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# The Masquerade Game: marine mimicry adaptation between egg-cowries and octocorals

Juan A Sánchez, Angela P Fuentes-Pardo, Íde Ní Almhain, Néstor E Ardila-Espitia, Jaime Cantera-Kintz, Manu Forero-Shelton

**Background.** Background matching, as a camouflage strategy, is one of the most outstanding examples of adaptation, where little error or mismatch means high vulnerability to predation. It is assumed that the interplay of natural selection and adaptation are the main evolutionary forces shaping the great diversity of phenotypes observed in mimicry, however there may be other significant processes that intervene in the development of mimicry such as phenotypic plasticity. Based on observations of background mismatching during reproduction events of egg-cowries, sea snails of the family Ovulidae that mimic the octocoral where they inhabit, we wondered if they match the host species diversity. Using observations in the field and molecular systematics, we set out to establish whether the different egg-cowrie color/shape polymorphisms correspond to distinct lineages restricted to specific octocoral species. **Methods.** Collection and observations of egg-cowries and their octocoral hosts were done using SCUBA diving between 2009-2012 at two localities in the Tropical Eastern Pacific (TEP), Malpelo Island and Cabo Corrientes (Colombia). Detailed host preference observations were done bi-annually at Malpelo Island. We analyzed the DNA sequence of the mitochondrial genes *COI* and *16S rDNA*, extensively used in phylogenetic and DNA barcoding studies, to assess the evolutionary relationship among different egg-cowrie colorations and morphologies. **Results.** No genetic divergence among egg-cowries associated to different species of the same octocoral genus was observed based on the two mitochondrial genes analyzed. For instance, all egg-cowrie individuals from the two sampled localities observed on 8 different *Pacifigorgia-Eugorgia* species showed negligible mitochondrial divergence yet large morphologic divergence, which suggests that morphologies belonging to at least two sea snail species, *Simnia avena* (= *S. aequalis*) and *Simnialena rufa*, can cross-fertilize. **Discussion.** Our study system comprised background-matching mimicry, of the masquerade type, between egg-cowries (*Simnia/Simnialena*) and octocorals (*Pacifigorgia/Eugorgia/Leptogorgia*). We observed mimicry mismatches related to fitness trade-offs, such as reproductive aggregations vs. vulnerability against predators. Despite the general assumption that coevolution of mimicry involves speciation, egg-cowries with different hosts and colorations comprise the same lineages. Consequently, we

infer that there would be significant tradeoffs between mimicry and the pursuit of reproductive aggregations in egg-cowries. The findings of this study not only contribute to the understanding of the evolution of mimicry in egg-cowries, a poorly studied group of marine gastropods, but also to the development of a new biologically meaningful board game that could be implemented as a learning tool.

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24

25 **Abstract**

26 **Background.** Background matching, as a camouflage strategy, is one of the most outstanding  
27 examples of adaptation, where little error or mismatch means high vulnerability to predation. It is  
28 assumed that the interplay of natural selection and adaptation are the main evolutionary forces  
29 shaping the great diversity of phenotypes observed in mimicry, however there may be other  
30 significant processes that intervene in the development of mimicry such as phenotypic plasticity.  
31 Based on observations of background mismatching during reproduction events of egg-cowries,  
32 sea snails of the family Ovulidae that mimic the octocoral where they inhabit, we wondered if  
33 they match the host species diversity. Using observations in the field and molecular systematics,  
34 we set out to establish whether the different egg-cowrie color/shape polymorphisms correspond  
35 to distinct lineages restricted to specific octocoral species.

36 **Methods.** Collection and observations of egg-cowries and their octocoral hosts were done using  
37 SCUBA diving between 2009-2012 at two localities in the Tropical Eastern Pacific (TEP),  
38 Malpelo Island and Cabo Corrientes (Colombia). Detailed host preference observations were  
39 done bi-annually at Malpelo Island. We analyzed the DNA sequence of the mitochondrial genes  
40 *COI* and *16S rDNA*, extensively used in phylogenetic and DNA barcoding studies, to assess the  
41 evolutionary relationship among different egg-cowrie colorations and morphologies.

42 **Results.** No genetic divergence among egg-cowries associated to different species of the same  
43 octocoral genus was observed based on the two mitochondrial genes analyzed. For instance, all  
44 egg-cowrie individuals from the two sampled localities observed on 8 different *Pacificorgia-*  
45 *Eugorgia* species showed negligible mitochondrial divergence yet large morphologic divergence,

46 which suggests that morphologies belonging to at least two sea snail species, *Simnia avena* (=S.  
47 *aequalis*) and *Simnialena rufa*, can cross-fertilize.

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49 type, between egg-cowries (*Simnia/Simnialena*) and octocorals  
50 (*Pacifigorgia/Eugorgia/Leptogorgia*). We observed mimicry mismatches related to fitness trade-  
51 offs, such as reproductive aggregations vs. vulnerability against predators. Despite the general  
52 assumption that coevolution of mimicry involves speciation, egg-cowries with different hosts  
53 and colorations comprise the same lineages. Consequently, we infer that there would be  
54 significant tradeoffs between mimicry and the pursuit of reproductive aggregations in egg-  
55 cowries. The findings of this study not only contribute to the understanding of the evolution of  
56 mimicry in egg-cowries, a poorly studied group of marine gastropods, but also to the  
57 development of a new biologically meaningful board game that could be implemented as a  
58 learning tool.

59

60 **Key words:** Masquerade camouflage, mimicry, octocoral, *Pacifigorgia*, *Neosimnia*, *Simnia*  
61 *avena*, *Simnialena rufa*, Tropical Eastern Pacific, Chocó, Cabo Corrientes, Malpelo Island,  
62 Colombia, evolution games, mitochondrial DNA.

63

64 **Background**

65

66 Mimicry provides some of the most spectacular outcomes of adaptation and evolution. It is  
67 usually a successful adaptation, where background matching provides concealing from predators  
68 (Kjernsmo & Merilaita, 2012) or prey (Stevens & Merilaita, 2009). However, how mimicry is

69 achieved and maintained is not entirely understood. It should involve selection and species  
70 interactions through many generations, but the evolutionary process itself is difficult to test  
71 (Cuthill et al., 2005). Model species exhibiting polymorphisms leading to background  
72 mismatches, such as the peppered moth (Van't Hof et al., 2013), are extremely useful to fully  
73 understand the evolution and genetics of mimicry. As far we are aware of, no such model for  
74 marine organisms has been well described yet.

75

76 There are many remarkable examples of mimicry and camouflage in marine animals. In fishes,  
77 for instance, there are repeated cases of mimicry, protective resemblance, and crypsis (Randall,  
78 2005). Marine invertebrates such as egg-cowries (Ovulidae:Gastropoda) are recognized  
79 symbiotic snails of several kinds of cnidarians (Schiaparelli et al., 2005; Reijnen, Hoeksema &  
80 Gittenberger, 2010), whose coloration includes aposematic and camouflage patterns (Rosenberg,  
81 1992; Lorenz & Fehse, 2009). Egg-cowries and true cowries exhibit special structures on the  
82 mantle (compound papillae), which accurately reconstruct the polyps and other structures of  
83 cnidarians (Gosliner & Behrens, 1990; Schiaparelli et al., 2005). It is presumed that part of the  
84 camouflage ability in cowries is due to developmental plasticity (Rosenberg, 1992), though a  
85 genetic component could also be involved, presumably very variable among the different types  
86 of cowries (Vermeij, 2012). The case of camouflage strategy exhibited by egg-cowries is a clear  
87 example of adaptive resemblance (Starrett, 1993), and it can be classified as a kind of  
88 'masquerade'. It is a background matching mimicry where the subject is slightly different to the  
89 background but if it is only glimpsed at, it is not recognized as an edible subject different from  
90 the background (Endler, 2006; Stoddard, 2012). This is the case of the ovulids genera *Simnia* and

91 *Simnialena* associated to octocorals of the genera *Pacifigorgia*, *Eugorgia*, and *Leptogorgia* at the  
92 Tropical Eastern Pacific-TEP (Sánchez, 2013).

93

94 Octocorals comprise some of the most conspicuous benthic organisms at rocky infralittorals  
95 throughout the TEP. Sea fans, sea whips, and sea candelabrum corals are dominant features on  
96 hard substrates in this area, reaching densities between 2 and 30 colonies m<sup>-2</sup> (Sánchez et al.,  
97 2014). Compared with only one species in the Atlantic, sea fans (*Pacifigorgia* spp.) seem to be  
98 particularly fit for the TEP, where they add up to about 35 species in tropical and subtropical  
99 waters (Vargas, Guzman & Breedy, 2008). Although morphological differences among species  
100 are very subtle, the color pattern at various traits comprises most of the interspecific variation  
101 (Breedy & Guzman, 2002). This may impose an adaptive challenge for their associated fauna,  
102 since most crustaceans and cowries seen on *Pacifigorgia* spp. match their colors (J.A. Sánchez,  
103 personal observation).

104

105 In this research, we studied the association between *Simnia/Simnialena* and octocorals in a  
106 system that includes three octocorals (two seafans and one seawhip) present at the oceanic island  
107 of Malpelo, Colombia (Sánchez et al., 2012) and over 10 sympatric sea fan and sea whip species  
108 in Cabo Corrientes, a coastal locality in Chocó, Colombia (Sánchez & Ballesteros, 2014),  
109 including the closely related genera of *Pacifigorgia*, *Eugorgia* and *Leptogorgia*. Our study was  
110 inspired by the remarkable accuracy of the camouflage strategy of egg-cowries inhabiting  
111 different octocoral hosts at the TEP. Are these specialized ectoparasites matching the host  
112 species diversity? In other words, does one egg-cowrie species colonize only one octocoral  
113 species, or several? Using observations in the field and molecular systematics, we tested the



114 hypothesis whether egg-cowrie shell (color and shape) polymorphisms, that currently are  
115 categorized as distinct species, correspond to different lineages (most likely due to a  
116 coevolutionary process) or, alternatively, plasticity or any other mechanism for maintaining  
117 polymorphism in shape and coloration within an interbreeding population could explain the  
118 phenotypic diversity observed in this group. Given the mimicry specialization observed between  
119 egg-cowries and coral hosts at lower taxonomic levels (e.g., genera), data supporting this  
120 hypothesis may provide great insight on the link between micro and macro-evolution of  
121 background matching as a camouflage strategy.

122

123 The study of this rather simple but unique system may provide important data on how color  
124 polymorphisms could be retained in mimicry and may contribute to the understanding of the  
125 natural processes leading to camouflage adaptation in marine organisms. This study had two  
126 main goals: (1) the description of host preference of different color variants of egg-cowries found  
127 in different octocoral species and (2) an assessment of the phylogenetic relationship among egg-  
128 cowries with particular emphasis on those that share closely related octocoral hosts. We surveyed  
129 egg-cowries at two localities in the Colombian Pacific (Malpelo Island and Cabo Corrientes) and  
130 conducted multiyear, detailed preference observations in one of the two locations (Malpelo  
131 Island). Inspired in our observations, and in order to integrate our outreach strategy with our  
132 research, we developed a board game where evolutionary and ecological themes, such as natural  
133 selection and adaptation, are implicit. The ultimate goal of this game was to facilitate the  
134 understanding of evolutionary processes, such as adaptation and natural selection, through a  
135 ludic activity that could be easily implemented in a learning setting.

136

137

138 **Methods**

139

140 **Study areas.** Between 2009 and 2012 using SCUBA diving we surveyed two localities at the  
141 Colombian Pacific (Fig. 1), Malpelo Island and Cabo Corrientes. Malpelo Island (4°0'N-  
142 81°36'20"W, Fig. 1A) is an oceanic rock escarpment 500 km off the continental coast of  
143 Colombia, which has been declared a conservation-dedicated national sanctuary since 1995 and a  
144 UNESCO Heritage area since 2006 (Chasqui Velasco, Gil-Agudelo & Nieto, 2011). There are  
145 only two sea fan species in Malpelo Island, *Pacifigorgia cairnsi* (Breedy and Guzman 2003) and  
146 *Pacifigorgia cf. curta* (Breedy and Guzman 2003), which reach an average density of 4 colonies  
147 m<sup>-2</sup> between 5 and 30 m depth around the island rocky littorals (Sánchez et al., 2012). The two  
148 species serve as a camouflage background for egg-cowries (Sánchez, 2013). The sea whip  
149 *Leptogorgia alba* is present in areas below 20 m and it also carries egg-cowries. As with many  
150 isolated oceanic islands, Malpelo has several endemic species (5 terrestrial and 7 marine) and  
151 particular ecological conditions (López-Victoria & Werding, 2008) that provide a unique natural  
152 experimental setting to study evolution. Endemic fish species include the Rubinoff's triplefin  
153 *Axoclinus rubinoffi* and twinspace triplefin *Lepidonectes bimaculata*, potential predators of small  
154 invertebrate such as egg-cowries (Chasqui Velasco, Gil-Agudelo & Nieto, 2011). We surveyed  
155 and sampled two reefs around Malpelo Island (El Arrecife and La Nevera) (Fig. 1A). The other  
156 locality studied corresponds to Cabo Corrientes, in Chocó, at the Pacific coast of Colombia (Fig.  
157 1B). The environmental conditions in this area are quite different compared to Malpelo Island  
158 due to constant run-off from one of the most humid areas in the world, yet, the octocoral  
159 community in this rocky region is more diverse than in Malpelo (Barrero-Canosa, Dueñas &

160 Sánchez, 2012). There are at least 10 octocoral species including mostly sea fans (*Pacifigorgia*)  
161 and a few species of *Leptogorgia* and *Eugorgia*, which all carry associated egg-cowries. The  
162 octocoral community has been recently affected by the invasive snow flake coral *Carijoa riisei*,  
163 which has decimated octocoral diversity including near local extinction of some octocorals such  
164 as *Muricea* spp. (Sánchez & Ballesteros, 2014). In Malpelo Island as well as in Cabo Corrientes,  
165 water temperature usually does not exceed 27 °C but there is a marked upwelling season between  
166 February and April, when water temperature can be as low as 17 °C (Sánchez et al., 2014).

167

168 **Host preference observations.** In 2008, 2009, and 2010 we surveyed four reefs at Cabo  
169 Corrientes (Roñosa, Piedra Bonita, Parguera, and Caló) (Fig. 1B). Observations and collection of  
170 egg-cowrie specimens on octorals were carried out for at least a 30 minutes dive per site per  
171 year. Sampling effort and observations in Malpelo Island were more intensive. Between 2009  
172 and 2010 two divers using SCUBA carried out egg-cowries and hosts surveys twice a year at the  
173 reefs El Arrecife and La Nevera (Malpelo Island) between 5 and 35 m depth, where permanent  
174 transects and tags for 174 *Pacifigorgia* colonies eased the biannual observations. Despite the  
175 high density of *Pacifigorgia* sea fans encountered in these surveys (Sánchez et al., 2012), the  
176 presence of egg-cowries and their encapsulated ovopositions were inconsistently and rarely  
177 spotted. Since some of the surveys were repeated at the same locations and depths, we realized  
178 that egg-cowries exhibit a gregarious pattern. In addition, our quantitative method, though fast  
179 and representative for surveying sea fans, was inaccurate for spotting *Simnia/Simnialena* egg-  
180 cowries and ovopositions given their small size and camouflage, which makes them very  
181 difficult to detect by eye in short surveys. Consequently, one more diver was added to the survey  
182 team in 2012 and 2013, whose main goal was thoroughly search for egg-cowries on sea fans

183 behind the divers surveying *Pacifigorgia* following the same tagged colonies. This method  
184 offered accurate information on their temporal, depth, and host preferences, including  
185 ovoposition. Most egg-masses were recorded with digital macro images (Nikon™ D7000,  
186 Nikkor micro 60 mm lens, Sea & Sea™ YS-D1 strobe and Aquatica™ AD7000 housing).

187

188 **Taxonomic identification and molecular phylogeny reconstruction of egg-cowries.** We  
189 collected complete individuals of egg-cowries and tissue samples of their octocoral hosts  
190 (Research permit No. 105 (2013), Autoridad Nacional de Licencias Ambientales-ANLA,  
191 Ministerio de Ambiente y Desarrollo Sostenible, Colombia). All samples were preserved  
192 separately in 96% ethanol and stored in the laboratory at -20 °C. We obtained a merged image of  
193 the dorsal and ventral view of each snail shell using a stereo-microscope camera and the software  
194 CombineZP (last accessed on October 5, 2015, [www.hadleyweb.pwp.blueyonder.co.uk](http://www.hadleyweb.pwp.blueyonder.co.uk)).  
195 Identification of egg-cowries to the lowest taxonomic level possible was achieved following the  
196 descriptions by Lorenz & Fehse, 2009 and Cate, 1973. For the octocorals we compared the  
197 vouchers with previously identified material deposited in the Museo de Historia Natural of the  
198 Universidad del los Andes (Sánchez et al., 2012, 2014). Total genomic DNA of each specimen  
199 was extracted from about 5 mm<sup>2</sup> of tissue following a standard CTAB  
200 Phenol:Chloroform:Isoamyl Alcohol protocol (Coffroth et al., 1992). DNA quality was assessed  
201 in 1% agarose gel electrophoresis in 1X TBE buffer. Gels were dyed with ethidium bromide and  
202 visualized in a Gel Doc™ XR (Biorad, U.S.). An approximate estimation of concentration in ng  
203 µl<sup>-1</sup> and purity (260/280 and 260/230 ratios) of each DNA sample was assessed with a NanoDrop  
204 (Thermo Scientific, U.S.). We amplified the egg-cowries' mitochondrial genes cytochrome  
205 oxidase I (*COI*) and ribosomal large sub-unit (*16S*) using the primer pairs COI HCO-2198 (5'-

206 TAA ACT TCA GGG TGA CCA AAA ATC A -3') and LCO-1490 (5'- GGT CAA CAA ATC  
207 ATA AAG ATA TTG G -3') (Folmer, O., M. Black, W. Hoeh, R. Lutz y R. Vrijenhoek, 1994),  
208 and 16S-br (5'- CCG GTC TGA ACT CAG ATC ACG T -3') and 16S-ar (5'- CGC CTG TTT  
209 ATC AAA AAC AT -3') (Palumbi, 1996). PCR reactions were performed in a C1000  
210 Thermocycler (Biorad, U.S.). All PCR reactions had a final volume of 15 µl including 1X buffer,  
211 3.5 mM of MgCl<sub>2</sub>, 0.2 mM dNTPs, 0,8 µg/µl of Bovine Serum Albumin, 1 µM of each primer,  
212 1U of *Taq* polymerase, and 1-20 ng/µl of total DNA; the PCR profile started with an initial  
213 denaturation at 94°C for 5 min., 35 cycles at 94 °C for 1 min., 44 °C for 30 sec. and 72 °C for 1  
214 min., with final extension at 72 °C for 7 min. PCR products were verified in 1.3% agarose gel  
215 electrophoresis in 1X TBE buffer; expected size of the amplified DNA regions were 710 bp for  
216 *COI* and 570 bp for *16S*. Contaminants remaining in the PCR products were removed following  
217 an alcohol-EDTA cleaning protocol. Sense and antisense strains of each amplified DNA region  
218 were sequenced using a Biosystems BigDye 3.1 kit and a capillary electrophoresis automated  
219 sequencer AB310 (Applied Biosystems). Raw electropherograms were checked visually using  
220 the software Geneious v4.8 (Drummond et al., 2009). Contigs and consensus sequences of each  
221 gene were also obtained using Geneious v4.8. We verified the overall taxonomic identity of the  
222 obtained sequences with the Basic Local Alignment Search Tool, BLAST (NCBI, U.S.).  
223 Sequence alignment, concatenation, and phylogenetic analyses were done in Geneious v8.0.4,  
224 including the implemented packages for maximum parsimony (PAUP\*), maximum likelihood  
225 (RAxML) and Bayesian inference (MrBayes), the last two analyses using the GTR model of  
226 sequence evolution as recommended by RAxML (Stamatakis, 2015) and default settings for  
227 getting 1000 replicates of bootstrapping node support. A sequence from the Caribbean flamingo  
228 tongue (*Cyphoma gibbosum*:Ovulidae) was included as outgroup.

229

### 230 **Integrated outreach: The masquerade game**

231 Inspired by the results obtained in this study, as well as on some elements of the classroom kits  
232 from the California Academy of Sciences, the “Coral Reef: Science and Conservation Game-  
233 The fragile coral reef (grades 3-7)” (Teaching and Student Services, 2008), we conceived a board  
234 game based on the mimicry adaptation of egg-cowries to coral hosts, which we think is useful for  
235 illustrating evolution and ecology concepts (see Supplementary Material for details and a game  
236 kit).

237

### 238 **Results**

#### 239 **Host preference in egg-cowries**

240 Egg-cowries in Cabo Corrientes and Malpelo Island colonized all surveyed octocoral species of  
241 *Leptogorgia*, *Pacifigorgia* and *Eugorgia* (Table 1, Figs. 2-3). Large (>10 individuals)  
242 reproductive aggregations were observed on *Pacifigorgia irene*, one of the most abundant sea  
243 fans at Cabo Corrientes (Fig 2A). Overall, all collected egg-cowries matched their mantle color  
244 pattern with those of the octocoral host; the shape and color of the snails associated to  
245 *Pacifigorgia* and *Eugorgia* were noticeably different respect to the snails associated to  
246 *Leptogorgia*, the first showing a red-purplish robust shell and the latter a white-pinkish elongated  
247 shell (Fig. 2).

248

249 Detailed observations at Malpelo Island revealed that about 10% of the 174 tagged colonies have  
250 at least one egg-cowrie and 4% can have an ovoposition, which corresponded to roughly 0.01  
251 and 0.04 egg-cowries or ovopositions per square meter assuming a seafan density of 4 col m<sup>-2</sup>

252 (Sánchez et al., 2012). Egg-cowries display a nearly perfect ‘masquerade’ background, matching  
253 the appearance of the sea fan *Pacifigorgia* by having polyp-like structures coming off the  
254 gastropod mantle (Fig. 3). There are only two species of sea fans in the infralittoral region of  
255 Malpelo Island, one has a red coenenchyme (octocoral branch tissue) with white polyps  
256 (*Pacifigorgia cairnsi*) and the other one has a blue-purplish coenenchyme with white, pink, or  
257 orange polyps (*Pacifigorgia cf. curta*). We observed that *Pacifigorgia cf. curta* egg-cowries  
258 match the background of the three polyp types present in these sea fans (Fig. 3A-C). The polyps  
259 of the sea fans are active most of the day, but when they are not, the sea fan background changes  
260 to the color of the coenenchyme. In this case egg-cowries have to retract their mantle and the  
261 color of their shell provides mimicry. In the 174 tagged colonies, we observed less than 5  
262 mismatches between shell color and coenenchyme color and those individuals usually moved  
263 towards the base of the colony. Other mismatches were observed during the reproductive period.  
264 The background matching of egg-cowries also included the color of the ovoposition, which is  
265 deposited as encapsulated eggs on sea fan branches (Fig. 4A-C). In this trait, mismatches were  
266 commonly seen during group mating at the zone of interaction of the two seafan species (Fig.  
267 4A-C). This behavior could increase the chance of interbreeding among different egg-cowries  
268 species associated to a similar type of octocoral. In Malpelo Island group ovopositions were  
269 observed in July, March, and November. The two sea fan species in Malpelo Island are usually  
270 distributed at different depth ranges (*Pacifigorgia cf. curta* shallow, 3-10 m, and *P. cairnsi* deep,  
271 10-30 m). We observed that snails with background mismatches were present at the boundary  
272 where the distribution of the sea fan species (*Pacifigorgia cairnsi* and *P. cf. curta*) coincide, or in  
273 overlapping areas where they coexist.  
274

275 Given our observations of the egg-cowries natural history, we can hypothesize that background  
276 matching is under selection because there are many potential natural predators that can take  
277 advantage of mismatches. For instance, hawkfishes, predators of small invertebrates (Froese &  
278 Pauly, 2015), were frequently seen near sea fan colonies with egg-cowries (Fig. 5A-B). The  
279 longnose hawkfish (*Oxycirrhites typus*) is adapted to hunt small invertebrates found on octocoral  
280 and black coral branches and comes in close contact with egg-cowries as it also settles on sea  
281 fans (Fig. 5A). The coral hawkfish (*Cirrhitichthys oxycephalus*) also patrols for small prey on the  
282 substrate in close contact with sea fans (Fig. 5B). Although these fish do not have a fixed  
283 territory, they spend enough time around sea fans to spot and take advantage of mismatched  
284 cowries.

285

286 Our observations suggest that color variants of egg-cowries could move freely throughout the  
287 two *Pacificorgia* species in the island. Sea fans of these two species were as near as 1-5 mm  
288 from each other at their overlapping depth interval (4-10 m). This implies that egg-cowries could  
289 go from one colony to another without leaving their hosts. Given the abundance of predators,  
290 there should be a trade-off between reproduction and protection against predation in egg-  
291 cowries.

292

293 We observed additional threats to egg-cowries survival related to habitat destruction, i.e., sea fan  
294 mortality. During the years of this survey (2009-2012) two sources of sea fan mortality were  
295 noted in Malpelo Island, fungal diseases and an invasive coral overgrowth. Mass mortalities  
296 were observed during 2009 and 2010, sometimes reaching 70% of sea fans (Sánchez et al.,  
297 2012). Affected colonies had the epizootiology of the fungal disease aspergillosis (Fig. 5C) that



298 has been recently detected elsewhere in the TEP (Barrero-Canosa, Dueñas & Sánchez, 2012). At  
299 two locations in Malpelo Island, ‘submarino’ (western most point of ‘La Nevera’) and some  
300 isolated rocky islets off the main island (‘La Catedral’), large infra-littoral areas are completely  
301 covered by the snowflake coral *Carijoa riisei* (Fig. 5D). This is an invasive octocoral presumably  
302 brought from the Western Atlantic, which overgrows and kills sea fans in Malpelo Island and  
303 elsewhere in the TEP (Sánchez & Ballesteros, 2014). Though egg-cowries were seen on sea fan  
304 colonies affected by these two stressors, most of them were observed on healthy ones.

305

### 306 **Morphologic and Molecular identification**

307 Egg-cowrie surveys revealed a species complex including the nominal species *Simnia avena*= *S.*  
308 *aequalis* (G.B. Sowerby II, 1832) fide Lorenz & Fehse (2009) and, *Simnialena rufa*=*Simnia*  
309 *inflexa* (G.B. Sowerby II, 1832) fide Cate (1973) and Lorenz & Fehse (2009). The *S. avena*  
310 morphology was observed on most *Pacifigorgia*, *Leptogorgia* and *Eugorgia* at Cabo Corrientes,  
311 whereas *Simnialena rufa* was observed on *Pacifigorgia* sea fans in Malpelo Island. (Table 1).  
312 Figure 6 shows the typical morphology of the two nominal egg-cowrie species observed in the  
313 Colombian Pacific. In general we encountered challenges in the taxonomic identification of egg-  
314 cowries, either because there is not a unified and updated taxonomic key for this group or due to  
315 the presence of intermediate morphologies. For instance, egg-cowries in Malpelo Island clearly  
316 looked like *S. rufa* when found on *Pacifigorgia* cf. *curta* and more like *S. avena* on *P. cairnsi*.

317

318 A phylogenetic analysis based on the sequence of the mitochondrial genes *COI* and *16S* showed  
319 two well supported clades for all the surveyed egg-cowries (Fig. 7). One clade comprised *S.*  
320 *avena* specimens associated to *Leptogorgia* spp and the other one included egg-cowries found on

321 *Eugorgia* and *Pacifigorgia*, both in Cabo Corrientes and Malpelo Island (Table 1). Within each  
322 clade there was neither well-supported sub-clades nor significant sequence divergence (Fig. 7).  
323 This result supports the assumption of an important role of developmental plasticity on the  
324 variation of camouflage patterns within egg-cowries species.

325

326

### 327 **Discussion**

328

329 Egg-cowries at the Colombian Pacific exhibit a remarkable camouflage strategy, in a  
330 masquerade fashion, mimicking over a dozen of octocoral hosts. The negligible genetic  
331 divergence observed within clades, that included multiple species and occasionally genera,  
332 suggests that developmental plasticity should play an important role on the determination of their  
333 delicate masquerade camouflage. Though the remarkable mimicry of egg-cowries has been  
334 previously studied, we found no former record on background matching for the encapsulated  
335 eggs nor the observed ovoposition mismatches at the zone of interaction of similar sea fan hosts.  
336 The main contribution of our natural history observations relies on the recognition of tradeoffs  
337 between mimicry and the pursuit of reproductive aggregations in egg-cowries.

338

339 Previous phylogenetic studies in Ovulidae provide a good framework to situate the evolutionary  
340 tempo among TEP egg-cowries. At a large phylogenetic scale, including several Ovulidae  
341 genera, cowries show some degree of host specialization within Anthozoa yet several  
342 morphologic traits used in taxonomy are polyphyletic (Schiaparelli et al., 2005). Likewise, there  
343 is a marked phylogenetic split between Indopacific and Atlantic Ovulidae; still, many groups at

344 each ocean lacked phylogenetic differentiation (Reijnen, Hoeksema & Gittenberger, 2010;  
345 Reijnen, 2015). Consequently, the paucity of genetic divergence among egg-cowries from  
346 closely related octocorals, as seen in our results, is not surprising.

347

348 Mitochondrial DNA genes, such as *COI*, have been extensively used for the taxonomic  
349 identification of mollusks, including ovulids, from different parts of the world (Layton, Martel &  
350 Hebert, 2014; Borges et al., 2016). For cowries, sister group of egg-cowries, *COI* barcoding has  
351 shown a species identification error between 4 and 17% (Meyer & Paulay, 2005). Whereas for  
352 the egg-cowries, *Crenavolva* spp., *COI* and *16S*, the same mtDNA genes used in this study,  
353 provided enough support for species differentiation and reviewing of the taxonomy of the genus  
354 (Reijnen, 2015). The modest phylogenetic divergence of the studied egg-cowries suggests a key  
355 role of phenotypic plasticity in the morphological variation.

356

357 Among the consequences of highly specialized parasitism and mimicry of the masquerade type is  
358 coevolution with their host. The case of egg-cowries is a nearly perfect masquerade to their  
359 octocoral hosts. Just in Malpelo Island there are at least four different color patterns in sea fan  
360 polyps that were matched by the egg-cowries. How did the same interbreeding population  
361 achieve this color variation? Our observations suggest that reproductive aggregation is a priority  
362 over concealment from predators and more importantly, regardless of the mates' color. This  
363 behavior is similar to what has been seen in the aposematic ovulid *Cyphoma gibbosum* for  
364 choosing among octocoral hosts (Nowlis, 1993). In addition, this supports the notion that  
365 conservation of polymorphisms in this trait would promote faster adaptation. Isolation with gene  
366 flow between different colorations of egg-cowries could contribute to maintain color  
367 polymorphism, which would promote faster background matching adaptation (Gray &

368 McKinnon, 2007). However, the question of how much of the camouflage ability is due to  
369 developmental plasticity in response to the environment (host) and how much is due to adaptive  
370 genetics (Rosenberg, 1992) remains unsolved.

371

372 The link between phenotypic plasticity and diversification processes remains one of the major  
373 questions in evolutionary biology (West-Eberhard, 2003; Fitzpatrick, 2012). Phenotypic  
374 plasticity provides the adaptive canvas for further adaptation and speciation. Yet, could  
375 phenotypic plasticity promote ecological speciation? Phenotypic plasticity could impede  
376 diversification since a single genotype is supposed to give rise to different phenotypes, as we  
377 observed in egg-cowries associated to sea fans. We assume phenotypic plasticity is allowing egg-  
378 cowries to colonize many hosts in the TEP, for which specialization resembles adaptive  
379 divergence or even radiation (Pfennig et al., 2010). Given the potential occurrence of mating  
380 among different egg-cowrie morphotypes, a detailed analysis of their adaptive genetic variation  
381 using more powerful molecular approaches would be necessary. We consider that the  
382 *Simnia/Simnialena* complex may constitute an ideal marine system to study and test this  
383 question.

384

385

## 386 **Conclusions**

387 Our study system comprised background-matching mimicry, of the masquerade type, between  
388 egg-cowries (*Simnia/Simnialena*) and octocorals (*Pacifigorgia/Eugorgia/Leptogorgia*). The  
389 ovoposition of the different egg-cowrie color variants also matches the host color. Egg-cowries  
390 with different color patterns but associated to similar octocoral hosts can indistinctively gather

391 for reproductive aggregations in Malpelo Island, which was consistent with their negligible  
392 phylogenetic divergence. Egg-cowries show background mismatches in ovoposition, which  
393 constitute a particular event that could help to understand how selection operates to refine  
394 mimicry traits and promote adaptation. These novel observations inspired us to develop a  
395 biologically meaningful game that could facilitate the teaching and learning process of ecology  
396 and evolution in the classroom as well as in outreach activities, while increasing the awareness  
397 and connection of students with their environment. We invite the readers to play and share this  
398 game, available in the supplementary material.

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405 Ballesteros, Carlos E. Gómez, Fabio Casas, Lina Gutierrez, Elena Quintanilla and Dairo Escobar  
406 among others. We appreciate the comments from our reviewers, Joana Robalo and an anonymous  
407 reviewer that greatly improved the manuscript. We recognize the participation and support from  
408 local communities in Cabo Corrientes.

409 **Table 1.** Egg-cowrie specimen information including sample label, collection date, the putative morphologic identification, location  
 410 and site of collection, depth of collection and coral host, and Genbank accession numbers for *16S* and *COI* sequences.

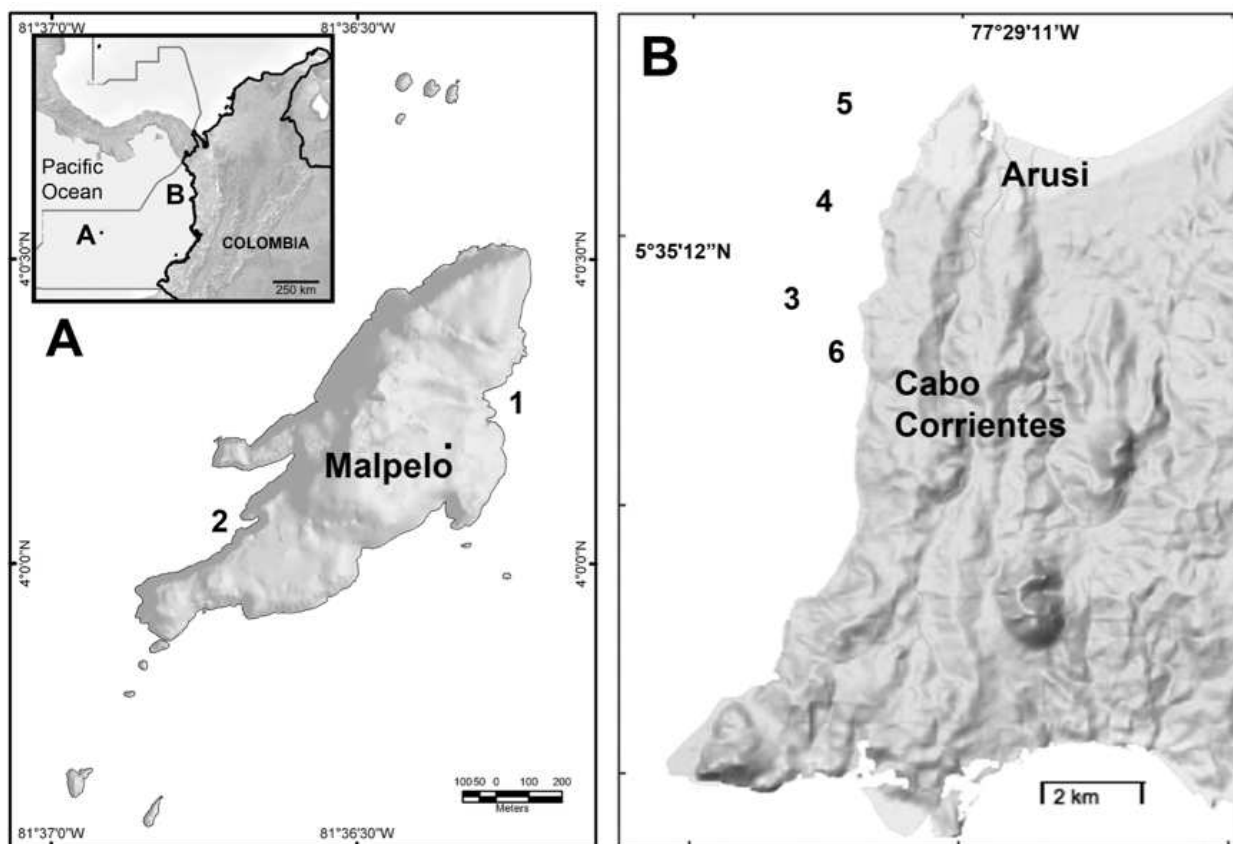
Sample label	Collection date	Morphologic ID	Location	Site	Depth (m)	Coral host species	<i>16S</i>	<i>COI</i>
<b><i>Pacifigorgia – Eugorgia clade</i></b>								
K136	19-Apr-11	<i>Simnia</i> sp.	Cabo Corrientes	Caló	15	<i>Pacifigorgia sculpta</i>	KU557467	KU557450
K175	16-Apr-11	<i>Simnia avena</i>	Cabo Corrientes	Roñosa	15	<i>P. stenobrochis</i>	KU557469	KU557452
K191	16-Apr-11	<i>Simnia avena</i>	Cabo Corrientes	Piedra Bonita	10	<i>P. eximia</i>	KU557470	KU557453
K193	16-Apr-11	<i>Simnia avena</i>	Cabo Corrientes	Roñosa	12	<i>Pacifigorgia</i> sp.	KU557471	KU557454
K237	19-Apr-11	<i>Simnia avena</i>	Cabo Corrientes	Caló	15	<i>P. stenobrochis</i>	KU557472	KU557455
Y098	26-Feb-11	<i>Simnialena rufa</i>	Malpelo Island	La Nevera	10	<i>P. cairnsi</i>	KU557473	KU557456
Y100	26-Feb-11	<i>Simnialena rufa</i>	Malpelo Island	La Nevera	10	<i>Pacifigorgia</i> sp. cf. <i>curta</i>	KU557474	KU557457
Y101	26-Feb-11	<i>Simnialena rufa</i>	Malpelo Island	La Nevera	10	<i>P. cairnsi</i>	KU557475	KU557458
Y109	26-Feb-11	<i>Simnialena rufa</i>	Malpelo Island	El Arrecife	15	<i>P. cairnsi</i>	KU557476	KU557459
Y183	18-Apr-11	<i>Simnia avena</i>	Cabo Corrientes	Piedra Bonita	12	<i>Pacifigorgia</i> sp.	KU557477	KU557460
Y185	18-Apr-11	<i>Simnia</i> sp.	Cabo Corrientes	Piedra Bonita	12	<i>Pacifigorgia</i> sp.	KU557478	KU557461
Y188	18-Apr-11	<i>Simnia avena</i>	Cabo Corrientes	Roñosa	10	<i>Eugorgia daniana</i>	KU557479	KU557462
Y197	18-Apr-11	<i>Simnia avena</i>	Cabo Corrientes	Piedra Bonita	12	<i>Pacifigorgia</i> sp.	KU557480	KU557463
Y199	18-Apr-11	<i>Simnia</i> sp.	Cabo Corrientes	Piedra Bonita	12	<i>P. eximia</i>	KU557482	KU557465
<b><i>Leptogorgia clade</i></b>								
K116	17-Apr-11	<i>Simnia avena</i>	Cabo Corrientes	Parguera 7	12	<i>Leptogorgia alba</i>	KU557466	KU557449
K168	16-Apr-11	<i>Simnia avena</i>	Cabo Corrientes	Roñosa	5	<i>L. ramulus</i>	KU557468	KU557451

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Y198	18-Apr-11	<i>Simnia avena</i>	Cabo Corrientes	Piedra Bonita	12	<i>Leptogorgia alba</i>	KU557481	KU557464
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412 **Figures**

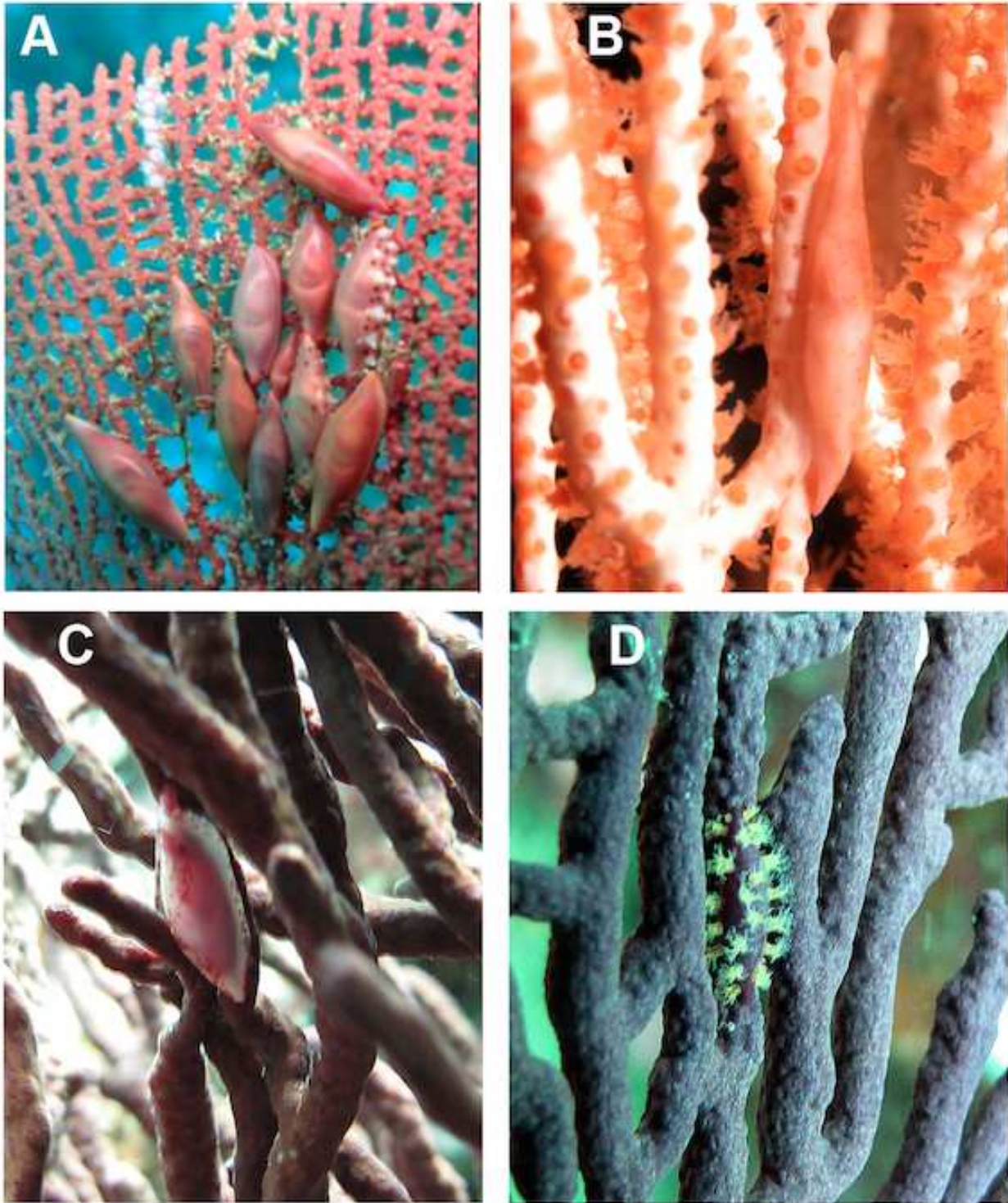


413

414 **Figure 1.** Study sites at the Colombian Pacific. A. Malpelo Island (1. El Arrecife; 2. La Nevera).

415 B. Cabo Corrientes, Chocó (3. Roñosa; 4. Piedra Bonita; 5. Parguera 7; 6. Caló).



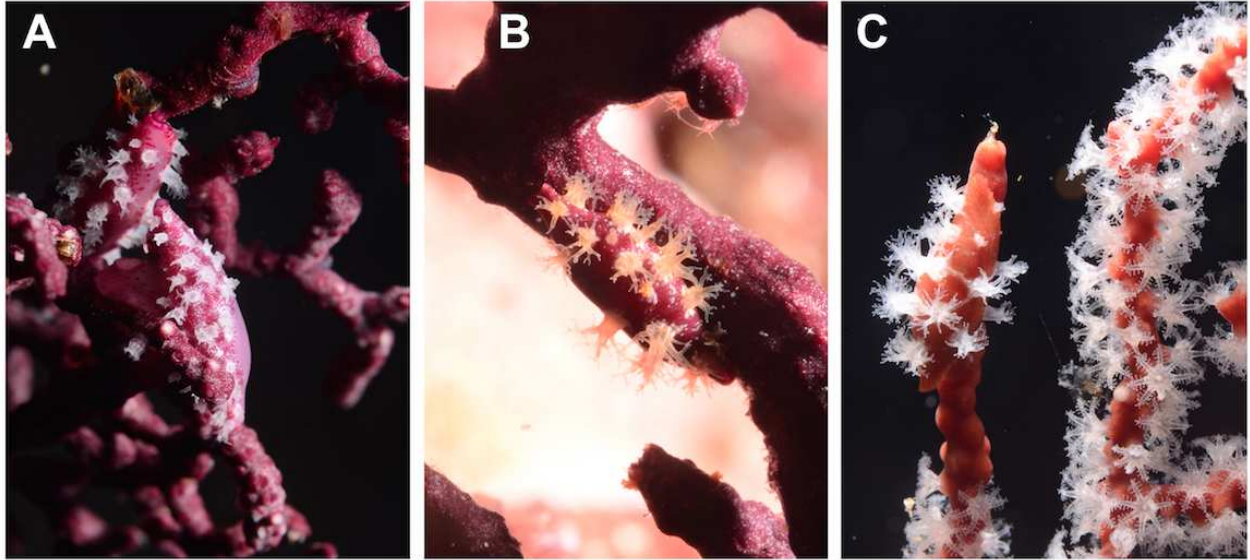


416

417 **Figure 2.** Egg-cowries (Ovulidae) observed in the Colombian Pacific (A, C and D in Cabo

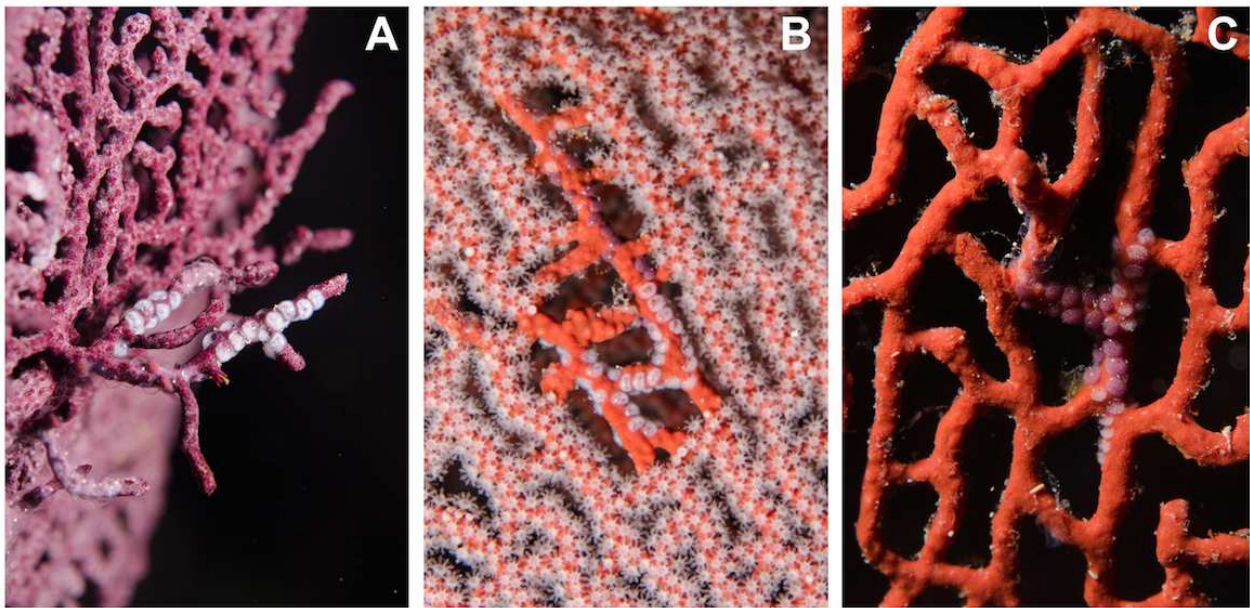
418 Corrientes, Chocó; B Malpelo Island). Coral hosts: A. *Pacifigorgia irene* (depth 12 m), B.

419 *Leptogorgia alba* (25 m) (Malpelo Island). C. *L. ramulus* (5 m). D. *P. stenobrochis* (15 m).



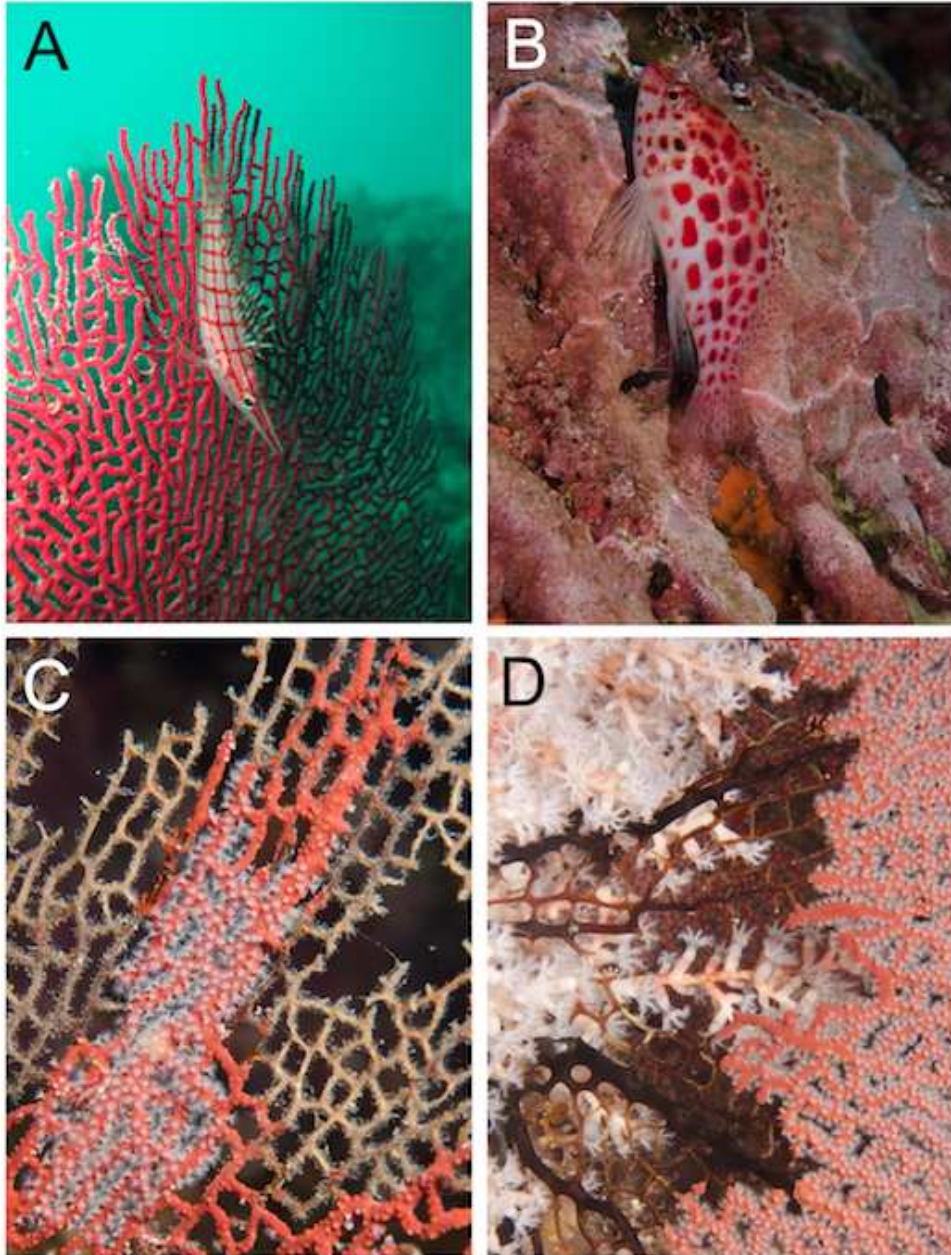
420

421 **Figure 3.** Egg-cowrie *Simnia avena* on *Pacifigorgia cairnsi* and *P. cf. curta* at Malpelo Island,  
 422 Colombian Pacific. (A) *S. avena* on *P. cf. curta* -white polyps; (B) *S. avena* on *P. cf. curta* -  
 423 orange polyps; (C) *S. avena* on *P. cairnsi*.



424

425 **Figure 4.** Mixed ovopositions (white and purple) left by the cowrie *Simnia avena* on sea fans at  
 426 Malpelo Island, Colombian Pacific. Pacific. A. Mixed ovoposition on purple background,  
 427 *Pacifigorgia cf. curta*; (B-C) mixed ovoposition on red background, *P. cairnsi*.



428

429 **Figure 5.** Potential threats to *Simnia* egg-cowries at Cabo Corrientes and Malpelo Island, Eastern

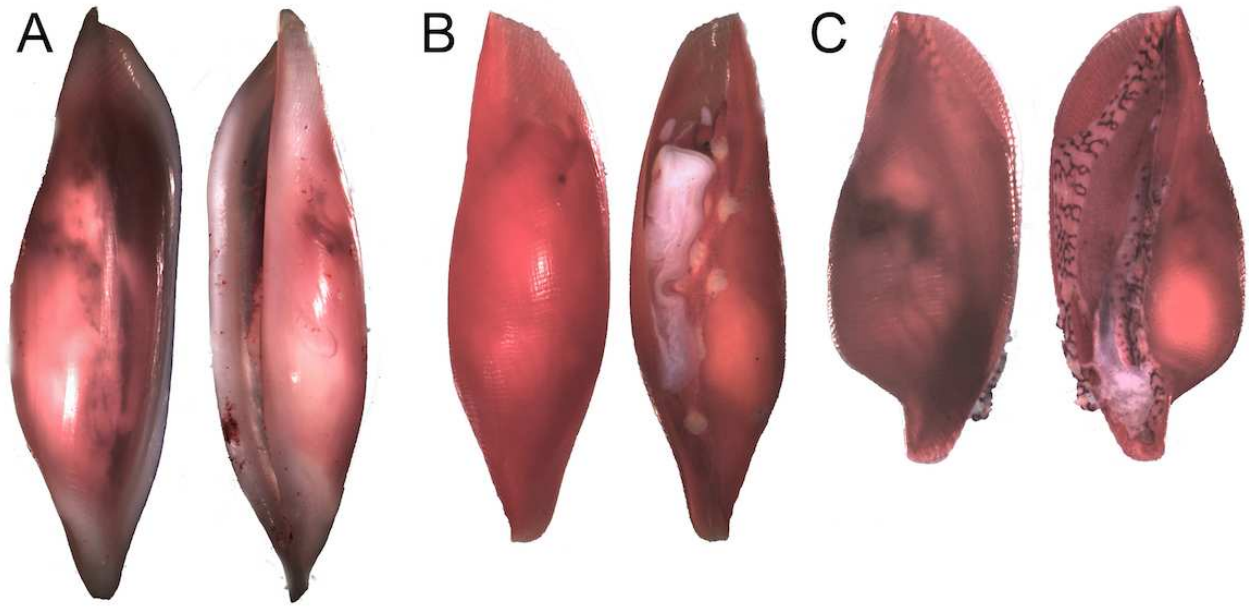
430 Tropical Pacific, Colombia. (A) Longnose hawkfish *Oxycirrhites typus* with a sea fan-like

431 background camouflage (Cabo Corrientes); (B) Coral hawkfish *Cirrhitichthys oxycephalus*; (C)

432 Diseased sea fan *Pacifigorgia cairnsi*; (D) The invasive snowflake coral, *Carijoa riisei*,

433 overgrowing *P. cairnsi* (B-D Malpelo Island).

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435

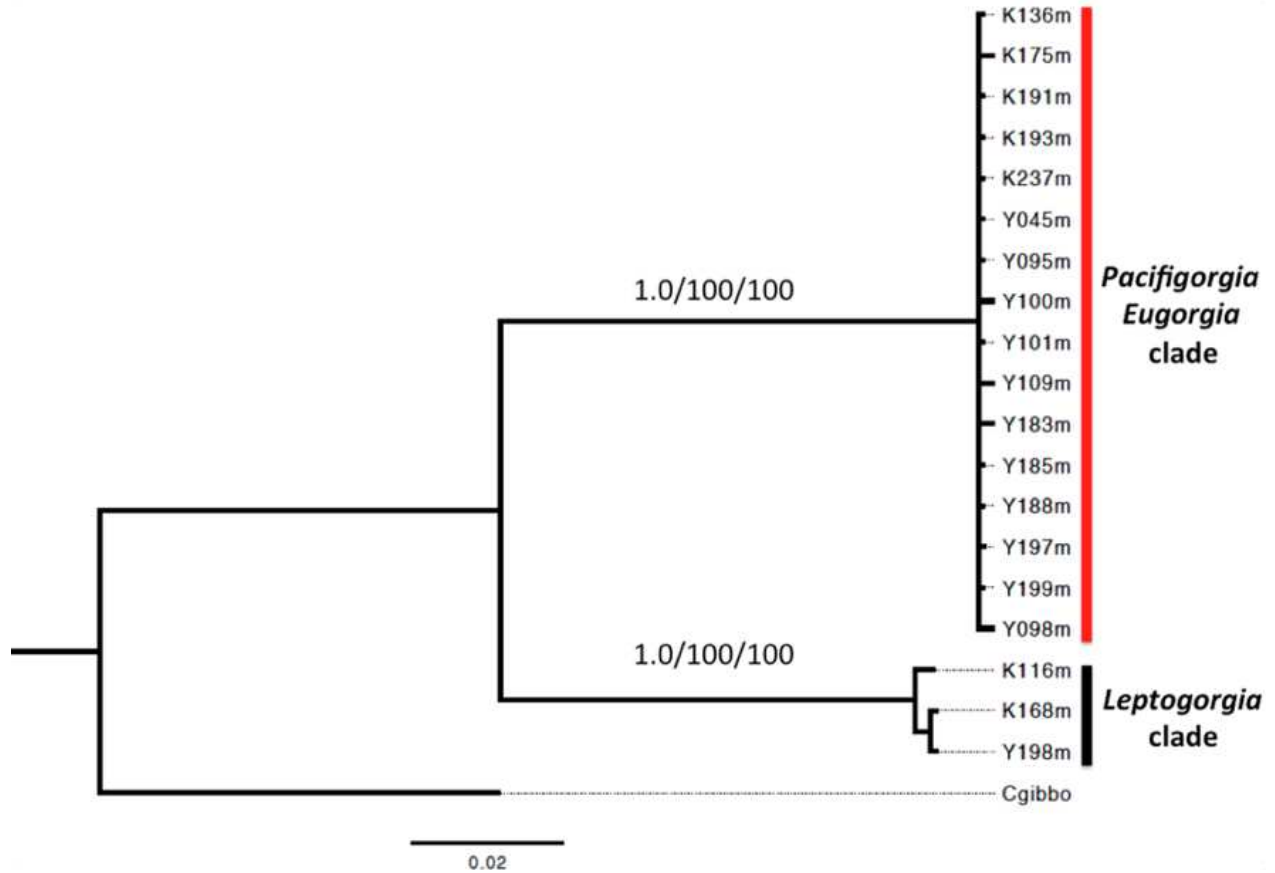
436 **Figure 6.** Distinct shell morphologies found in egg-cowries at the Colombian Pacific. A. *Simnia*

437 *avena*, adult specimen K168 found on *Leptogorgia ramulus* at Cabo Corrientes, 12.6 mm (max

438 length). B. *Simnia avena*, juvenil specimen K191 found on *Pacifigorgia eximia*, Cabo

439 Corrientes, 5.8 mm. C. *Simnialena rufa*, Y100, on *Pacifigorgia cf. curta*, Malpelo Island, 4 mm.

440



441

442 **Figure 7.** Bayesian inference phylogram using concatenated 16S and COI mitochondrial  
 443 sequences. Above node support are presented for 1000-replicates bootstrapping values >0.7  
 444 (Bayesian posterior probabilities) and >70% maximum parsimony/maximum likelihood.

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453 **References**

454

455 Bandel K. 1973. Notes on *Cypraea cinerea* Gmelin and *Cyphoma gibbosum* (Linnaeus) from  
456 the Caribbean Sea and description of their spawn. *Veliger* 15:335–337.

457 Barrero-Canosa J., Dueñas LF., Sánchez JA. 2012. Isolation of potential fungal pathogens in  
458 gorgonian corals at the Tropical Eastern Pacific. *Coral Reefs* 32:35–41. DOI:

459 10.1007/s00338-012-0972-2.

460 Béarez P., Bujard J-T., Campoverde R. 2007. Description of four small reef fishes from

461 Ecuador: *Oxycirrhites typus* (Cirrhitidae), *Acanthemblemaria balanorum*

462 (Chaenopsidae), *Arcos decoris* (Gobiesocidae) and *Lythrypnus dalli* (Gobiidae).

463 *Cybiurn* 31:477–479.

464 Borges LM., Hollatz C., Lobo J., Cunha AM., Vilela AP., Calado G., Coelho R., Costa AC.,

465 Ferreira MS., Costa MH. 2016. With a little help from DNA barcoding: investigating

466 the diversity of Gastropoda from the Portuguese coast. *Scientific Reports* 6.

467 Breedy O., Guzman HM. 2002. A revision of the genus *Pacifigorgia* (Coelenterata:

468 Octocorallia: Gorgoniidae). *Proceedings of the Biological Society of Washington*

469 115:782–839.

470 Calcinaï B., Bavestrello G., Cerrano C. 2004. Dispersal and association of two alien species in

471 the Indonesian coral reefs: the octocoral *Carijoa riisei* and the demosponge

472 *Desmapsamma anchorata*. *Journal of the Marine Biological Association of the United*

473 *Kingdom* 84:937–941.

474 Cate CN. 1973. *A systematic revision of the recent cypraeid family ovulidae (Mollusca:*

475 *Gastropoda)*. California Malacozoological Society.

476 Chasqui Velasco L., Gil-Agudelo DL., Nieto R. 2011. Endemic shallow reef fishes from  
477 Malpelo island: abundance and distribution. *Boletín de Investigaciones Marinas y*  
478 *Costeras-INVEMAR* 40:107–116.

479 Coffroth MA., Lasker HR., Diamond ME., Bruenn JA., Bermingham E. 1992. DNA fingerprints  
480 of a gorgonian coral: A method for detecting clonal structure in a vegetative species.  
481 *Marine Biology* 114.

482 Cuthill IC., Stevens M., Sheppard J., Maddocks T., Párraga CA., Troscianko TS. 2005.  
483 Disruptive coloration and background pattern matching. *Nature* 434:72–74.

484 Drummond AJ., Ashton B., Cheung M., Heled J., Kearse M., Moir R., Stones-Havas S., Thierer  
485 T., Wilson A. 2009. Geneious 4.8. *Biomatters, Auckland, New Zealand*.

486 Endler JA. 2006. Disruptive and cryptic coloration. *Proceedings of the Royal Society B:*  
487 *Biological Sciences* 273:2425–2426.

488 Fitzpatrick BM. 2012. Underappreciated consequences of phenotypic plasticity for  
489 ecological speciation. *International Journal of Ecology* 2012.

490 Folmer, O., M. Black, W. Hoeh, R. Lutz y R. Vrijenhoek R. 1994. DNA primers for  
491 amplification of mitochondrial cytochrome c oxidase subunit I from diverse  
492 metazoan invertebrates. *Molecular marine biology and biotechnology* 3:294–299.

493 Froese R., Pauly D. 2015. Fish Base. *World Wide Web, Electronic Publication*. [http://www.](http://www.fishbase.org)  
494 [fishbase.org](http://www.fishbase.org).

495 Gosliner TM., Behrens DW. 1990. Special resemblance, aposematic coloration and mimicry  
496 in opisthobranch gastropods. *Adaptive coloration in invertebrates*. *Texas A&M*  
497 *University Sea Grant College Program, College Station*:127–138.

498 Gray SM., McKinnon JS. 2007. Linking color polymorphism maintenance and speciation.  
499 *Trends Ecol Evol* 22:71–9. DOI: 10.1016/j.tree.2006.10.005.

500 Kjernsmo K., Merilaita S. 2012. Background choice as an anti-predator strategy: the roles of  
501 background matching and visual complexity in the habitat choice of the least  
502 killifish. *Proceedings of the Royal Society B: Biological Sciences*:rsob20121547.

503 Layton KK., Martel AL., Hebert PD. 2014. Patterns of DNA barcode variation in Canadian  
504 marine molluscs. *PloS one* 9:e95003.

505 Long DE. 2012. The politics of teaching evolution, science education standards, and being a  
506 creationist. *Journal of Research in Science Teaching* 49:122–139.

507 López-Victoria M., Werding B. 2008. Ecology of the Endemic Land Crab *Johngarthia*  
508 *malpilensis* (Decapoda: Brachyura: Gecarcinidae), a Poorly Known Species from the  
509 Tropical Eastern Pacific 1. *Pacific Science* 62:483–493.

510 Lorenz F., Fehse D. 2009. *The living Ovulidae: a manual of the families of allied cowries:*  
511 *Ovulidae, Pediculariidae and Eocypraeidae*. ConchBooks.

512 Meyer CP., Paulay G. 2005. DNA barcoding: error rates based on comprehensive sampling.  
513 *PLoS Biol* 3:e422.

514 Nowlis JP. 1993. Mate-and oviposition-influenced host preferences in the coral-feeding  
515 snail *Cyphoma gibbosum*. *Ecology*:1959–1969.

516 Palumbi SR. 1996. Nucleic acids II: the polymerase chain reaction. *Molecular systematics*  
517 2:205–247.

518 Pfennig DW., Wund MA., Snell-Rood EC., Cruickshank T., Schlichting CD., Moczek AP. 2010.  
519 Phenotypic plasticity's impacts on diversification and speciation. *Trends in Ecology*  
520 *& Evolution* 25:459–467. DOI: 10.1016/j.tree.2010.05.006.



521 Randall JE. 2005. A review of mimicry in marine fishes. *ZOOLOGICAL STUDIES-TAIPEI-*  
522 44:299.

523 Reijnen BT. 2015. Molecular data for *Crenavolva* species (Gastropoda, Ovulidae) reveals the  
524 synonymy of *C. chiapponii*. *ZooKeys*:15.

525 Reijnen BT., Hoeksema BW., Gittenberger E. 2010. Host specificity and phylogenetic  
526 relationships among Atlantic Ovulidae (Mollusca: Gastropoda). *Contributions to*  
527 *Zoology* 79:69–78.

528 Rosenberg G. 1992. An introduction to the Ovulidae (Gastropoda: Cypraeacea). *American*  
529 *Conchologist* 20:4–7.

530 Sadler TD., Romine WL., Stuart PE., Merle-Johnson D. 2013. Game-Based Curricula in  
531 Biology Classes: Differential Effects Among Varying Academic Levels. *Journal of*  
532 *Research in Science Teaching* 50:479–499.

533 Sánchez JA., Gómez CE., Escobar D., Dueñas LF. 2012. Diversidad, abundancia, y amenazas  
534 de los octocorales de isla Malpelo, Pacífico Oriental Tropical, Colombia. *Revista de*  
535 *Investigaciones Marinas & Costeras* 41.

536 Sánchez JA. 2013. Remarkable specialization in Eastern Pacific sea fan ectoparasites  
537 (*Neosimnia*). *Coral Reefs* 32:891–891. DOI: 10.1007/s00338-013-1049-6.

538 Sánchez JA., N. E. Ardila., J. Andrade., L. F. Dueñas., R. Navas., D. Ballesteros. 2014. Octocoral  
539 densities and mortalities in Gorgona Island, Colombia, Tropical Eastern Pacific.  
540 *Revista de Biología Tropical* 62:209–219.

541 Sánchez JA., Ballesteros D. 2014. The invasive snowflake coral (*Carijoa riisei*) in the  
542 Tropical Eastern Pacific, Colombia. *Revista de Biología Tropical* 62:197–207.

543 Schiaparelli S., Barucca M., Olmo E., Boyer M., Canapa A. 2005. Phylogenetic relationships  
544 within Ovulidae (Gastropoda: Cypraeoidea) based on molecular data from the 16S  
545 rRNA gene. *Marine Biology* 147:411–420.

546 Stamatakis A. 2015. The RAxML v8. 2. X Manual. *Structure*.

547 Starrett A. 1993. Adaptive resemblance: a unifying concept for mimicry and crypsis.  
548 *Biological Journal of the Linnean Society* 48:299–317.

549 Stevens M., Merilaita S. 2009. Animal camouflage: current issues and new perspectives.  
550 *Philosophical Transactions of the Royal Society B: Biological Sciences* 364:423–427.

551 Stoddard MC. 2012. Mimicry and masquerade from the avian visual perspective. *Current*  
552 *Zoology* 58:630–648.

553 Teaching and Student Services. 2008. Coral Reefs: Science and COnservation.

554 Van't Hof AE., Nguyen P., Dalíková M., Edmonds N., Marec F., Saccheri IJ. 2013. Linkage map  
555 of the peppered moth, *Biston betularia* (Lepidoptera, Geometridae): a model of  
556 industrial melanism. *Heredity* 110:283–295.

557 Vargas S., Guzman HM., Breedy O. 2008. Distribution patterns of the genus *Pacifigorgia*  
558 (Octocorallia: Gorgoniidae): track compatibility analysis and parsimony analysis of  
559 endemicity. *Journal of biogeography* 35:241–247.

560 Vermeij GJ. 2012. Crucibles of creativity: the geographic origins of tropical molluscan  
561 innovations. *Evolutionary Ecology* 26:357–373.

562 West-Eberhard MJ. 2003. *Developmental plasticity and evolution*. Oxford University Press.

563 Yates TB., Marek EA. 2014. Teachers teaching misconceptions: a study of factors  
564 contributing to high school biology students' acquisition of biological evolution-  
565 related misconceptions. *Evolution: Education and Outreach* 7:7.

