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Shell shape, morphometrics and relative growth of four sympatric limpet species from the Algarve coast (southern Portugal)

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Abstract

This study analysed and compared the shell shape, morphometrics and relative growth of four sympatric limpet species (*Patella depressa*, *Patella ulyssiponensis*, *Patella vulgata* and *Siphonaria pectinata*) collected at Praia da Luz in Lagos (Algarve coast – southern Portugal). Morphometric relationships were established through regression analysis between linear (shell length, width and height), ponderal (total weight), area (shell base and surface areas) and volume variables (shell internal and total volumes). Relative growth (isometry *vs* allometry) was analysed to assess variation in the growth rate of morphometric variables throughout the species ontogeny. In addition, morphometric indices (ellipticity, conicity, density, surface area and volumetry) were calculated to further characterize shell shape. Overall, 1482 individuals with broad size and weight ranges were analysed (*P. depressa* = 354; *P. ulyssiponensis* = 306; *P. vulgata* = 408; *S. pectinata* = 414). All regressions were highly significant ($P < 0.001$) and the morphometric variables were strongly correlated ($r = 0.761$ to 0.994). Among 28 morphometric relationships, there were 14 isometries, 13 positive allometries and only one negative allometry. The morphometric indices revealed clear morphological differences between species and were mostly size-dependent, reflecting gradual changes in shell shape during growth. The main results are compared with a compilation of analogous data reported for these limpet species throughout their distributional range. Overall, the general trends in relative growth are discussed in terms of the species life habits, main traits and functional morphology.

Introduction

Limpets are common inhabitants and recognized keystone species on intertidal rocky shores worldwide, playing a crucial role in structuring local communities and ensuring ecosystem balance, integrity and stability (Jenkins *et al.*, 2005; Coleman *et al.*, 2006; Burgos-Rubio *et al.*, 2015; Henriques *et al.*, 2017). In addition, due to the easy access to intertidal areas, diverse limpet species have been harvested for human consumption since the establishment of ancestral populations along the coastline. For instance, in the Iberian Peninsula, true limpets (patellogastropods) have been traditional seafood since prehistoric times (Middle Palaeolithic) (Bicho & Haws, 2008; Fa *et al.*, 2016; Verdún-Castelló & Casabó i Bernad, 2020). Nowadays, various limpet species are collected for seafood by both professional fishermen and recreational harvesters, under exploitation levels that depend on the geographic location, ease of access to intertidal areas and species abundance, and that reflect local/regional heritage, cultural legacy and gastronomic tradition (Sousa *et al.*, 2020*a*). In Portugal, limpets are professionally and/or recreationally harvested in some scattered locations sporadically exploited along the mainland (Vasconcelos *et al.*, 2019), whereas these activities are ancestral, popular, widespread and intense in the archipelagos of Madeira (Henriques *et al.*, 2012; Sousa *et al.*, 2019*a*, 2019*b*, 2020*a*, 2020*b*, 2020*c*; Cañizares *et al.*, 2021) and Azores (Santos *et al.*, 1995; Côrte-Real *et al.*, 1996; Martins *et al.*, 2011, 2017; Diogo *et al.*, 2016).

Studies on the general morphology, morphometric relationships and relative growth of molluscs are performed with distinct purposes and provide useful information for diverse research fields, namely systematics and taxonomy, biology and ecology, fisheries assessment and management (Gaspar *et al.*, 2001, 2002; Mauro *et al.*, 2003; Vasconcelos *et al.*, 2016, 2018*a*, 2018*b*, 2022; Faria *et al.*, 2017). The study of relative growth (isometry *vs* allometry, i.e. comparison of growth rates between body parts or measurements) is still the basis and founding principle for analysing morphometrics and investigating shape variation among closely related organisms (Huxley, 1932; Huxley & Teissier, 1936). In the particular case of limpets, such studies aim mainly to assess the influence of diverse abiotic factors as drivers of changes in shell growth, shape and dimensions, mostly environmental variables such as shore topography, wave exposure and intensity, tidal height and desiccation stress (Baxter, 1983; Nolan, 1991; Côrte-Real *et al.*, 1996; Cabral & Silva, 2003; Lomovasky *et al.*, 2020; Vafidis *et al.*, 2020).

In this general context, the present work analysed and compared morphometric relationships (between shell length, width, height, total weight, area and volume), morphometric indices (ellipticity, conicity, density, surface area and volumetry) and relative growth (isometry *vs* allometry) among four sympatric limpet species from the Algarve coast (southern Portugal). The study comprised three true limpet species, namely the black-footed limpet (*Patella depressa* Pennant, 1777), the rough limpet (*Patella ulyssiponensis* Gmelin, 1791) and the common limpet (*Patella vulgata* Linnaeus, 1758), as well as the striped false limpet (*Siphonaria pectinata* Linnaeus, 1758). Overall, the study was based on the following working hypotheses regarding potential ecological implications of diverse morphological and morphometric features of these limpet species: (a) different limpet species display dissimilar morphometric relationships, indices and relative growth; (b) different morphometrics and relative growth reflect intra- and inter-specific variation in the limpet species' main ecological traits, habitat features, distribution and position in the intertidal, and prevailing environmental conditions.

Materials and methods

Studied limpet species

Due to their broad distributional range along the NE Atlantic, limpets are quite common along European rocky shores and some species have their meridional and septentrional biogeographic limits in Portugal (Guerra & Gaudêncio, 1986; Boaventura, 2000; Cabral, 2007; Borges *et al.*, 2015; Simone & Seabra, 2017). Accordingly, diverse limpets co-occur in southern Portugal and the following four species inhabit rocky shores in the lower eulittoral zone along the Algarve coast: the true limpets *P. depressa*, *P. ulyssiponensis* and *P. vulgata* and the striped false limpet *S. pectinata*.

Both *P. depressa* and *P. vulgata* have their meridional biogeographic limit in southern Portugal (Fretter & Graham, 1976; Guerra & Gaudêncio, 1986; Southward *et al.*, 1995; Boaventura, 2000; Borges *et al.*, 2015). In general, *P. depressa* (more wave-exposed areas) and *P. vulgata* (more sheltered areas) predominate in the mid-shore, whereas *P. ulyssiponensis* is a low-shore species that prevails in the lower algal zone or in shallow tidal pools, although their distribution might vary depending on local features of the rocky shore (Ballantine, 1961; Fretter & Graham, 1976; Boaventura, 2000; Cabral, 2007; Antit *et al.*, 2008; Casal *et al.*, 2018). In contrast, the false limpet *S. pectinata* is an upper-shore species that occurs mainly on rocky surfaces subjected to moderate wave-action, which reduce the risk of dislodgement and provide suitable conditions for prolonged foraging activity (Ocaña, 2003; Crocetta, 2016).

Study area and sample collection

Field sampling was performed monthly during two consecutive years (January 2017–December 2018), at Praia da Luz (37° 05′06.5″N 08°43′45.1″W) in Lagos (Algarve coast – southern Portugal) (Figure 1). The study area is moderately sheltered by near headlands and capes that protect this rocky shore against the North-west Atlantic Ocean swell, softening the local hydrodynamics due to lower wave energy, wind exposure and coast steepness (Boaventura *et al.*, 2002; Vasconcelos *et al.*, 2019). In the sampling zone, the rocky shoreline eroded by the wave action and seawater runoff creates small intertidal pools that preserve seawater for long periods.

The four limpet species (*P. depressa*, *P. ulyssiponensis*, *P. vulgata* and *S. pectinata*) were caught manually using a harvesting knife along an intertidal area of ~3000 m^2 (~100 m long × 30 m wide). Specimens (~15–20 individuals/month) were collected randomly during low tide, roughly at the same tidal level. Immediately after field sampling, individuals were kept in identified plastic bags and preserved in ice until further laboratory procedures.

Biological sampling and shell morphometrics

In the laboratory, species identification was confirmed based on the main shell features described and illustrated in specialized literature (Christiaens, 1973; Fretter & Graham, 1976; Titselaar, 1998) and species names followed the most recent taxonomic nomenclature available at the World Register of Marine Species – WoRMS (WoRMS Editorial Board, 2021; http://www.marinespecies.org). Damaged specimens (eroded or broken shell border) were discarded and epibionts (seaweeds and encrusting invertebrates) were removed from the shell surface with a scalpel and/or hard brush to avoid biased measurements and weighing.

Individuals were separated per species, counted, measured using a digital calliper (precision of 0.01 mm) and weighed on a top loading digital balance (precision of 0.01 g). The morphometric variables included the measurement of the three shell axes, namely shell length (SL), shell width (SW) and shell height (SH) (Figure 2), complemented by the determination of total weight (TW) after blotting dry on absorbent paper to drain seawater from the shell surface and mantle cavity to avoid biased weighing.

In addition, based on these measurements and weights, the following shell areas and volumes were calculated using specific equations for parabolic cones, previously employed in other studies involving diverse limpet species (Jones *et al.*, 1979; Baxter, 1983; Lowell, 1984; Khouw, 2006; Cabral, 2007; Cabral & Natal Jorge, 2007):

- Shell base area: $SbA = \pi \times [(SL + SW)/4)]^2$
- Shell surface area: $SsA = 3.6 \times [(SL + SW)/4] \times \sqrt{\{[(SL + SW)/4)]^2 + [(4/3) \times SH)]\}}$
- Shell internal volume: $SiV = \pi \times SL \times SW \times SH/12$
- Shell total volume: $StV = \{\pi \times [(SL + SW)/4]^2 \times SH\}/2$

Data treatment and statistical analyses

Initially, all data were checked for the occurrence of outliers, which were corrected or eliminated before further treatment and analyses. Morphometric relationships were established through regression analysis (least squares method on raw data) by fitting the power function ($Y = aX^b$) and the degree of association between variables was assessed through the correlation coefficient (r).

Independently of the type of variables (linear, ponderal, area or volume), relative growth was analysed through the regression slope (allometry coefficient – b). In relationships between linear variables (SW and SH *vs* SL) isometry occurs for $b = 1$, between linear and area variables (SbA and SsA *vs* SL) isometry occurs for $b = 2$, and between linear and ponderal or volume variables (TW, SiV and StV *vs* SL) isometry occurs for $b = 3$, in practice reflecting a similar growth rate of both variables throughout ontogeny (Huxley & Teissier, 1936; Mayrat, 1970). Accordingly, a t-test (H_0: $b = 1$ or 2 or 3; H_A: $b \neq 1$ or 2 or 3) was applied to confirm whether the regression slope denotes isometric growth ($b = 1$ or 2 or 3) or allometric growth (negative allometry: $b < 1$ or 2 or 3; positive allometry: $b > 1$ or 2 or 3).

In addition, aiming to further analyse the shell shape and better describe the general morphology of limpet species, five morphometric indices (ellipticity, conicity, density, surface area and volumetry) based on coupled ratios between the linear, ponderal,

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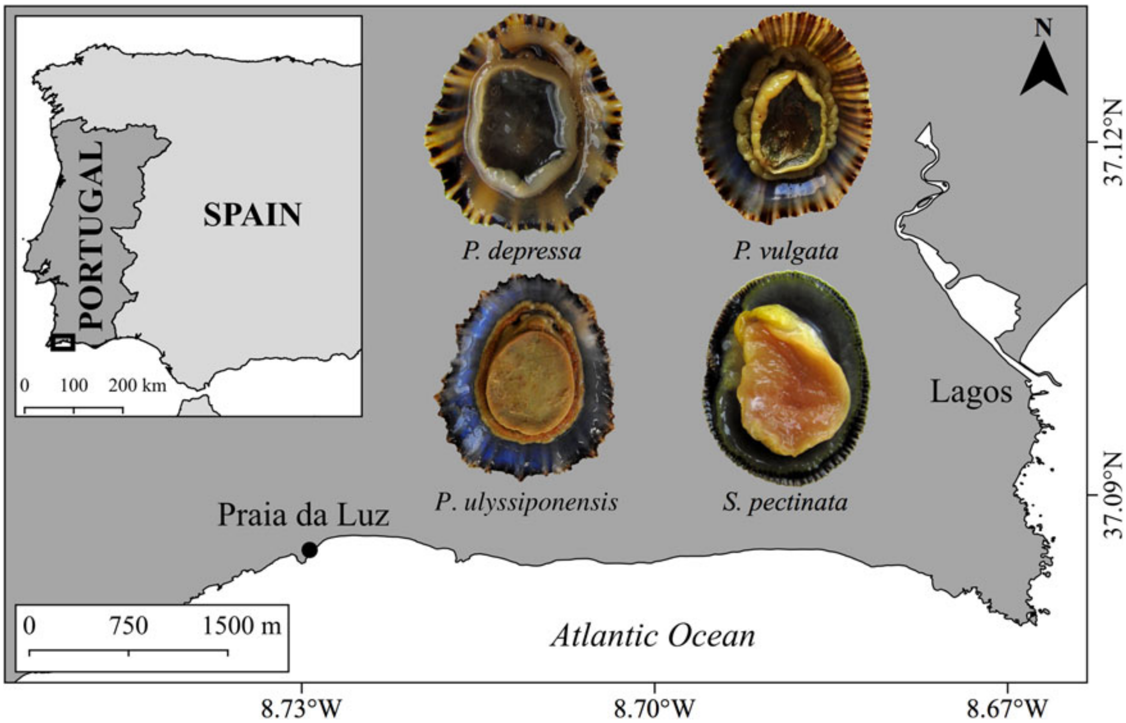

Fig. 1. Map highlighting the geographic location of the sampling site at Praia da Luz (Algarve coast – southern Portugal), together with photographs (ventral view) of the studied species: *Patella depressa*, *Patella ulyssiponensis*, *Patella vulgata* and *Siphonaria pectinata*.

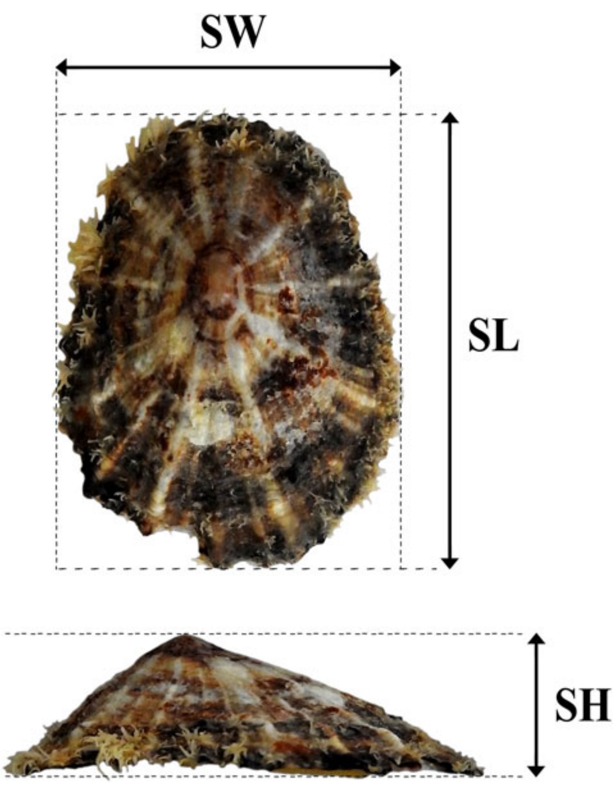

Fig. 2. Schematic illustration of the three shell axes measured in the four limpet species (*Patella depressa*, *Patella ulyssiponensis*, *Patella vulgata* and *Siphonaria pectinata*): shell length (SL), shell width (SW) and shell height (SH).

area or volume variables were calculated through the following equations (some concepts and terminologies adapted from Cabral, 2003, 2007; Cabral & Silva, 2003; Cabral & Natal Jorge, 2007; Battelli, 2016):

- Ellipticity index (elongation ratio): EI = SW/SL
- Conicity index (convexity ratio): CI = SH/SL
- Density index (weight ratio): DI = TW/SL
- Surface area index (area ratio): SI = SsA/SL
- Volumetry index (volume ratio): VI = StV/SL

These morphometric indices were compared between species through analysis of variance (ANOVA). Whenever ANOVA assumptions (normality of data and homogeneity of variances) were not achieved, the non-parametric Kruskal–Wallis test (ANOVA on ranks) was performed. In addition, variation in the morphometric indices during growth was analysed by plotting EI, CI, DI, SI and VI against individual size (SL). For each species, the main trends and eventual size-dependency (variation throughout ontogeny) in the morphometric indices was assessed through a *t*-test (H_0: $b = 0$; H_A: $b \neq 0$) applied to the respective regression slope. All statistical analyses were performed following Sokal & Rohlf (1987) with significance level considered at $P < 0.05$.

Results

The descriptive statistics, morphometric relationships and relative growth of the four limpet species are compiled in Table 1. A total of 1482 individuals were analysed (*P. depressa* = 354; *P. ulyssiponensis* = 306; *P. vulgata* = 408; *S. pectinata* = 414). These fairly representative samples presented a broad range in individual size and weight for all species analysed, namely *P. depressa* (17.2–41.6 mm SL/0.4–9.1 g TW), *P. ulyssiponensis* (24.6–52.5 mm SL/2.2–34.8 g TW), *P. vulgata* (19.5–42.7 mm SL/1.6–16.0 g TW) and *S. pectinata* (9.7–31.3 mm SL/0.1–5.1 g TW) (Table 1).

Independently of the species and variables (linear, area or ponderal), all morphometric relationships were highly significant ($P < 0.001$) and characterized by high correlation coefficients (r = 0.761–0.994) (Table 1). The correlations were always higher in relationships involving shell areas (r = 0.988–0.994) and volumes (r = 0.959–0.981), compared with those involving total weight

Table 1. Descriptive statistics, morphometric relationships and relative growth in four limpet species from the Algarve coast (southern Portugal)

		Size and weight		Morphometric relationship			Relative growth	
Species	*N*	SL	TW	Equation	*r*	*b* ± SE (95% CI)	*t*-test	Type
Patella depressa (Pennant, 1777)	354	30.2 ± 5.0 (17.2–41.6)	3.5 ± 1.8 (0.4–9.1)	SW = 0.563 $SL^{1.117}$	0.962***	1.117 ± 0.017 (1.084–1.150)	6.913***	A+
				SH = 0.111 $SL^{1.248}$	0.910***	1.248 ± 0.030 (1.188–1.307)	8.166***	A+
				TW = 0.00003 $SL^{3.362}$	0.970***	3.362 ± 0.045 (3.274–3.450)	8.087***	A+
				SbA = 0.005 $SL^{2.105}$	0.991***	2.105 ± 0.015 (2.075–2.135)	6.863***	A+
				SsA = 0.006 $SL^{2.092}$	0.991***	2.092 ± 0.015 (2.062–2.121)	6.048***	A+
				SiV = 0.00002 $SL^{3.365}$	0.980***	3.365 ± 0.037 (3.293–3.437)	9.991***	A+
				StV = 0.00003 $SL^{3.353}$	0.981***	3.353 ± 0.036 (3.283–3.423)	9.908***	A+
Patella ulyssiponensis (Gmelin, 1791)	306	38.4 ± 5.4 (24.6–52.5)	11.0 ± 5.5 (2.2–34.8)	SW = 0.679 $SL^{1.033}$	0.967***	1.033 ± 0.016 (1.002–1.063)	2.092*	A+
				SH = 0.275 $SL^{1.026}$	0.770***	1.026 ± 0.049 (0.930–1.122)	$0.531^{n.s.}$	I=
				TW = 0.00006 $SL^{3.298}$	0.930***	3.298 ± 0.075 (3.151–3.445)	3.992***	A+
				SbA = 0.006 $SL^{2.028}$	0.993***	2.028 ± 0.013 (2.002–2.055)	2.087*	A+
				SsA = 0.007 $SL^{2.012}$	0.993***	2.012 ± 0.013 (1.986–2.039)	$0.927^{n.s.}$	I=
				SiV = 0.00005 $SL^{3.058}$	0.959***	3.058 ± 0.052 (2.956–3.161)	$1.128^{n.s.}$	I=
				StV = 0.00008 $SL^{3.054}$	0.960***	3.054 ± 0.051 (2.953–3.155)	$1.056^{n.s.}$	I=
Patella vulgata (Linnaeus, 1758)	408	31.0 ± 4.1 (19.5–42.7)	6.2 ± 2.6 (1.6–16.0)	SW = 0.753 $SL^{1.033}$	0.947***	1.033 ± 0.017 (0.999–1.067)	$1.912^{n.s.}$	I=
				SH = 0.529 $SL^{0.904}$	0.761***	0.904 ± 0.038 (0.828–0.979)	2.521*	A–
				TW = 0.0002 $SL^{2.967}$	0.916***	2.967 ± 0.065 (2.840–3.094)	$0.510^{n.s.}$	I=
				SbA = 0.006 $SL^{2.030}$	0.988***	2.030 ± 0.016 (1.999–2.061)	$1.917^{n.s.}$	I=
				SsA = 0.008 $SL^{2.005}$	0.988***	2.005 ± 0.016 (1.974–2.036)	$0.319^{n.s.}$	I=
				SiV = 0.0001 $SL^{2.937}$	0.959***	2.937 ± 0.043 (2.852–3.021)	$1.476^{n.s.}$	I=
				StV = 0.0002 $SL^{2.934}$	0.960***	2.934 ± 0.042 (2.851–3.017)	$1.564^{n.s.}$	I=
Siphonaria pectinata (Linnaeus, 1758)	414	20.5 ± 4.4 (9.7–31.3)	1.4 ± 0.8 (0.1–5.1)	SW = 0.724 $SL^{1.006}$	0.968***	1.006 ± 0.013 (0.981–1.031)	$0.448^{n.s.}$	I=
				SH = 0.167 $SL^{1.092}$	0.855***	1.092 ± 0.033 (1.028–1.157)	2.826**	A+
				TW = 0.0001 $SL^{2.981}$	0.977***	2.981 ± 0.032 (2.919–3.043)	$0.597^{n.s.}$	I=
				SbA = 0.006 $SL^{2.004}$	0.994***	2.004 ± 0.011 (1.982–2.025)	$0.336^{n.s.}$	I=
				SsA = 0.007 $SL^{1.980}$	0.994***	1.980 ± 0.011 (1.959–2.001)	$1.896^{n.s.}$	I=
				SiV = 0.00003 $SL^{3.098}$	0.973***	3.098 ± 0.036 (3.027–3.169)	2.726**	A+
				StV = 0.00005 $SL^{3.096}$	0.974***	3.096 ± 0.035 (3.027–3.165)	2.727**	A+

N, number of individuals; SL, shell length (mm); SW, shell width (mm); SH, shell height (mm); TW, total weight (g); SbA, shell base area (cm^2); SsA, shell surface area (cm^2); SiV, shell internal volume (cm^3); StV, shell total volume (cm^3); Size and weight data presented as mean ± SD and respective range (minimum–maximum); *r*, correlation coefficient; *b*, allometry coefficient; SE, standard error; 95% CI, 95% confidence interval. Asterisks denote statistical level (*P*-value): $^{n.s.}$not significant, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; A–, negative allometry; I =, isometry; A+, positive allometry.

($r = 0.916$–0.977), shell width ($r = 0.947$–0.968) and shell height ($r = 0.761$–0.910). The regression slopes (allometry coefficients) ranged in the intervals $b = 0.904$–1.248 (linear variables), $b = 1.980$–2.105 (area variables) and $b = 2.934$–3.365 (ponderal and volume variables). Among the 28 morphometric relationships, isometries (14 = 50.0%) and positive allometries (13 = 46.4%) clearly prevailed over negative allometries (1 = 3.6%). In *P. depressa*, all morphometric relationships were hyperallometric (7 A+), being mostly isometric in *P vulgata* (6 I =), *P. ulyssiponensis* (4 I =) and *S. pectinata* (4 I =). The only hypoallometry (1 A−) was recorded in the relationship between SH and SL of *P. vulgata* (Table 1).

The morphometric indices (ellipticity, conicity, density, surface area and volumetry) of the four limpet species are compiled in Table 2 and illustrated in Figure 3. These five indices revealed a remarkable variation in shell shape and clear morphological diversity between species: EI ranged from 0.737 in *S. pectinata* to 0.844 in *P. vulgata*, CI varied between 0.223 in *S. pectinata* and 0.382 in *P. vulgata*, DI ranged from 0.061 in *S. pectinata* to 0.275 in *P. ulyssiponensis*, SI varied between 0.142 in *S. pectinata* and 0.274 in *P. ulyssiponensis*, and VI ranged from 0.029 in *S. pectinata* to 0.141 in *P. ulyssiponensis* (Table 2). The true limpets (*P. depressa*, *P. ulyssiponensis* and *P. vulgata*) displayed invariably higher morphometric indices than the false limpet (*S. pectinata*). All morphometric indices presented highly significant differences (Kruskal–Wallis: $P < 0.001$) among limpet species, namely EI ($H = 866.935$), CI ($H = 1123.419$), DI ($H = 1053.906$), SI ($H = 900.314$) and VI ($H = 1019.370$), excepting the ellipticity (Dunn's test: $Q = 1.287$; $P > 0.05$) and surface area (Dunn's test: $Q = 1.653$; $P > 0.05$) of *P. depressa* and *P. vulgata* (Table 2). Overall, these indices highlight diverse morphological features of the species, namely the wider and rounder shells of *P. vulgata* and *P. depressa*, compared with the longer and more elliptic shells of *P. ulyssiponensis* and *S. pectinata*. All species displayed shells with significantly different conicity, which was highest in the more conical *P. vulgata* and lowest in the more flattened *S.*

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Table 2. Morphometric indices (ellipticity, conicity, density, surface area and volumetry) in four limpet species from the Algarve coast (southern Portugal)

	Patella depressa (Pennant, 1777)	*Patella ulyssiponensis* (Gmelin, 1791)	*Patella vulgata* (Linnaeus, 1758)	*Siphonaria pectinata* (Linnaeus, 1758)
Ellipticity	0.839 ± 0.049^a	0.765 ± 0.030^b	0.844 ± 0.040^a	0.737 ± 0.045^c
(SW/SL)	(0.699–0.957)	(0.686–0.838)	(0.742–0.958)	(0.613–0.854)
Conicity	0.260 ± 0.028^a	0.305 ± 0.037^b	0.382 ± 0.040^c	0.223 ± 0.034^d
(SH/SL)	(0.187–0.325)	(0.228–0.400)	(0.304–0.481)	(0.129–0.312)
Density	0.109 ± 0.043^a	0.275 ± 0.104^b	0.194 ± 0.060^c	0.061 ± 0.027^d
(TW/SL)	(0.023–0.227)	(0.089–0.718)	(0.076–0.385)	(0.012–0.167)
Surface area	0.234 ± 0.043^a	0.274 ± 0.040^b	0.242 ± 0.034^a	0.142 ± 0.031^c
(SsA/SL)	(0.120–0.341)	(0.171–0.384)	(0.151–0.344)	(0.064–0.223)
Volumetry	0.083 ± 0.031^a	0.141 ± 0.046^b	0.124 ± 0.034^c	0.029 ± 0.014^d
(StV/SL)	(0.018–0.163)	(0.050–0.290)	(0.051–0.245)	(0.006–0.081)

SL, shell length (mm); SW, shell width (mm); SH, shell height (mm); TW, total weight (g); SsA, shell surface area (cm^2); StV, shell total volume (cm^3); Data presented as mean ± SD and respective range (minimum–maximum). In each morphometric index, different superscript letters (^{a}, ^{b}, ^{c} or ^{d}) denote statistically significant differences between species (K–W: $P < 0.05$).

pectinata. Similarly, all species had diverse density indices, ranging from the clearly lighter *S. pectinata* to the gradually heavier *P. depressa*, *P. vulgata* and *P. ulyssiponensis*. Accordingly, both the surface area and volumetry indices were invariably lowest in *S. pectinata* and highest in *P. ulyssiponensis* compared with the remaining limpet species (Table 2).

Most morphometric indices were size-dependent in the four limpet species, except for the ellipticity of *P. vulgata* and *S. pectinata* and the conicity of *P. ulyssiponensis*, whose linear regressions against specimen size were not statistically significant ($r = 0.014$–0.093; $P > 0.05$) (Figure 3). However, all the remaining relationships displayed slopes significantly different from zero reflecting gradual changes in shell shape during growth, almost invariably positive slopes ($b = 0.0007$–0.0084) indicative of increasing trends in those morphometric indices during growth and only one negative slope ($b = -0.0012$) denoting the declining shell conicity throughout the ontogeny of *P. vulgata*. Overall, although with variable levels of statistical significance ($P < 0.05$–0.001), the density, surface area and volumetry indices of all species were clearly size-dependent and increased markedly during the limpets' growth and lifespan (Figure 3).

Discussion

Limpets are keystone and foundation species in intertidal rocky shores, playing a crucial role in shaping and structuring the local communities. However, despite being extensively studied worldwide, for diverse purposes mostly related to the species' general biology and ecology, the information available on limpets' morphometric relationships, indices and relative growth is still relatively scarce and dispersed. In fact, to the authors' best knowledge concerning the present limpet species (*P. depressa*, *P. ulyssiponensis*, *P. vulgata* and *S. pectinata*), comparisons with previous studies on those subjects are limited to populations of *P. ulyssiponensis* from mainland Portugal (Cabral, 2003, 2007; Cabral & Silva, 2003) and Tunisia (Boukhicha *et al.*, 2013) and to populations of *P. vulgata* from Scotland (Jones *et al.*, 1979; Baxter, 1983) and mainland Portugal (Cabral, 2003, 2007; Cabral & Silva, 2003) (Table 3). In this context, the present study provided valuable information to further analyse and compare limpets' shape, morphometrics and relative growth, as well as to discuss their main trends and connections with species' ecological traits, distribution, habitat and environment, within this highly dynamic and complex scenario of intertidal ecosystems.

The present limpet species survive and thrive in very harsh and unstable environments, therefore some characteristics of the coast (exposed or sheltered), shore level (upper, middle or lower limits), wave exposure, hydrodynamic fluxes and tidal cycle, with consequent physical, chemical and biological abrupt changes (Boaventura *et al.*, 2002, 2003), are reflected and correlated with particular features of their shell shape (Cabral, 2007). Accordingly, the morphometric relationships established in this study revealed diverse trends and patterns in the relative growth of these four limpet species. The relationship SW *vs* SL revealed diverse trends in the relative growth of *P. depressa* ($b = 1.117$) and *P. ulyssiponensis* ($b = 1.033$) with positive allometries indicative of progressive widening of the shell, compared with *P. vulgata* ($b = 1.033$) and *S. pectinata* ($b = 1.006$) with isometries suggestive of balanced growth rates in shell length and width throughout ontogeny.

For comparison purposes, and certainly reflecting contrasting environmental conditions between study areas, especially in terms of higher exposure and stronger hydrodynamics, a previous study registered isometric growth in *P. ulyssiponensis* ($b = 1.022$) from western Portugal (Cabral, 2007), whereas for *P. vulgata* hypoallometry ($b = 0.924$) was reported in Scotland (Jones *et al.*, 1979) and there are reports of hyperallometries in Scotland ($b = 1.062$–1.080) (Baxter, 1983) and western Portugal ($b = 1.042$) (Cabral, 2007) (Table 3). Limpets' shell shape is strongly influenced by their latitudinal distribution and vertical position on the shore (Bouzaza & Mezali, 2018). In fact, other studies that recorded hyperallometric growth between SW and SL suggested that limpets at higher tidal levels (compared with those lower down the shore) and limpets inhabiting sheltered sites (compared with those in more exposed areas), both tended to have slightly broader shells (Balaparameswara Rao & Ganapati, 1971; Bannister, 1975; Jones *et al.*, 1979; Baxter, 1983). Apparently, narrower shells are helpful and advantageous to reduce drag and avoid dislodgement under stronger wave action (Branch & Marsh, 1978; Baxter, 1983).

In the present study, the relationship SH *vs* SL also displayed clear inter-specific differences, ranging from positive allometries in *P. depressa* ($b = 1.248$) and *S. pectinata* ($b = 1.092$), isometric growth in *P. ulyssiponensis* ($b = 1.026$) and a negative allometry in *P. vulgata* ($b = 0.904$), reflecting differential and divergent trends in the expression of shell height compared with shell length throughout the species ontogeny. In the case of *S. pectinata*, hyperallometric growth in shell height is probably related to its

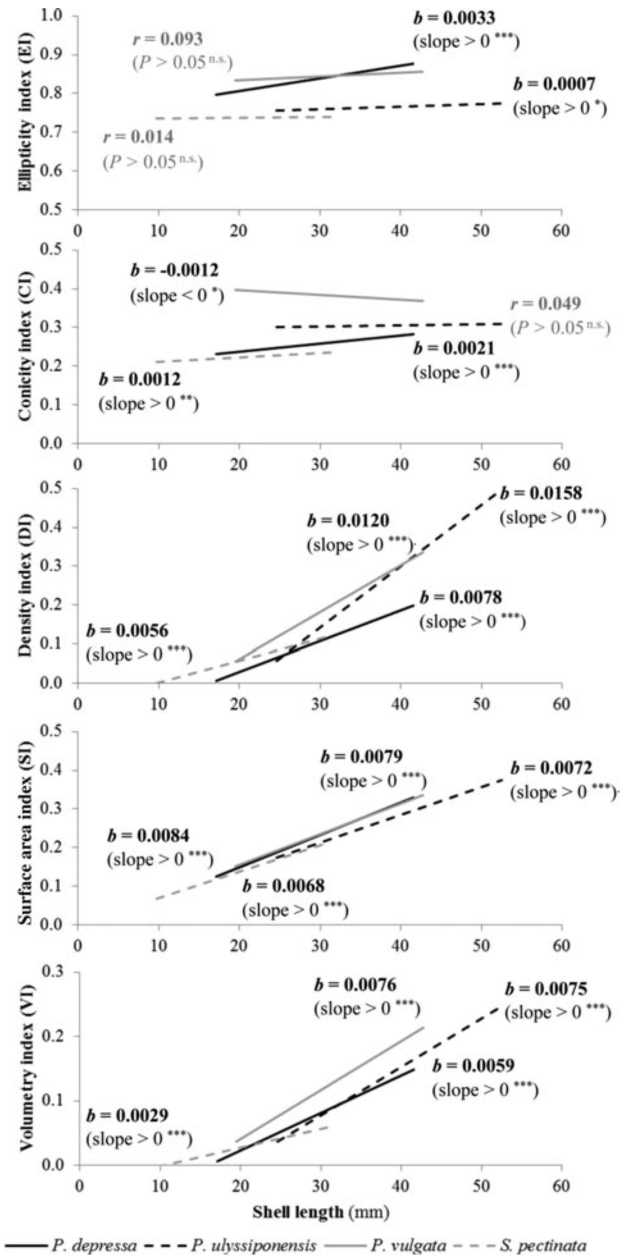

Fig. 3. Variation in the morphometric indices (ellipticity, conicity, density, surface area and volumetry) as a function of specimen size in four limpet species (*Patella depressa*, *Patella ulyssiponensis*, *Patella vulgata* and *Siphonaria pectinata*) from the Algarve coast (southern Portugal). *r*, correlation coefficient; *b*, regression slope. Asterisks denote statistical level (*P*-value): n.s. not significant, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

quite harsh intertidal habitat, subject to long periods of aerial exposure and prone to desiccation (Vermeij, 1973), where higher and heavily ridged shells (strong radial ribs) help to dissipate heat and keep soft body temperature (Vermeij, 1973; Cabral, 2007; Boukhicha *et al.*, 2013). The same principle applies to the positive allometry in *P. depressa* that occurs mainly in the middle shore level in both exposed and sheltered coasts along mainland Portugal, strongly influenced by the tidal cycle and repeatedly emerged for considerable periods, thus more susceptible to desiccation than species inhabiting lower shore levels (Guerra & Gaudêncio, 1986; Boaventura *et al.*, 2002, 2003). However, although being advantageous under thermally stressful conditions, taller shells are energetically more expensive in highly hydrodynamic environments (Baxter, 1983), compared with flattened shells better adapted for handling stronger wave impact and current flow (Khouw, 2006). In the particular case of *P. ulyssiponensis* this isometric growth, indicative of equivalent growth rates between shell length and height, probably reflects the fact that this species inhabits lower shore levels and is submerged most of the time (Cabral, 2007).

Proportionally flatter shells are more common in limpets highly exposed to strong wave action at higher shore levels, where this morphometric/morphological feature helps them to adhere firmly and remain attached to the substratum, avoiding being swept away by hydrodynamic forces and alleviating desiccation stress (Orton, 1928; Bannister, 1975; Branch & Marsh, 1978; Baxter, 1983; Khouw, 2006; Cabral, 2007; Harley *et al.*, 2009). In addition, since predators tend to select smaller prey that are easier to handle, flattened shells (i.e. proportionally greater investment in increasing shell length and/or width compared with shell height) is probably an advantageous strategy of limpets to avoid predation (Silva *et al.*, 2008). Similarly, previous studies also reported isometric growth in the relationship SH *vs* SL of *P. ulyssiponensis* from mainland Portugal ($b = 1.035$ and $b = 1.059$) (Cabral & Silva, 2003; Cabral, 2007), whereas possibly due to specific shell shape adaptations to particular environmental conditions, *P. vulgata* population displayed positive allometries ($b = 1.216–1.322$) in Scotland (Baxter, 1983) and mainland Portugal ($b = 1.045$ and $b = 1.216$) (Cabral & Silva, 2003; Cabral, 2007) (Table 3). In addition, some differences might also be due to the population geographic positioning within the species distributional range (i.e. weaker adaptation and lower fitness towards the northward and southward limits of each species), eventually reinforced by local features and stressors such as wave exposure and hydrodynamics, shore level and tidal height, availability of intertidal pools and shadow, predation and harvesting. For instance, the occurrence and abundance of the boreal *P. vulgata* decreases southwards (Borges *et al.*, 2015), being scarcer in southern Portugal where it reaches its meridional biogeographic limit, thus becoming more sensitive to water temperature, suffering stronger thermal stress and higher risk of desiccation in this southern edge of its distributional range (Guerra & Gaudêncio, 1986). Consequently, in this area *P. vulgata* tends to inhabit microhabitats, namely tidal pools and shade zones, especially on vertical and humid surfaces (Guerra & Gaudêncio, 1986), displaying a behavioural adaptation to adverse environments that also influences and modulates limpet morphology and morphometrics (Harley *et al.*, 2009).

In the present study, limpets' total weight was composed of both shell weight (deposition of shell material) and tissues weight (somatic growth). The morphometric relationship TW *vs* SL presented distinct trends between species, with hyperallometries in *P. depressa* ($b = 3.362$) and *P. ulyssiponensis* ($b = 3.298$) against isometric growth in *P. vulgata* ($b = 2.967$) and *S. pectinata* ($b = 2.981$). These positive allometries in both *P. depressa* and *P. ulyssiponensis* reflect a proportionally higher growth rate in total weight compared with shell length, probably associated to increased shell deposition that improved shell thickness and weight throughout ontogeny (Jones *et al.*, 1979), which indicates suitable feeding conditions for those species in the study area because starvation reduces calcium deposition and decreases the growth rate in shell weight (Zischke *et al.*, 1970). In general, limpets inhabiting higher shore levels develop heavier shells to improve protection against solar radiation (Balaparameswara Rao & Ganapati, 1971), but the continuous deposition of material and increased shell thickness during growth also helps to maintain the limpets' resistance against compression forces (Cabral & Natal Jorge, 2007). For example, boreal populations of *P. vulgata* from the Orkney Islands (Scotland), subjected to severe environments and intense hydrodynamics, presented hyperallometries ($b = 3.341–3.610$) in their weight–length relationships (Baxter, 1983) (Table 3). In addition, by also including tissues

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Table 3. Comparison of morphometric relationships and relative growth in *Patella ulyssiponensis* and *Patella vulgata* populations from the Algarve coast (southern Portugal) and from other geographic locations throughout their distributional range in the North-east Atlantic Ocean

		Morphometric relationship				Relative growth		
Species	Location	Variables	N	*r*	*b* ± SE (95% CI)	*t*-test	Type	Reference
Patella ulyssiponensis	Póvoa de Varzim (Portugal)	SW *vs* SL	65	0.958	0.791			Cabral (2003)
(Gmelin, 1791)	Afife to Telheiro (Portugal)		413	0.958	1.022 (0.992–1.051)	$^{n.s.}$	I=	Cabral (2007)
	Lagos (Portugal)		306	0.967	1.033 ± 0.016 (1.002–1.063)	2.092***	A+	Present study
	Póvoa de Varzim (Portugal)	SH *vs* SL	65	0.773	1.035			Cabral (2003)
	Póvoa de Varzim (Portugal)		75		1.035	0.320$^{n.s.}$	I=	Cabral and Silva (2003)
	Afife to Telheiro (Portugal)		413	0.786	1.059 (0.978–1.139)	$^{n.s.}$	I=	Cabral (2007)
	Lagos (Portugal)		306	0.770	1.026 ± 0.049 (0.930–1.122)	0.531$^{n.s.}$	I=	Present study
Patella vulgata	Easthaven (Scotland)	SW *vs* SL	50	0.992	0.924 ± 0.017	4.540***	A–	Jones *et al.* (1979)
(Linnaeus, 1758)	Orkney Islands, Sites 1 to 3 (Scotland)		50	0.983 to 0.995	1.062 ± 0.015 to 1.080 ± 0.015	3.660*** to 5.497***	A+	Baxter (1983)
	Póvoa de Varzim (Portugal)		239	0.964	0.821			Cabral (2003)
	Afife to Telheiro (Portugal)		381	0.970	1.042 (1.016–1.068)	***	A+	Cabral (2007)
	Lagos (Portugal)		408	0.947	1.033 ± 0.017 (0.999–1.067)	1.912$^{n.s.}$	I=	Present study
	Orkney Islands, Sites 1 to 3 (Scotland)	SH *vs* SL	50	0.969 to 0.981	1.216 ± 0.028 to 1.322 ± 0.035	7.791*** to 9.091***	A+	Baxter (1983)
	Póvoa de Varzim (Portugal)		239	0.868	1.043			Cabral (2003)
	Póvoa de Varzim (Portugal)		253		1.045	4.820***	A+	Cabral and Silva (2003)
	Afife to Telheiro (Portugal)		381	0.869	1.216 (1.146–1.285)	***	A+	Cabral (2007)
	Lagos (Portugal)		408	0.761	0.904 ± 0.038 (0.828–0.979)	2.521***	A–	Present study
	Orkney Islands, Sites 1 to 3, summer (Scotland)	TW *vs* SL	50	0.985 to 0.995	3.457 ± 0.014 to 3.610 ± 0.019	21.438*** to 41.058***	A+	Baxter (1983)
	Orkney Islands, Sites 1 to 3, winter (Scotland)		50	0.988 to 0.995	3.341 ± 0.022 to 3.469 ± 0.014	3.421*** to 32.961***	A+	Baxter (1983)
	Lagos (Portugal)		408	0.916	2.967 ± 0.065 (2.840–3.094)	0.510$^{n.s.}$	I=	Present study
	Easthaven (Scotland)	SiV *vs* SL	50	0.991	3.256 + 0.023	11.290***	A+	Jones *et al.* (1979)
	Orkney Islands, Sites 1 to 3 (Scotland)		50	0.993 to 0.997	3.290 ± 0.013 to 3.394 ± 0.016	23.224*** to 30.681***	A+	Baxter (1983)
	Lagos (Portugal)		408	0.959	2.937 ± 0.043 (2.852–3.021)	1.476$^{n.s.}$	I=	Present study

SL, shell length (mm); SW, shell width (mm); SH, shell height (mm); TW, total weight (g); SiV, shell internal volume (cm^3); N, number of individuals; *r*, correlation coefficient; *b*, allometry coefficient; SE, standard error; 95% CI, 95% confidence interval. Asterisks denote statistical level (*P*-value): $^{n.s.}$not significant, $P > 0.05$; ***, $P < 0.001$; A–, negative allometry; I = , isometry; A+, positive allometry. Some *r* values were square-root transformed and some *b* values were anti-log transformed from original data.

weight (somatic growth), weight–length relationships constitute a simple and practical condition index (Anderson & Gutreuter, 1983; Richter *et al.*, 2000). Similarly to the presently non-harvested populations from southern Portugal (isometries in *P. vulgata* and *S. pectinata* and hyperallometries in *P. depressa* and *P. ulyssiponensis*), isometric and positive allometric growth in the relationship TW *vs* SL were considered indicators of ecosystem health and population fitness in *P. aspera* populations from Marine Protected Areas (MPAs) in the archipelago of Madeira (Sousa *et al.*, 2020*c*).

As expected, resulting from calculations based on mathematical equations involving the three linear measurements already discussed above (SL, SW and SH), limpets' shell areas (SbA and SsA) and volumes (SiV and StV) also displayed some similar trends in terms of relative growth. For instance, the positive allometries in shell base area presented by *P. depressa* and *P. ulyssiponensis* (denoting increased growth rate in SbA during growth) are usually influenced by the species' vertical distribution on the shore and prevailing conditions (Khouw, 2006). On the one hand, a smaller shell base area helps to reduce water loss and avoid desiccation under exposed conditions (Lowell, 1984; Khouw, 2006; Cabral, 2007), while on the other hand a larger contact area improves a limpet's tenacity, because the adhesion force to hard substrate (attachment strength to the home scar) is proportional to the foot surface area (Branch & Marsh, 1978; Jones *et al.*, 1979; Grenon & Walker, 1981; Baxter, 1983; Cabral, 2007). Regarding the shell surface area, this morphometric feature is essentially related with functional trade-off between limpets and the surrounding temperature, i.e. heat loss and cooling using seawater retained inside the shell to decrease body temperature, alleviate thermal stress and avoid desiccation (Vermeij, 1973; Cabral, 2007; Boukhicha *et al.*, 2013). Accordingly, one positive allometry (*P. depressa*) and three isometries (*P. ulyssiponensis*, *P. vulgata* and *S. pectinata*) recorded in the relationships SsA *vs* SL of these limpet species in this study area, further confirms their adaptation and ability to cope with the aerial exposure and thermal stress during low tide. Following some general trends recorded in shell dimensions and areas, enhanced shell volumes (SiV and StV) throughout ontogeny also constitute a useful morphological adaptation against heating stress and desiccation risk (Cabral, 2007). In practice, more voluminous limpets have a larger reservoir of seawater (i.e. store more inner water because a higher portion of the available shell volume is void of tissue), which allows losing a smaller fraction of body water, lowering body temperature and alleviating desiccation during periods of environmental stress (Vermeij, 1973; Branch & Marsh, 1978; Lowell, 1984; Nolan, 1991; Cabral, 2007). In the present study, the relationships SL *vs* SiV and SL *vs* StV revealed the same type of relative growth in *P. ulyssiponensis* and *P. vulgata* (isometries) as well as in *P. depressa* and *S. pectinata* (hyperallometries), suggesting a differential adaptation of these limpet species to thermal stress induced by the aerial exposition during emersion periods (variable depending on the shore level) in intertidal areas along southern Portugal. Just for comparison purposes, positive allometric growth was recorded in the relationship SiV *vs* SL in two Scottish populations of *P. vulgata* from Easthaven (Jones *et al.*, 1979) and from the Orkney Islands (Baxter, 1983) (Table 3).

Subsequently, the calculation of morphometric indices (ellipticity, conicity, density, surface area and volumetry) clearly confirmed their practicality and usefulness for further describing and interpreting limpets' shell shape. In fact, despite consisting of simple ratios between some variables, these morphometric indices corroborated data on shell morphometrics and relative growth, providing valuable insights of inter- and/or intra-specific variation in some shell features of these limpet species. Confirming high diversity in shell shape, the conicity (CI: *P. vulgata* > *P. ulyssiponensis* > *P. depressa* > *S. pectinata*), density and volumetry (DI and VI: *P. ulyssiponensis* > *P. vulgata* > *P. depressa* > *S. pectinata*) were significantly different among all limpet species. The ellipticity (EI: *P. depressa* = *P. vulgata* > *P. ulyssiponensis* > *S. pectinata*) and surface area indices (SI: *P. ulyssiponensis* > *P. depressa* = *P. vulgata* > *S. pectinata*) also displayed considerable inter-specific variation among most limpet species. Unfortunately, intra- and inter-specific comparisons of these morphometric indices with analogous data available from previous studies with these limpet species are quite scarce and limited to the ellipticity and conicity indices of *P. ulyssiponensis* and *P. vulgata* from Portugal and Tunisia (Cabral, 2003, 2007; Cabral & Silva, 2003; Boukhicha *et al.*, 2013). Following some general trends in shell shape and morphometrics already discussed above, the present population of *P. ulyssiponensis* scored an ellipticity index of 0.765, quite similar to those previously recorded along mainland Portugal, namely 0.764 (Cabral, 2003) to 0.769 (Cabral, 2007), and all higher than that reported in Tunisia (0.707) (Boukhicha *et al.*, 2013), whereas *P. vulgata* from this study area presented a higher EI (0.844) compared with other populations from the Portuguese coast, which ranged from 0.793 (Cabral, 2003) to 0.799 (Cabral, 2007). The conicity index of *P. ulyssiponensis* from the Algarve coast (CI = 0.305), fell within the range previously registered along mainland Portugal, namely 0.303 (Cabral, 2007), 0.318 (Cabral, 2003) and 0.322 (Cabral & Silva, 2003), being slightly higher than in Tunisia (CI = 0.296) (Boukhicha *et al.*, 2013), while *P. vulgata* recorded a CI of 0.382 in this study area, also comparatively higher than in other populations from mainland Portugal, with reported CIs of 0.345 (Cabral & Silva, 2003), 0.346 (Cabral, 2003) and 0.356 (Cabral, 2007).

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