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

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**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.

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

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24

## 25 Abstract

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 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.  
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36 **Methods.** Collection and observations of egg-cowries and their octocoral hosts were done using  
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 38 Malpelo Island and Cabo Corrientes (Colombia). Detailed host preference observations were  
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 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  
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 44 egg-cowrie individuals from the two sampled localities observed on 8 different *Pacifigorgia*-  
 45 *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.

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

## Background

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

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

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

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

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

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



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

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

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>

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

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

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

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



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

### **Morphologic and Molecular identification**

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

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

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

## Discussion

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

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

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

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

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

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

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

## Conclusions

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

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

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

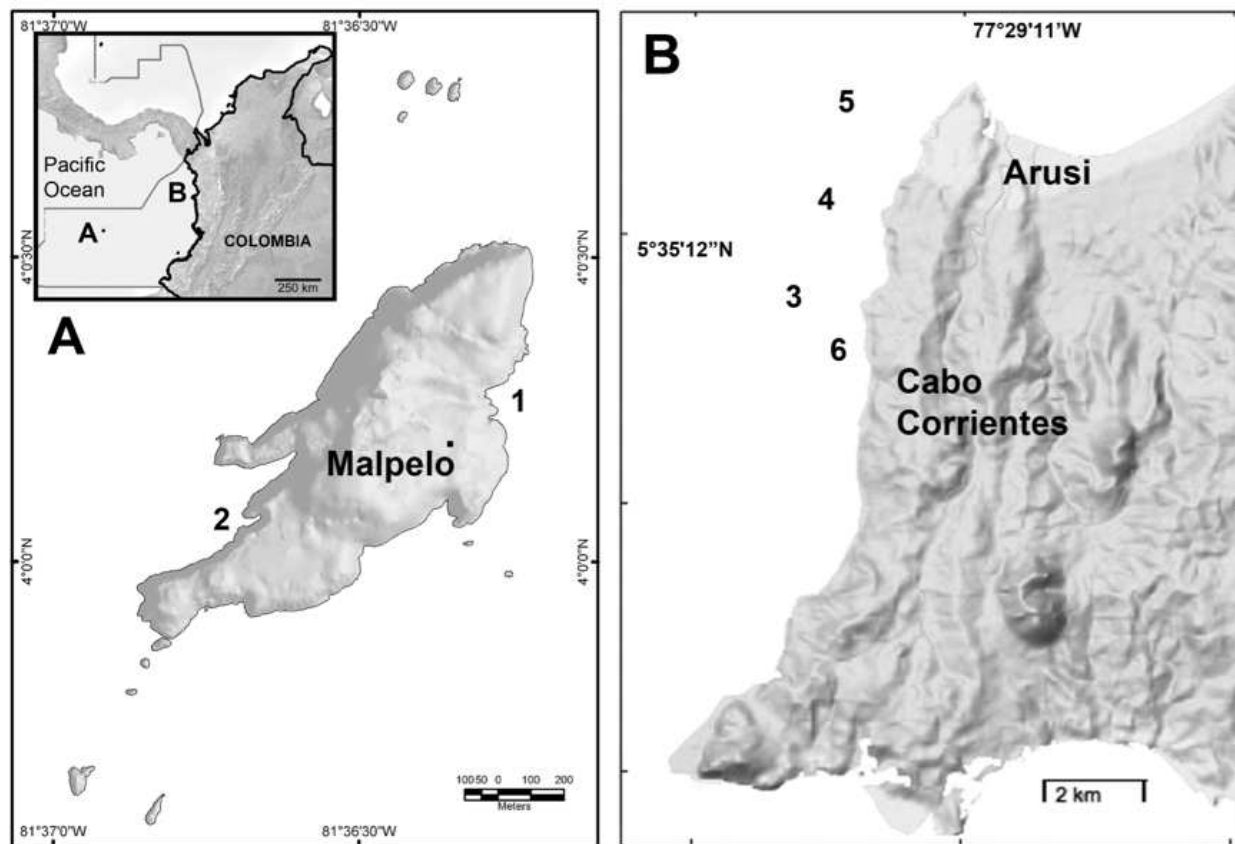
Sample label	Collection date	Morphologic ID	Location	Site	Depth (m)	Coral host species	16S	COI
<b><i>Pacifigorgia</i> – <i>Eugorgia</i> clade</b>								
K136	19-Apr-11	<i>Simnia</i> sp.	Cabo Corrientes	Caló	15	<i>Pacifigorgia sculpta</i>	KU557467	KU557450
K175	16-Apr-11	<i>Simnia avena</i>	Cabo Corrientes	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</i> clade</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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# Figures

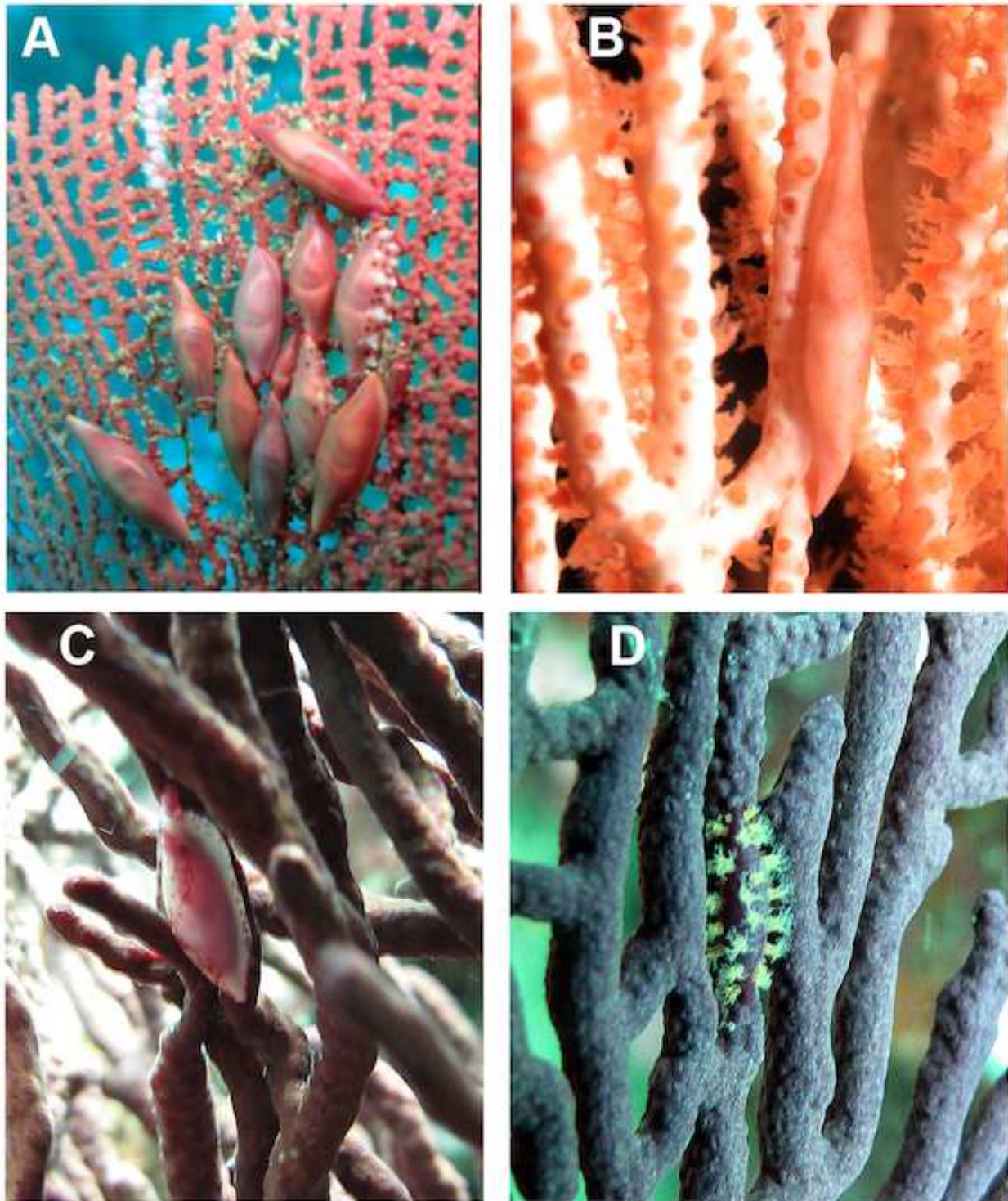


413

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).





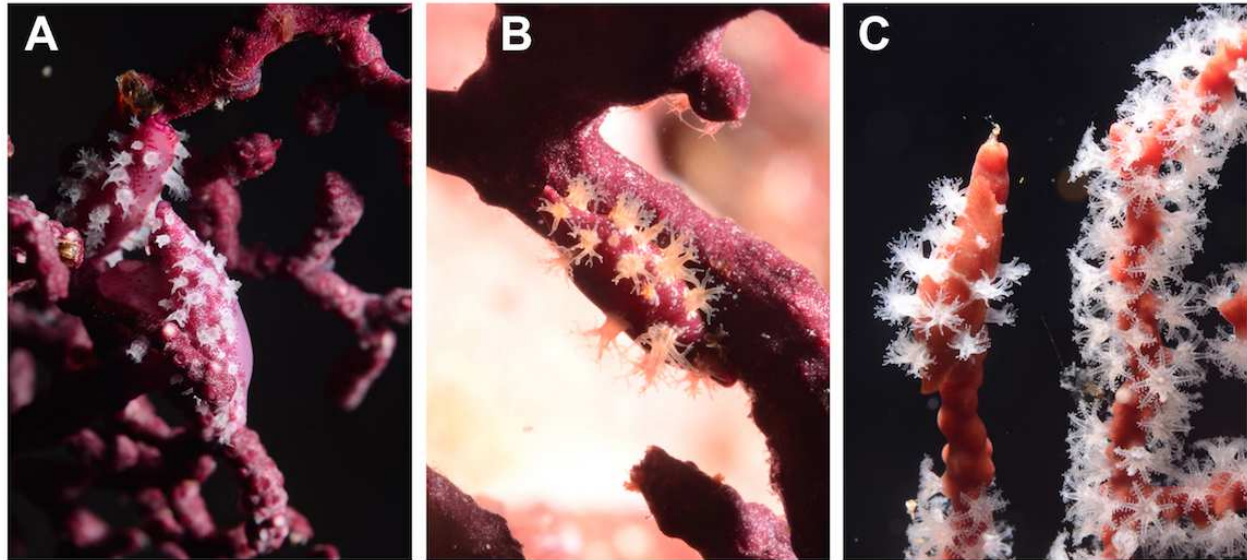
416

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

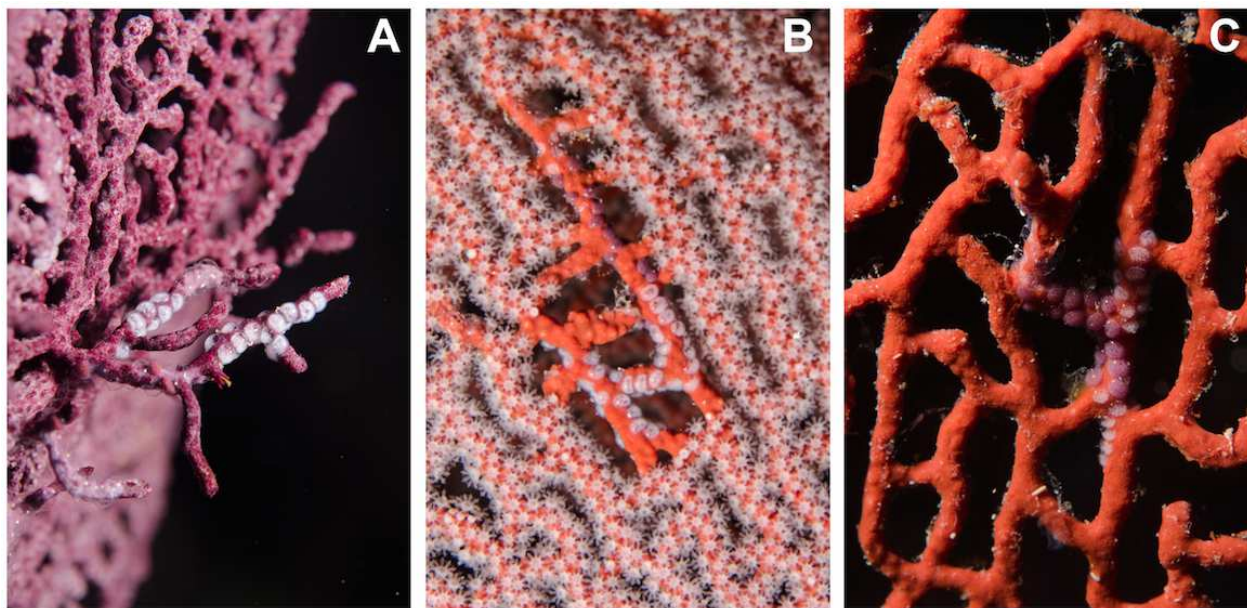
418 Corrientes, Chocó; B Malpelo Island). Coral hosts: A. *Pacifigorgia irene* (depth 12 m), B.

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

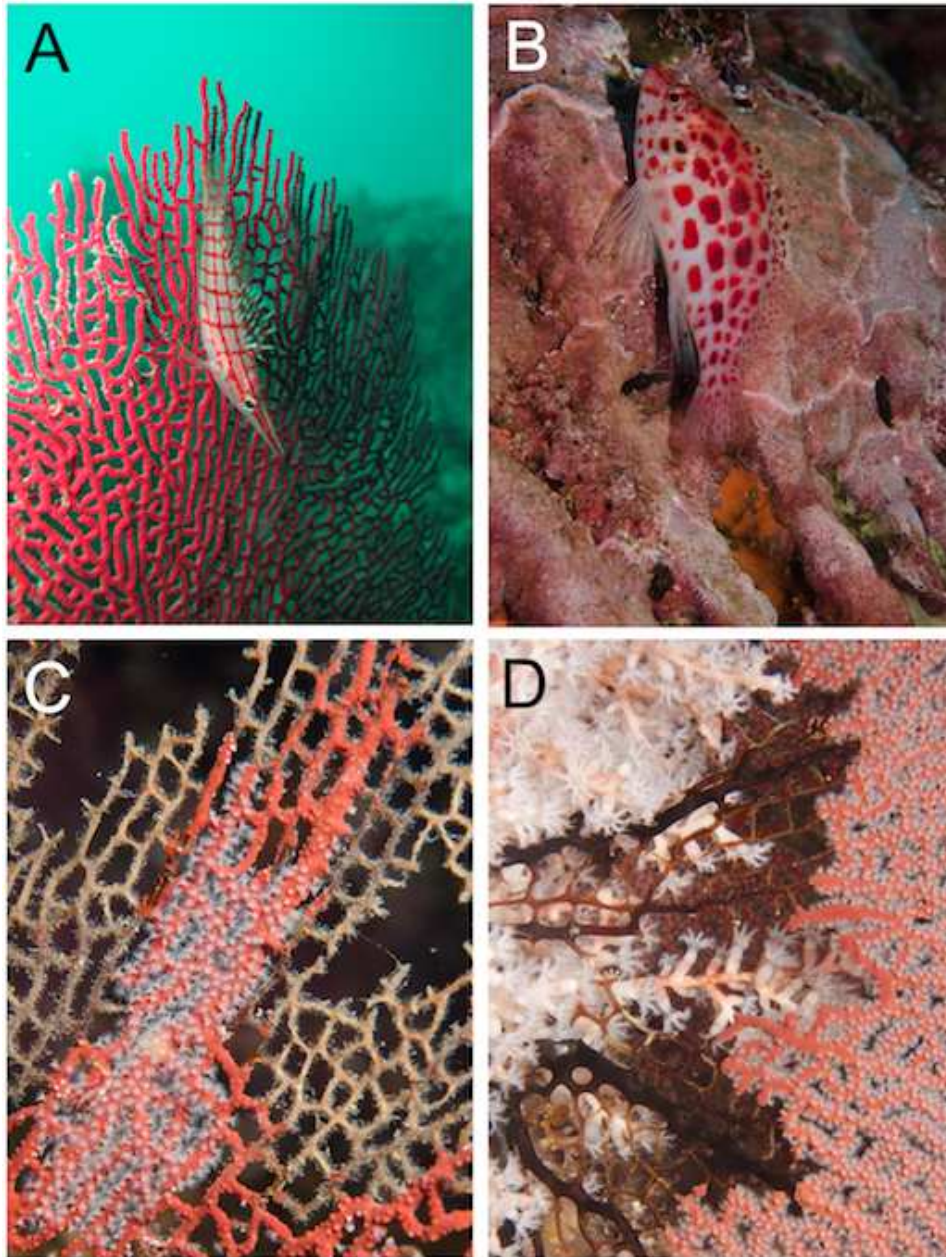




**Figure 3.** Egg-cowrie *Simnia avena* on *Pacifigorgia cairnsi* and *P. cf. curta* at Malpelo Island, Colombian Pacific. (A) *S. avena* on *P. cf. curta* -white polyps; (B) *S. avena* on *P. cf. curta* - orange polyps; (C) *S. avena* on *P. cairnsi*.

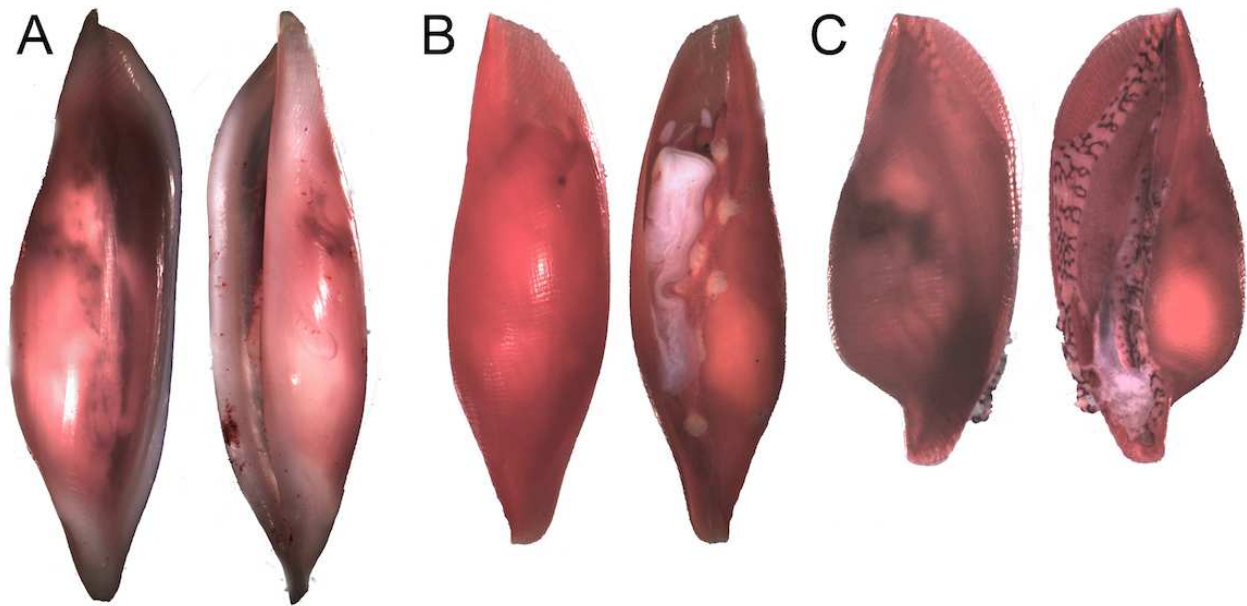


**Figure 4.** Mixed ovopositions (white and purple) left by the cowrie *Simnia avena* on sea fans at Malpelo Island, Colombian Pacific. (A) Mixed ovoposition on purple background, *Pacifigorgia cf. curta*; (B-C) mixed ovoposition on red background, *P. cairnsi*.



**Figure 5.** Potential threats to *Simnia* egg-cowries at Cabo Corrientes and Malpelo Island, Eastern Tropical Pacific, Colombia. (A) Longnose hawkfish *Oxycirrhites typus* with a sea fan-like background camouflage (Cabo Corrientes); (B) Coral hawkfish *Cirrhilabrus oxycephalus*; (C) Diseased sea fan *Pacifigorgia cairnsi*; (D) The invasive snowflake coral, *Carijoa riisei*, overgrowing *P. cairnsi* (B-D Malpelo Island).





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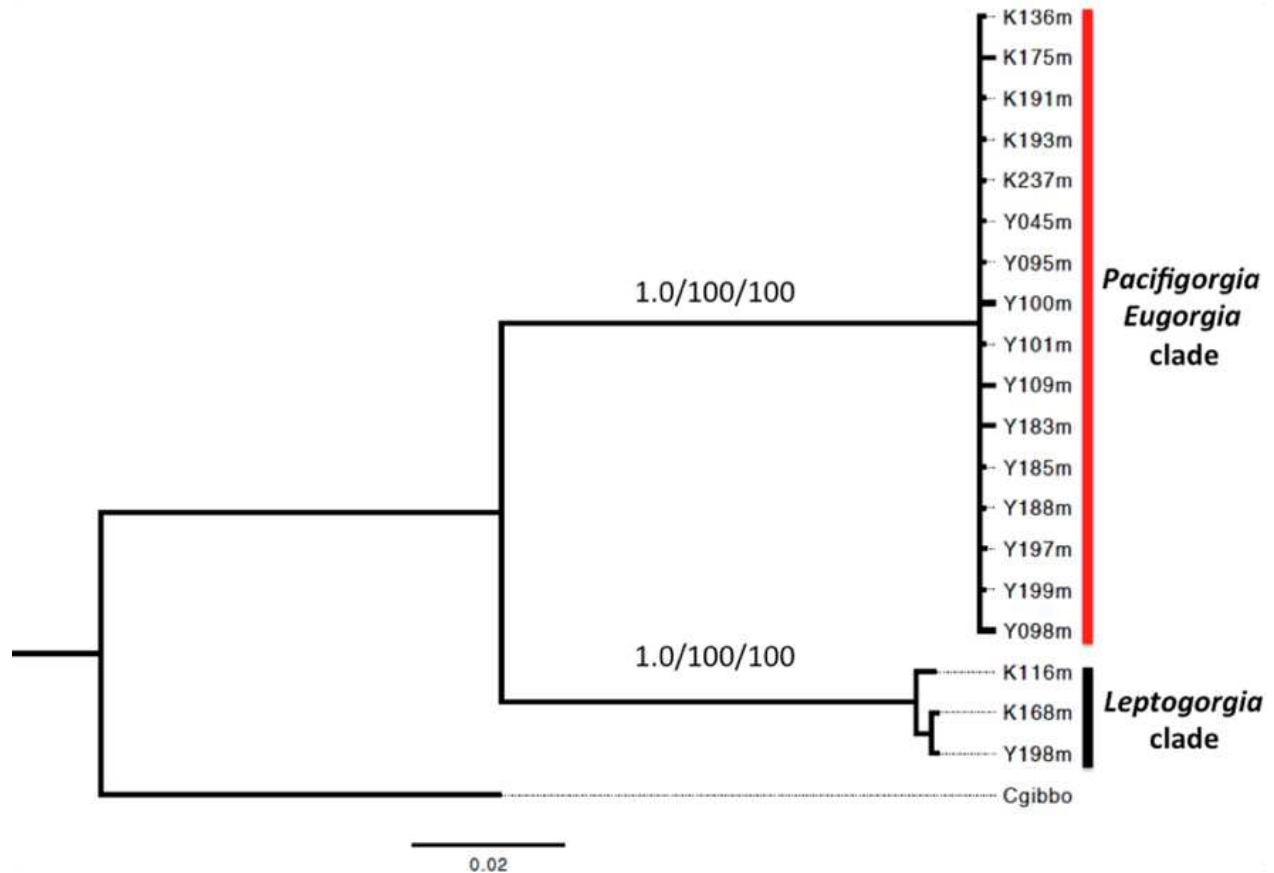
436 **Figure 6.** Distinct shell morphologies found in egg-cowries at the Colombian Pacific. A. *Simnia*

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



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

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