamarckii* form. Whereas flattened outlines are associated to the opposite values of the aforementioned morphometric variables corresponding to *Lamarckii* form (Fig. 4D, F). However, conical outlined shapes are shared by individuals with low and high values of DA/DP that correspond to both *Rouxii* and *Lamarckii* forms, but flattened shapes are exclusively associated to *Lamarckii* form individuals (Fig. 4E). A combined projection of PC1\_ORAL and PC1\_LAT/PC2\_LAT shows that *Rouxii* form tends to circular and conical shell shape with shifted apex to the

anterior edge, and *Lamarckii* form tends to elliptic and flattened concentric shell shape (Fig. 5).

## DISCUSSION

The plasticity of shell shape is one of the most remarkable phenomena resulting from the adaptive capacity of limpets to different environmental conditions (Branch 1985, Sá Pinto *et al.* 2008). This is the case for *Patella ferruginea* having two different forms (*Rouxii* and *Lamarckii*). In fact, morphometric analysis shows that *Rouxii* form is high and voluminous with a shifted apex toward the anterior edge of the shell and an outline tending to a circular shape. Whereas, *Lamarckii* form is flattened and concentric with an outline tending to elliptic shape. The morphometric dissimilarity between the two forms (*Rouxii* and *Lamarckii*) could be due to many ecological factors impacting the distribution of *P. ferruginea* all over the intertidal zone: immersion time, substratum type and the surrounding physicochemical factors (Grandfils

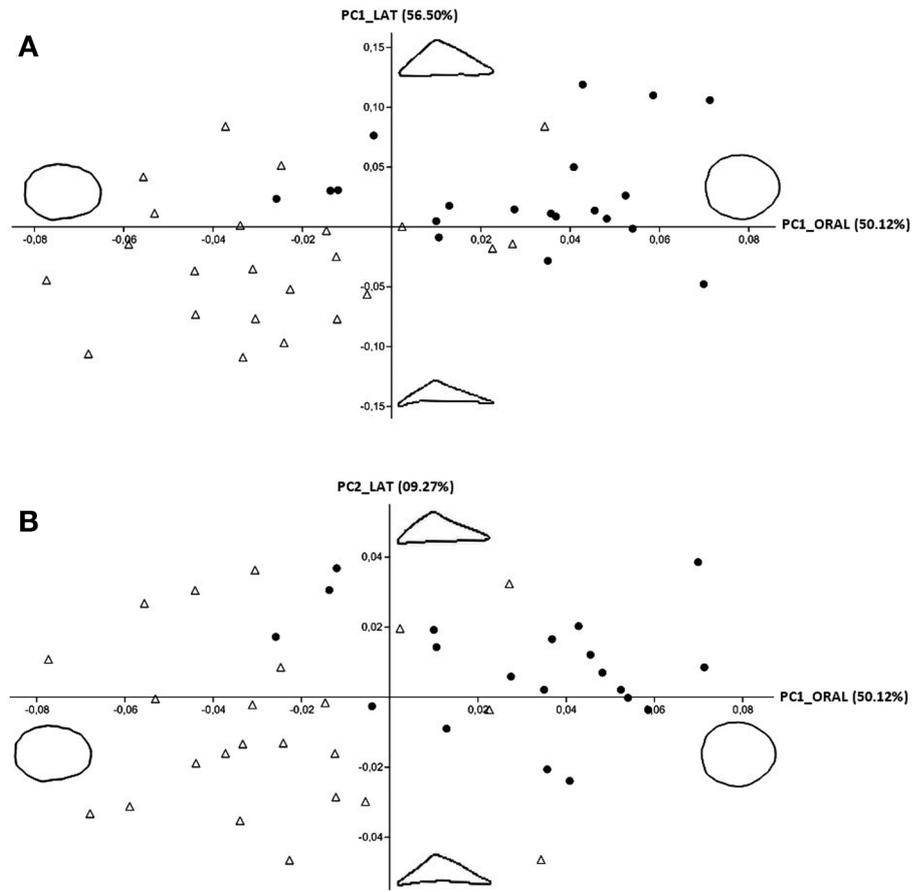


Fig. 5. – Combined projection of the most relevant principal components of oral and lateral views. **A:** Combination between PC1\_ORAL and PC1\_LAT; **B:** Combination between PC1\_ORAL and PC2\_LAT.

1982, Gray & Hodgson 2003, Espinosa *et al.* 2009). Limpet tenacity in adhering to the substrate can largely determine their distribution related to wave exposure. Giant limpets (i.e. *P. ferruginea*), exhibit a high tenacity that allows them to settle on wave-beaten shores (Espinosa & Rivera-Ingraham 2017). This adhering specificity could affect the shell morphology. Indeed, Denny & Blanchette (2001) showed in their study of hydrodynamics effect on limpet survivorship that the tenacious cling of “the owl limpet” *Lottia gigantea* to its substratum facing water velocity reduces shell outline shape to rotundity with a shifted apex toward the anterior edge (such as *Rouxii* form) for a better and quick adhesion to wave-swept rocky shores (reducing of grabbing surface), allowing the increase and decrease lift in extreme conditions. As a consequence of the cling surface narrowing, the shell shape becomes high and conical (such as *Rouxii* form) (Figs 3, 4, 5). However, all *Rouxii* individuals considered in this study were observed more or less in the highest level of the seashore. Thus, circular outline shape of *Rouxii* form (as described for *L. gigantea*) is very advantageous for *P. ferruginea* to cling easily to its substratum. This could explain the shell height with a shifted apex towards the anterior edge of *Rouxii* form (high values of H/L and H/W with low value of DA/DP); unlike *Lamarckii* form which possesses flattened and concentric shells (low values of

H/L, H/W with high values of DA/DP) (Figs 3, 4, 5; Table II). The fact that GM values are low for *Lamarckii* form and high for *Rouxii* form (Table II; Fig. 4) suggests that *Lamarckii* form corresponds to *P. ferruginea* juvenile individuals, whereas *Rouxii* form corresponds to adult ones. Moreover, almost all *Lamarckii* individuals of this study, especially small ones, were observed in the lowest part of the seashore where larvae are recruited (Rivera-Ingraham 2010). The *Rouxii* form could be a consequence of *P. ferruginea* vertical migration toward upper intertidal level facing desiccation and high hydrodynamism. However, some adult individuals of *P. ferruginea*, having high values of GM, possess a *Lamarckii* form or intermediate. These lasts were found in the lower part of the intertidal area, encrusted to their scar and trapped by the relief hindering them from moving upper. Furthermore, the voluminous size of *Rouxii* form (high values of GM, Table II) could help the foraging excursion in extended areas of the upper intertidal zone. Indeed, Espinosa *et al.* (2008a) displayed that large individuals of *P. ferruginea* (i.e. *Rouxii* form) show larger foraging excursion and more extended areas than do small ones. Therefore, their foraging path shows a low incidence of trail following that could be a mechanism to avoid passing over previously grazed area. This behavior could force the largest individuals of *P. ferruginea* to spend a long period of time

far from their scar in difficult conditions of the upper intertidal area. However, Gray & Hodgson (1998) recorded a reduction in limpet feeding activity in upper shore individuals (i.e. *P. ferruginea*). Likewise, the *Rouxii* form (high upstream shifted apex) could help to store much as possible water and absorb a considerable amount of oxygen in the upper intertidal area (Branch 1985, Paracuellos *et al.* 2003). In fact, Lindberg & Ponder (2001) assumed that the high shape shells is an adaptation increasing the size of the pallial cavity for larger gills as a consequence of long periods spent in extreme conditions with low oxygen availability. This phenomenon is observed in *Patella rustica* (having circular outline shape and high conical shell) inhabiting the upper mediolittoral and the first level of supralittoral (Titselaar 1998, Lima *et al.* 2007). Similar case is observed in *Patella caerulea* cohabiting with *P. ferruginea* which has two morphotypes, one very flattened (such as *Lamarckii* form) found exclusively in the immersed areas and the other high and short (such as *Rouxii* form) inhabiting the emerged areas (Mauro *et al.* 2003, Bouzaza & Mezali 2018, Bouzaza 2018). Moreover, Tlig-Zouari *et al.* (2011) noted in their study on the morphometry of *P. ferruginea* of the Tunisian coast that the existence of *Rouxii* and *Lamarckii* forms could be due to inclination of substratum and duration of exposure to solar radiation. Furthermore, Branch (1981) assumed that desiccation is one of the main reasons for extending limpet higher on the shore where wave action is strong and the aspect of the rocks reduces exposure to the sun. The shell shape of *Rouxii* form seems to be advantageous to face such conditions, unlike *Lamarckii* form which seems to be associated to damp intertidal area. This finding corroborates the work of Yamamori & Kato (2018) who showed that species of the genus *Broderipia* (Gray, 1847) living in immersed water have very flattened shells (such as *Lamarckii* form) compared with species of the sister genus *Roya* (Iredale, 1912) having higher shells (such as *Rouxii* form) and inhabiting wave-exposed rock reef. In addition, Lowell (1986) suggested that the low-spired shape of limpet shells (such as *Lamarckii* form) is an adaptation to avoiding crab predation. Tablado & Lopez-Gappa (2001) showed in their work on morphometric diversity of *Siphonaria lessoni* that the morphotypic differentiation could be due to a change in the growth rate on micro-habitats and environmental pressures (wave exposure, food availability and intraspecific competition). The low number of individuals considered in this study (43 individuals), due to the endangered status of *P. ferruginea*, could significantly impact the robustness of the statistical analysis.

In conclusion, the presence of the two ecotype forms *Rouxii* and *Lamarckii* could be an adaptive response of *P. ferruginea* to different environmental conditions of its habitats. The *Rouxii* form seems to be a consequence to the long time spent of *P. ferruginea* in the upper part of intertidal area where large individuals are occasionally

immersed in water but exposed to wave action, whereas the *Lamarckii* form is related to the lower part of intertidal area where the limpet is frequently immersed. For future work, it would be interesting to study deeply the ecological factors that could influence the morphology of *P. ferruginea* to better understand the phenomena inducing dissimilarity between *Rouxii* and *Lamarckii* forms. However, nuclear molecular markers should be used in order to elucidate definitively the genetic relationship state between these two forms.

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