Sexual dimorphism in shell size of the land snail Leptopoma perlucidum (Caenogastropoda: Cyclophoridae)

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Sexual dimorphism in the shell size and shape of land snails has been less explored compared to that of other marine and freshwater snail taxa. This study examined the differences in shell size and shape across both sexes of *Leptopoma perlucidum* land snails. We collected 84 land snails of both sexes from two isolated populations on two islands off Borneo. A total of five shell size variables were measured: (1) shell height, (2) shell width, (3) shell spire height, (4) aperture height, and (5) aperture width. We performed frequentist and Bayesian t-tests to determine if there was a significant difference between the two sexes of *L. perlucidum* on each of the five shell measurements. Additionally, the shell shape was quantified based on nine landmark points using the geometric morphometric approach. We used generalised Procrustes and principal component analyses to test the effects of sex and location on shell shape. The results showed that female shells were larger than male shells across all five measurements (all with p-values < 0.05), but particularly in regards to shell height and shell width. Future taxonomic studies looking to resolve the *Leptopoma* species' status should consider the variability of shell size caused by sexual dimorphism.

1 **Sexual dimorphism in shell size of the land snail *Leptopoma***

2 ***perlucidum* (Caenogastropoda: Cyclophoridae)**

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29 **Abstract**

30 Sexual dimorphism in the shell size and shape of land snails has been less explored compared to

31 that of other marine and freshwater snail taxa. This study examined the differences in shell size

32 and shape across both sexes of *Leptopoma perlucidum* land snails. We collected 84 land snails of

33 both sexes from two isolated populations on two islands off Borneo. A total of five shell size

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35 height, and (5) aperture width. We performed frequentist and Bayesian t-tests to determine if

36 there was a significant difference between the two sexes of *L. perlucidum* on each of the five shell

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39 component analyses to test the effects of sex and location on shell shape. The results showed

40 that female shells were larger than male shells across all five measurements (all with p-values <

41 0.05), but particularly in regards to shell height and shell width. Future taxonomic studies looking

42 to resolve the *Leptopoma* species' status should consider the variability of shell size caused by

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Introduction

Molluscs exhibit a wide variety of sexual systems and strategies, with the superfamilies of gastropods being dioecious, simultaneously hermaphroditic, or sequentially hermaphroditic (Collin, 2013). Among these, terrestrial gonochoristic gastropods make up several superfamilies under the orders Architaenioglossa (clades Caenogastropoda) and Cycloneritida (clade Neritimorpha); the rest are primarily hermaphroditic. Additionally, there is little research on sexual dimorphism in shell forms of land snail superfamilies compared to freshwater and marine snail superfamilies.

Not all species within a genus exhibit sexual dimorphism (Glöer et al., 2007; Lazutkina et al., 2009; Riasco & Guzman, 2010; Andreeva et al., 2017). Because shell size and shape are often used as diagnostic characteristics in species' taxonomy, it is important to understand the effects of sexual dimorphism on these traits. Sexual dimorphism can be observed in a shell's surface ornamentations (Dutta et al., 2017), size (Jokinen et al., 1982; Son, 1997; Estebenet & Cazzaniga, 1998; Glöer et al., 2007; Pastorino, 2007; Kurata & Kikuchi, 2000; Son & Hughes, 2000; Minton & Wang, 2011; Ng et al., 2019; Páll-Gergely et al., 2020), shape (Jokinen et al., 1982; Keawjam, 1987; Son & Hughes, 2000; Minton & Wang, 2011; Márquez & Averbuj, 2017), and pigmentation (Gofas, 2001; Schilthuizen et al., 2017). The driving forces that cause dimorphisms in shell characteristics are generally related to reproductive selection (Pastorino, 2007; Colin, 2018).

To our knowledge, sexual dimorphism in shell size and shape of terrestrial caenogastropod shells has only been studied in five genera: *Cochlostoma*, *Obscurella*, *Plectostoma*, *Barnaia,* and *Streptaulus* (Raven, 1990; Gofas, 2001; Schilthuizen et al., 2003, Reichenbach et al., 2012; Páll-Gergely et al., 2020). With the exception of *Plectostoma*, the species have elongate conical shells where female shells are more slender than males. Schilthuizen et al. (2013) found no differences in shape between the two sexes in the sinistroid shells of *Plectostoma*. In the present study, we investigate sexual dimorphism in the land snail - *Leptopoma perlucidum* (Grateloup, 1840) (Cyclophoridea). The species exhibits high polymorphism in shell colour pattern (Phung et al., 2007) and it is not known whether this shell feature, as well as its size and shape, reflect sexual

86 dimorphism. Therefore, we tested the differences of five linear measurements (i.e. size)

87 corresponding to the nine referenced landmarks (i.e. shape) on the shell of male and female

88 individuals.

89

Materials & methods

91 **Collection of specimens**

92 We collected living *L. perlucidum* adults (shells with reflected lips), as snails without lips are likely

93 to be immature from two islands, Tiga Island (N 5°43'28", E 115°39'20") and Gaya Island (N 6°1'3",

94 E 116°1'50"), both located at the west coast of Sabah, between January and August 2016. Sabah

95 Parks approved this work (permit no. TS/PTD/5/4 Jld. 54 (112)). The snails were drowned until

96 the animal's soft body fully extended so that the sexes could be determined and examined under

97 a stereomicroscope as described by Jonges (1980) (Figure 1B and C). A total of 84 *L. perlucidum*

98 specimens were collected: nine females and 12 males from Gaya Island, and 33 females and 30

99 males from Tiga Island. All specimens were deposited in the *BORNEENSIS* collection at the

100 Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah (BOR/MOL 6651, 6653-

101 6654, 7873-7875, 7877, 8739-8748, 8750-8754, 8756-8784, 8786-8794, 8797-8802, 8805-8809,

102 8813, 8816-8817, 9444-9447, 9449-9451, and 9726-9728).

103

104 **Shell morphology data**

105 Each shell was photographed from the shell's aperture view using a Leica Image Analyzer M205.

106 The shell size and shape measurements were obtained using the photographs. The shell size

107 consisted of five linear measurements, measured to the nearest 0.1 mm: aperture height (AH),

108 aperture width (AW), shell height (SH), shell width (SW), and spire height (SpH) (Figure 1A). The

109 shell shape was quantified using nine landmark coordinates corresponding to the dimensions of

110 the different parts of the shell and recorded with ImageJ (Figure 1A). The measurements and

111 landmarks were selected based on the traits used for taxonomic purposes (Vermeulen, 1999;

112 Vermeulen & Liew, 2022). Furthermore, these landmarks correspond to some of the landmarks

113   used by Larsson et al. (2020) as developmentally descriptive shape parameters to simulate the

114   three-dimensional logarithmic spiral growth of the shell.

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117

118   **Data analysis**

119   *Sexual dimorphism in shell size*

120   We used two independent sample tests to determine whether there was a significant difference

121   across each of the five shell measurements between both sexes of *L. perlucidum* for the two

122   islands, respectively. No subset data (two locations vs. two sexes) violated the assumption of

123   homogeneity of variances (Levene test) for all five shell measurements. However, three data

124   subsets from Tiga Island (female AH, and male SW and SH) violated the normality assumption

125   (Shapiro–Wilk test). Q-Q plots demonstrated that all five measurements had approximately

126   normal distributed residuals. Because sampling was opportunistic and effect size (Cohen's d,

127   Cohen, 1988) cannot be determined prior to sampling, we calculated effect size based on the

128   differences between male and female snails in the five shell measurements for each location. The

129   very large effect sizes found in the measurements for both sexes on Tiga Island ranged from 0.75

130   to 1.20, while on Gaya Island, the values ranged from 1.15 to 1.92. Therefore, we checked the

131   power of the tests after the experiment had been conducted by using the calculated effect size

132   (d), significant level of 0.05, and the smaller n for each group, n = 30 and 9 for Tiga and Gaya

133   Island respectively.

134

135   We conducted frequentist student's t-tests since the deviations from the normality assumption

136   in these datasets were considered not too serious and we rejected the null hypothesis when p

137   <0.05. Simultaneously, we also performed Bayesian t-tests (BayesFactor – BF; Morey & Rouder,

138   2015) because the Bayesian framework could supplement the frequentist p-value (Rouder et al.,

139   2012). Typically, $BF_{10} > 1$ is used to quantify evidence in favour of the alternative hypothesis.

140   Ultimately, we based our conclusions on the inference of both frequentist (p-values) and

141   Bayesian (BF_{10}) tests. All statistical tests and effect size calculations were performed using JASP

142   software (version 0.12.2; JASP Team, 2020) while the power of the tests was assessed using the

143   function "pwr.t.test" implemented in the 'pwr' packages for R (Champely et al., 2020).

144

145   *Sexual dimorphism in shell shape*

146   Shell shape was analysed using landmark-based geometric morphometrics. The digitised

147   coordinate configurations of all specimens were subjected to Generalised Procrustes Analysis

148   (GPA; Rohlf & Slice, 1990) to hold constant variations in size, orientation, and position. We then

149   scaled them to standard unit centroid size. For the size comparison between the sexes, we did

150   not use the centroid size of the set of landmarks, as the exact linear measurements were used in

151   this study. GPA was done using the 'gpagen' function in the R package 'geomorph' (Adams &

152   Otárola-Castillo, 2013). The aligned landmark coordinates produced by GPA were used as a set

153   of shell shape variables for further analysis. First, principal component analysis (PCA) was applied

154   using the 'plotTangentSpace' function in the same package to visualise the shape pattern

155   variations. After that, we performed Procrustes ANOVA (regression for shape data) using the

156   'procD' function in the R package 'geomorph' to determine the effects of sex and location on shell

157   shape. The analyses were performed in R (version 4.0.3; R Core Team, 2015). The completed R

158   script can be found in Supplemental File 1.

159

160   **Results**

161   **Sexual dimorphism in shell size**

162   All five boxplots showed a difference across all shell size measurements between male and

163   female *L. perlucidum* (Figure 2). Both frequentist and Bayesian t-tests showed significant effect

164   of sex on shell measurements, especially with respect to SH and SW (Table 1). The power of all

165   the tests was above 0.8 for all shell measurements of both land snail populations, with the

166   exception of AW for the Gaya Island population (power = 0.6). There were significant differences

167   across all five measurements between female and male shells for both locations as revealed by

168   the frequentist t-test (all with p-values < 0.05) and the Bayesian t-test (BF inclusion > 1). The

169   female shell appeared to be larger than the male shell across all five measurements (Table 2,

170   Supplemental File 2).

171

Sexual dimorphism in shell shape

173   A total of 56% (PC1 – 31.8%, PC2 – 23%) of the shape variation in the nine-landmark

174   coordinate dataset was explained by the first two principal components (Figure 3). The thin-plate

175   spline (TPS) transformation grids showed that the main source of the shape variations in the

176   morphospace were from the aperture shape, i.e., landmarks 5, 6, 7, 8, and 9. The scatterplot

177   showed significant overlaps between the sex and location of *L. perlucidum* in their shell shape.

178   There were no significant differences between the shell shapes of male and female *L. perlucidum*

179   from the two different locations (Procrustes ANOVA – Sexes: df = 1, F = 1.5247, p = 0.150;

180   locations: df = 1, F = 1.6907, p = 0.117; sex and location interaction: df = 1, F = 0.4359, p = 0.879)

181   (Supplemental File 3). Shell images of all specimens used in this study can be found in

182   Supplemental File 4.

183

Discussion

Sexual dimorphism in *L. perlucidum* shell form

186   This is the first investigation into sexual dimorphism in shell size and shape in the Cyclophoridae.

187   This species exhibits sexual dimorphism in shell size but not in shell shape. Females have larger

188   shells than males despite shell size variations. To date, only a handful of land snail studies have

189   investigated the size variations between both sexes, and all studies showed that females are

190   more slender and larger than males (Gofas, 2001; Reichenbach et al., 2012; Páll-Gergely et al.,

191   2020). Although females can be at least 6% (~ 1 mm) larger than males in the same *L. perlucidum*

192   population, this may not be noticeable even when comparing the shells of both sexes side by

193   side. Páll-Gergely et al. (2020) pointed out that these differences can only be revealed when

194   rigorous statistical methods are used, as is the case in most other studies.

195

196   On the other hand, there is an abundance of sexual dimorphism studies on the shell form of

197   aquatic and marine snails. These studies overwhelmingly show that females are larger than males

198   (Jokinen et al., 1982; Son, 1997; Estebenet & Cazzaniga, 1998; Kurata & Kikuchi, 2000; Son &

199   Hughes, 2000; Minton & Wang, 2011; Ng et al., 2019). However, there has been a few exceptions

200 in which males were larger than females (Kurata & Kikuchi, 2000) or where there was no sexual

201 dimorphism in shell size (Tripoli et al., 2015; Vaux et al., 2017). In addition to the overall shell size

202 in terms of total height and width, some studies also showed that females had a larger aperture

203 size compared to males (Cazzaniga, 1990; Son, 1997; Minton & Wang, 2011), or that the shells of

204 females were more globose than males' (Jokinen et al., 1982; Keawjam, 1987; Son & Hughes,

205 2000; Minton & Wang, 2011).

206

207 Currently, the biology, specifically the mating process, of the *Leptopoma* species remains

208 unexplored. Therefore, we can only hypothesise that females have larger shells than males

209 because of the different morphologies of their reproductive systems. In studies on other taxa, it

210 has been hypothesised that sexual dimorphism in caenogastropod shells (females either have a

211 larger shell size or a more globose shell) appears to be primarily related to female fecundity or

212 egg mass production (Colin et al., 2018). Females generally have larger sized shells, especially in

213 the last whorl, resulting in a higher shell volume for egg deposition (Gofas, 2001).

214

215 Studies on other taxa found that the driving forces for sexual dimorphism in shell form include

216 sexual selection and the two sexes' different growth rates (Jokinen et al., 1982; Kurata & Kikuchi,

217 2000; Riasco & Guzman, 2010). The underlying driving forces of sexual dimorphism in the shell

218 size of *L. perlucidum* need to be similarly investigated in future studies with more field

219 observations and experiments to determine whether females are larger than males in mating

220 pairs (e.g., Ng et al., 2019) and the growth rate of both sexes.

221

222 **The implications to taxonomic studies on the genus *Leptopoma***

223 Future taxonomic research to resolve the status of the *Leptopoma* species would need to take

224 into account the variability of shell size caused by sexual dimorphism and geographical variations

225 (Phung et al., 2017). There are 125 valid names for *Leptopoma* species, and there are another

226 154 invalid names due to various nomenclature reasons (MolluscaBase, 2021). The last intensive

227 review, conducted by Kobelt (1902) on 105 *Leptopoma* is outdated, and subsequent taxonomic

228 works have mainly dealt with a handful of species in relatively small geographic areas (Gude,

229   1921; Vermeulen, 1999; Phung et al., 2017). There has been no quantitative comparison of shell

230   shapes among species, except Phung et al. (2017). The species diversity hotspot is in the

231   Philippines archipelago, where many species occur sympatrically over thousands of islands (GBIF,

232   2021). Our study shows that in *L. perlucidum* at least, no shape differences (which would further

233   complicate a taxonomic revision of the genus) are found between males and females.

234

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Frequentist and Bayesian t-test results for the effect of sexes on five shell measurements.

Frequentist t-tests with significant p-values were annotated with asterisks.

1   **Table 1.** Results of frequentist t-test, and Bayesian t-test for the effect of sexes and locations on five shell

2   measurements. Frequentist t-tests with significant p-values were annotated with asterisks. Significant p-

3   values: * < 0.05, ** < 0.01, *** < 0.001.

Measurements	Tiga Island			Gaya Island		
	Frequentist t-test	Effect size	Bayesian t-test	Frequentist t-test	Effect size	Bayesian t-test
	t	Cohen's d	BF_{incl}	t	Cohen's d	BF_{incl}
Shell height	3.941***	0.99	115.8	4.363***	1.92	72.5
Shell width	4.770***	1.20	1451.8	4.034***	1.78	39.4
Aperture height	3.716***	0.94	61.7	3.798**	1.68	25.7
Aperture width	4.753***	1.20	1374.5	2.607*	1.15	3.5
Shell spire height	2.971**	0.75	9.3	3.928***	1.73	32.5

Shell measurements summaries for female and male *L. perlucidum* snails from Gaya and Tiga Islands.

1 **Table 2.** Summary of the shell measurements for the female and male *Leptopoma perlucidum* snails in two locations (Gaya Island and Tiga Island).

Measurements (mm)	Gaya Island			Tiga Island		
	female	male	Differences between female and male (%)	female	male	Differences between female and male (%)
	Mean ± S.D.	Mean ± S.D.		Mean ± S.D.	Mean ± S.D.	
Shell height	14.3 ± 0.5	13.2 ± 0.6	+ 8.3%	13.8 ± 0.9	13.0 ± 0.9	+ 6.2%
Shell width	14.0 ± 0.5	13.0 ± 0.6	+ 7.7%	13.5 ± 0.7	12.6 ± 0.8	+ 7.1%
Aperture height	7.7 ± 0.3	7.1 ± 0.4	+ 8.5%	7.4 ± 0.4	7 .0 ± 0.5	+ 5.7%
Aperture width	8.5 ± 0.5	7.9 ± 0.4	+ 7.6%	8.2 ± 0.5	7.6 ± 0.4	+ 7.9%
Shell spire height	3.6 ± 0.1	3.3 ± 0.2	+ 9.1%	3.4 ± 0.4	3.2 ± 0.3	+ 6.2%

Figure 1

L. perlucidum shell and animals.

(A) Shell size and shape measurements for *L. perlucidum.* Shell sizes were measured in five ways: from the apertural view: SH = shell height, SpH = shell spire height, SW= shell width, AH=aperture height, and AW=aperture width. Red points designated the nine landmarks for geometric morphometric. (B) Male specimen; red arrow indicated the penis. (C) The female specimen. The penis was not seen and the reproductive organ can be observed.
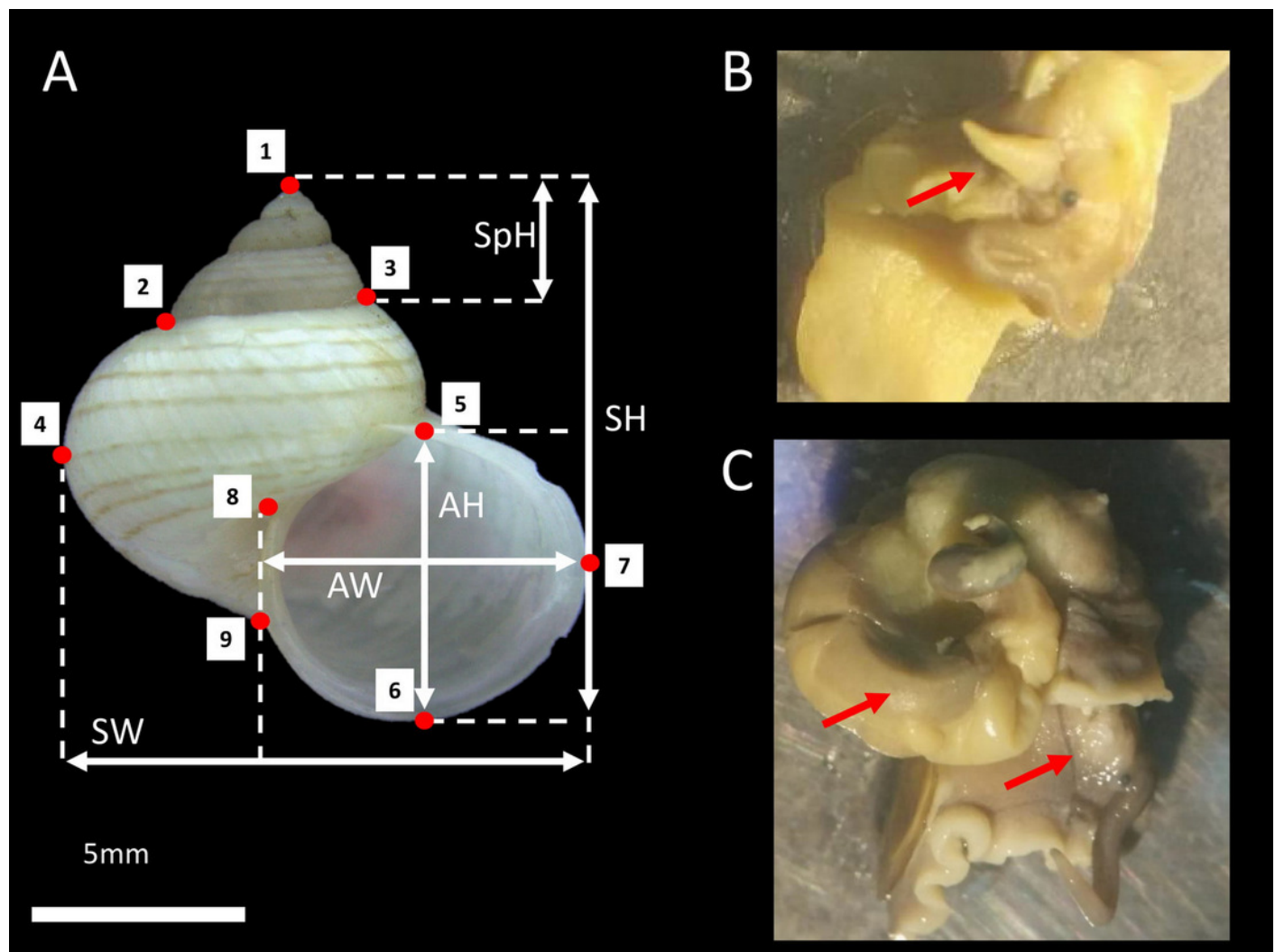
Figure 2

Boxplots show the differences in five quantitative shell measurements between specimens of opposite sex sampled from two locations.

Female, Gaya Island (n = 9); male, Gaya Island (n = 12); female, Tiga Island (n = 33); male, Tiga Island (n = 30). (A) Shell height. (B) Shell width. (C) Aperture height. (D) Aperture width. (E) Shell spire height.
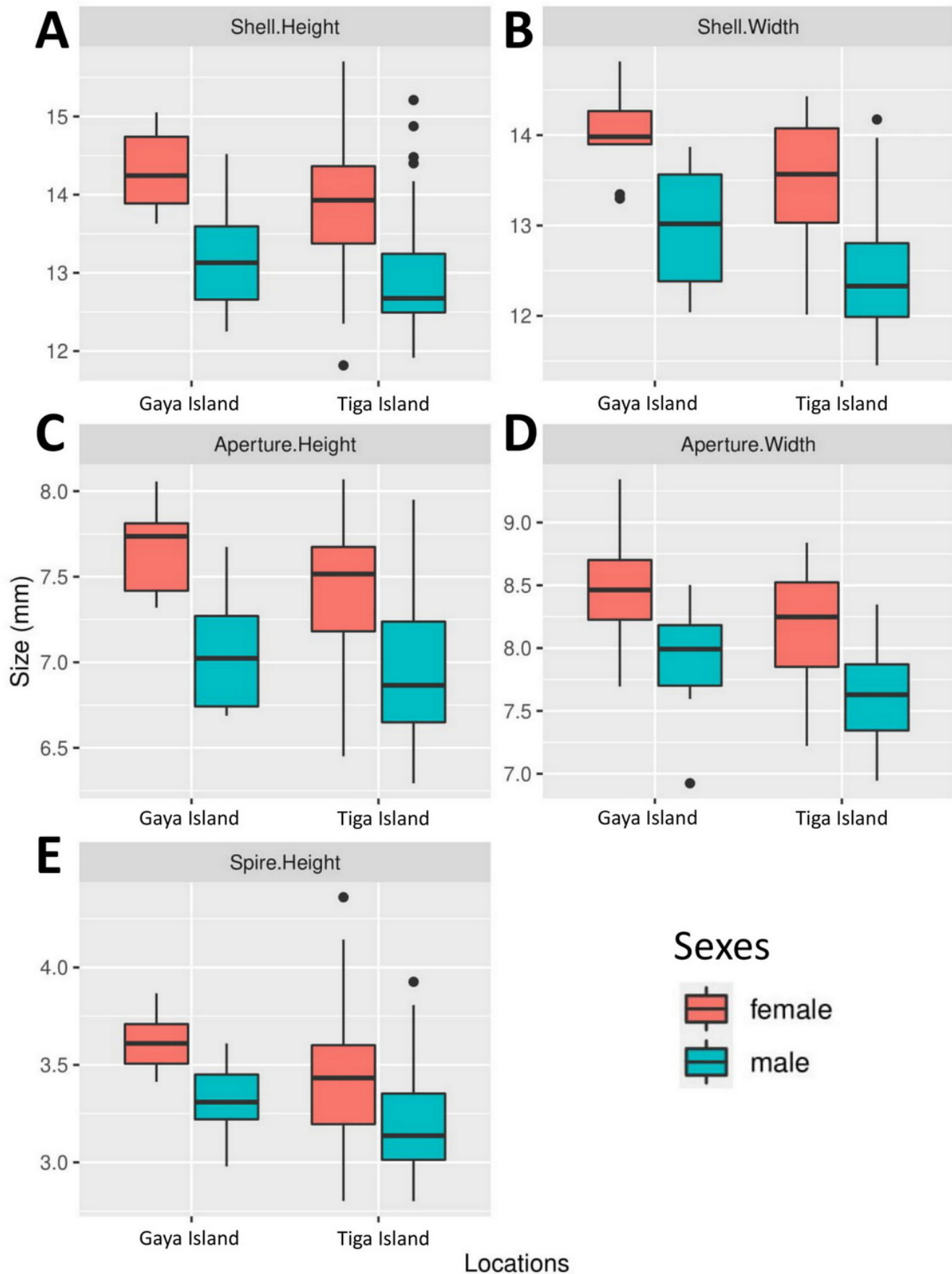
Figure 3

Principal component analysis (PCA) for shell shape of *L. perlucidum*.

Morphospace is represented by a scatterplot of the scores from the first two principal components of the geometric morphometric analysis of the nine shell landmarks. Thin-plate spline (TPS) transformation grids represent shape variation at the extremes of the two principal component axes.