

# Population structure and morphology of *Canarium* (*Canarium*) *incisum* and *Canarium* (*Canarium*) *esculentum* (Mollusca: Neostromboidae: Strombidae) from the Philippines with preliminary notes on aperture colouration based on DArTseq data

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## Abstract

*Canarium* (*Canarium*) *incisum* and *Canarium* (*Canarium*) *esculentum* are small members of the molluscan Strombidae family. Little is known of their population structure. Therefore, we explored this using samples from a population of each. The first sample from Corong Corong Beach, El Nido, Philippines, consisted of 81 adult *C. incisum*, of which 33 were female and 48 were male. The second sample from Olango Island, Philippines consisted of 73 adult *C. esculentum*, of which 40 were female and 33 were male. Bias in sex ratio between species was not significant. However, there was bias in sex ratio within species, where males from both species were smaller in axial length than females. We found no evidence of pseudohermaphroditism. The black colouration of the aperture is a phenotype shared by many stromboidians, and 7.4% of *C. incisum* population exhibited this trait, while the *C. esculentum* population contained 50.1% black apertures specimens. Preliminary DArTseq analysis indicates that organisms with the black aperture colouration are nested within the populations. Our study fills a knowledge gap on *C. incisum* and *C. esculentum* population structure, and gives greater insights to size dynamics of stromboidian taxa in general.

## KEYWORDS

aperture, colour, pseudohermaphroditism, sex bias, size dimorphism

## 1 | INTRODUCTION

The Philippines is a hotspot for mollusc divergence, having great species richness and morphological variability (Abbott, 1960; Kreipl et al., 1999). This diversity is emphasised with the recent taxonomic revisions of many groups

in this region, with many new species having recently been circumscribed within the clade Neostromboidae Maxwell, Dekkers, et al., 2019a, including Rostellariidae (Morrison, 2008), Seraphsidae Jung, 1974 (Poppe & Tagaro, 2016; Dekkers et al., 2019; Maxwell et al., 2021a) and Strombidae Rafinesque, 1815 (Dekkers et al., 2021).

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However, few studies have sought to understand the population structures of these taxa (Maxwell et al., 2022).

Some members of the Strombidae express sexually dimorphic characteristics in both physiology and shell morphometrics (Abbott, 1949, 1960, 1961; Reed, 1993a; Mutlu 2004; Maxwell, Rowell, et al., 2020a; Maxwell, Rymer, et al., 2021b, Maxwell et al., 2022). While the phenomenon of sex-ratio bias is reported from numerous members of the Strombidae, this may simply be an artefact of aggregation and sampling size (Maxwell et al., 2017; Maxwell, Rymer, et al., 2021b). The shells of many species also show a high degree of variability in colour and form (Abbott, 1960; Maxwell, Rymer, et al., 2020b). Some species, such as *Strombus pugilis* Linné, 1758 (Reed, 1993b), have demonstrated pseudohermaphroditism in observable genitalia, with individuals having both male and female external sex organs (Jenner, 1979; Nicolaus & Barry, 2015). A recent study in *Canarium (Canarium) esculentum* Maxwell, Rymer, 2020b (not *Canarium urceus urceus* (Linné, 1758) as identified in Ruaza, 2019) from Caraga, Philippines showed an abnormally high incidence of pseudohermaphroditism in females (36%; Ruaza, 2019). Despite these recent studies, many stromboidean species still remain unstudied in terms of morphological variability, sex-ratio bias and pseudohermaphroditism.

*Canarium (Canarium) incisum* (Wood, 1828) is one these overlooked species, while *Canarium (Canarium) esculentum* Maxwell, Rymer, et al., 2020b is represented by a single study (Ruaza, 2019). These species are economically important and are used as an affordable protein source in many Philippine coastal communities. Until recently, these species have been misidentified and synonymised within the *Canarium (Canarium) urceus* (Linné, 1758) complex (Abbott, 1960; Kreipl et al., 1999). They have recently been restated and recircumscribed, providing a more solid taxonomic footing (Maxwell, Rymer, et al., 2020b).

There are two known aperture colour morphs in these species: a form with an orange callus and aperture in *C. incisum*, while *C. esculentum* is typically white, and both species share a form with varying degrees of black colouring in the aperture. This colour dimorphism is shared with at least two other species of *Canarium*: *C. (C.) anatellum* (Duclos, 1844) and *C. (Elegantum) radians* (Duclos, 1844). However, there have been no studies that have sought to understand the frequency of this colour trait in stromboidians and how it relates to population structure.

This study had five aims to inform on the population characteristics of *C. incisum* and *C. esculentum*: first, we assessed whether sexual dimorphism in axial shell length was present; second, we assessed whether there was a sex-ratio bias; third, we assessed whether

there was evidence of pseudohermaphroditism in these species; fourth, we determined the ratio of aperture colour morphology within the populations; and fifth, we examined the genetic structure of aperture colour morphology.

## 2 | METHODS

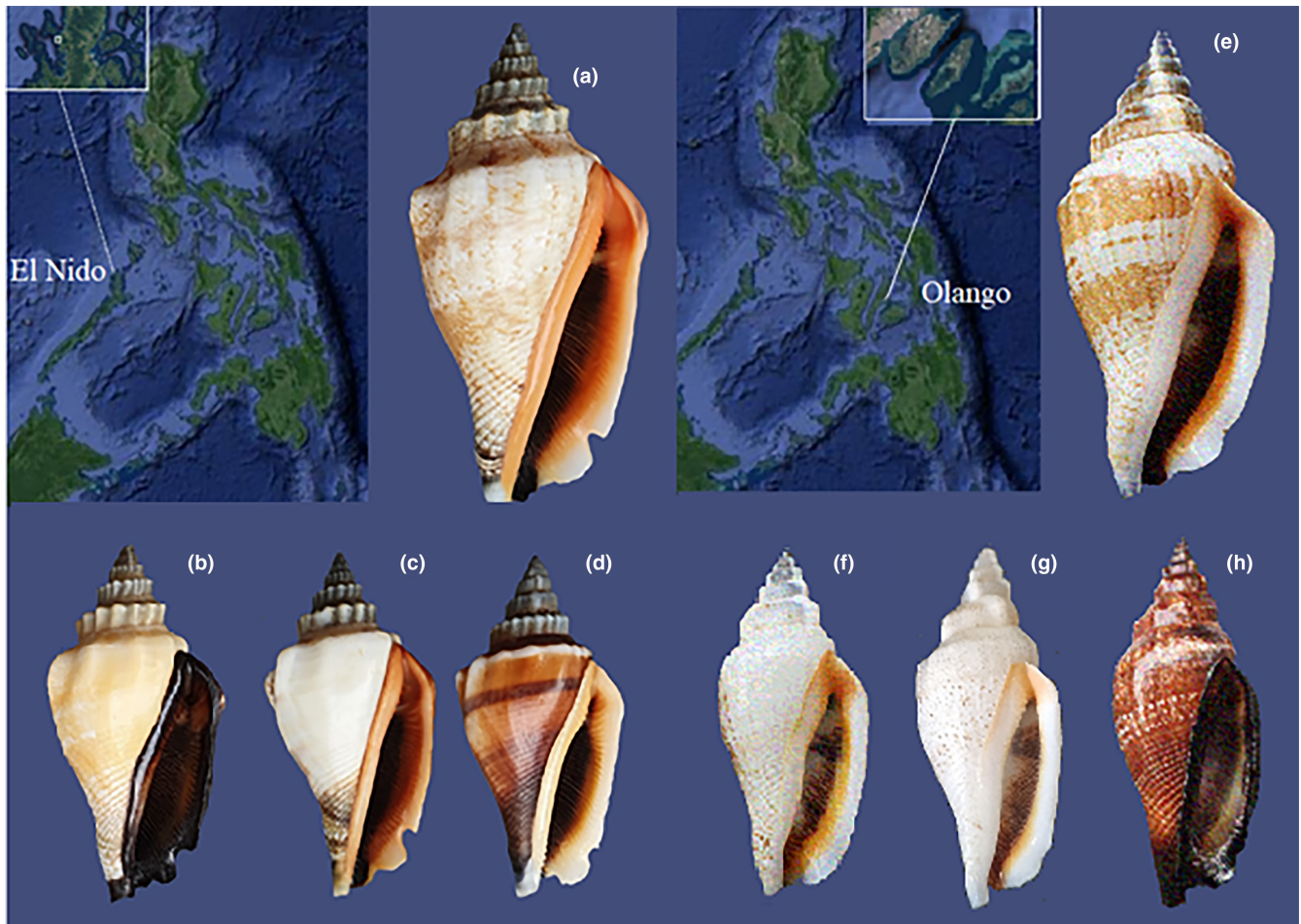
### 2.1 | Sampling

Both target species are collected regularly for domestic consumption and sold at local markets as “sikad sikad” or “anikad.” We contracted local fishermen in August 2020 to collect stromboidean species, including *C. incisum*, from Corong Corong Beach, El Nido, Philippines (11.35N, 119.46 E; Figure 1). The collection was explicitly requested to be non-selective for size to avoid bias. The sample represented the total number of organisms collected during one low-tide period. The fishermen are experienced collectors for the shell trade, and are able to recognise mature organisms through the presence of the thickened outer lip. No information on aggregations of individuals was provided by the collectors. After collection, specimens were placed in alcohol and shipped to James Cook University, Cairns, Australia (following customs approval and clearance).

The, *C. esculentum*, sample represents a dealer-obtained sample from Olango Island, Philippines (10.01 N, 124.09 E; Figure 1) collected in June 2020. No other information on the sample or aggregations of individuals was provided by the dealer. The samples were prepared and shipped as for *C. incisum*.

### 2.2 | Morphology

Once in Australia, specimens from each sample were sorted. Thereafter, the animals were removed from their shells, and the following information was documented for each specimen: total axial length; colouration of the aperture; sex (presence of a verge indicated a male, while presence of an oviduct indicated a female); presence or absence of pseudohermaphroditism – masculinised females are readily distinguished from males and normal females by a deformed and vestigial verge (Reed, 1995; see Ruaza, 2019 for illustrations of sexual organs and pseudohermaphroditism). The masculinised female verge is muscular, may be multi-lobed and may contain superficial channels with ciliated epithelia (Reed, 1993b). Shells were catalogued into the Stephen Maxwell Collection (SMC) for future reference.



**FIGURE 1** Location and representatives of two samples examined in this study – *Canarium (Canarium) incisum* (Wood, 1828) Corong Corong Beach, El Nido Philippines: (a) female, 47.0 mm (SMC 19db.001d = pr2f); (b) female, 37.5 mm (SMC 19db.001e = pr4bf); (c) male, 31.75 mm (SMC 19db.001w = pr4m); and (d) male, 32.5 mm (SMC 19db.001a = prt1m); and *Canarium (Canarium) esculentum* Maxwell, Rymer, Congdon and Dekkers, 2020b Olango Island, Philippines: (e) female, 58.8 mm (SMC 19a.004e = phf1); (f) male, 48.1 mm (SMC 19a.004a = phm3); (g) male, 51.4 mm (SMC 19a.004j = phm5); (h) male, 51.1 mm (SMC 19a.004h = phbm4) (shells not to scale, map image modified from Google earth, accessed August 2021)

### 2.3 | Statistical analyses

Statistical analyses for each population were conducted using SPSS Statistics v 28 (IBM). For each sex, shell summary statistics were generated, and the means and standard errors for each sex presented to statistically demonstrate the presence/absence of sexual dimorphism. A box plot of each sex was generated to illustrate the size-frequency distributions of each sex. An independent-sample *t*-test was conducted to determine if there were significant differences in the size of each sex. The proportion of males was tested against a hypothesised proportion of 0.5 using an exact binomial test to determine if a sex ratio bias was present. Aperture colour ratios were calculated as a percentage of the total sample. Pseudohermaphroditism was scored as present or absent.

### 2.4 | Genetic analyses

A trial of seven specimens from the *C. esculentum* sample (male:  $n = 4$ ; female:  $n = 3$ ), of which three specimens had a black aperture (male:  $n = 2$ ; female:  $n = 1$ ), and six *C. incisum* specimens (male:  $n = 3$ ; female:  $n = 3$ ), of which two were black aperture morphs (male:  $n = 1$ ; female:  $n = 1$ ), were selected for trial single-nucleotide polymorphism (SNP) genotyping. We also included a female *Canarium (Canarium) urceus* (Linné, 1758) from Singapore, where all animals have black apertures, as an outgroup. DNA extraction, library preparation, array-based sequencing and in silico genotyping of SNPs were conducted by Diversity Arrays Technology (DArT), Canberra, at a depth of 2.5 million reads. This technology, service and the data it produces, is known as “DArTseq.” The following data filtering criteria were sequentially applied: reproducibility  $\geq 90\%$ ;

all secondaries were removed; average read depth  $\geq 10$ ; individual call rate  $\geq 50\%$ ; locus call rate = 100%. After filtering, 13 individuals and 5361 SNP loci with no missing data remained. One *C. esculentum* female from Cebu was removed due to poor sample sequencing quality.

Genetic variance across the sample was visualised using Pearson Principal Component Analysis (PCA) using the R package *dartR* (Gruber et al., 2018), which simplifies multidimensional data along ordination axes (Pearson, 1901; Jolliffe, 2003). The positions of black aperture individuals among the taxa were examined.

### 3 | RESULTS

The *C. incisum* sample contained only adults (Total:  $n = 81$ ; females:  $n = 33$ ; males:  $n = 48$ ). The mean size of females was 41.91 mm ( $\pm 0.73$  SE) in contrast to males, which had a mean size of 35.10 mm ( $\pm 0.60$  SE). This difference in size, with a tendency towards larger females, was significant ( $t_{2,79} = -7.21$ ,  $p < 0.001$ ; Figure 2). The number of females collected was smaller than the number of males (1:1.45), although this difference was not statistically significant ( $p = 0.12$ ;  $\alpha = 0.95$ ). While most (92.6%) of the sample exhibited typical aperture colouration of shades of orange, 7.4% showed atypical colouration with a black aperture (females:  $n = 3$  (9% of females); males:  $n = 3$  (6.3% of males)).

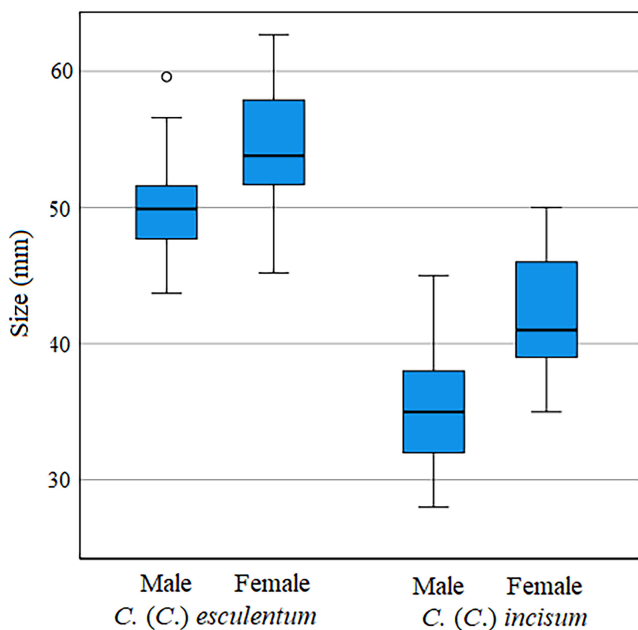


FIGURE 2 Boxplot of median and quartile of the axial lengths of each sex of *Canarium (Canarium) incisum* (Wood, 1828) from Corong Corong Beach, El Nido, Philippines and *Canarium (Canarium) esculentum* Maxwell, Rymer, Congdon and Dekkers, 2020b from Cebu, Philippines

The *C. esculentum* sample also contained only adults (Total:  $n = 73$ ; females:  $n = 40$ ; males:  $n = 33$ ). The mean size of females was 54.77 mm ( $\pm 0.65$  SE) in contrast to males, which had a mean size of 49.74 mm ( $\pm 0.62$  SE). This difference in size, biased towards larger females, was significant ( $t_{2,77} = -5.27$ ,  $p < 0.001$ ; Figure 2). The number of males collected was smaller than the number of females (1:1.21), although this difference was not statistically significant ( $p = 0.483$ ;  $\alpha = 0.95$ ). There was no evidence of pseudohermaphroditism in visible genitalia in either population. The sample exhibited equal-coloured apertures, with the aperture colouration of shades of white being 49.9%, while 50.1% showed the black aperture colouration (females:  $n = 22$  (55% of females); males:  $n = 15$  (45.5% of males)).

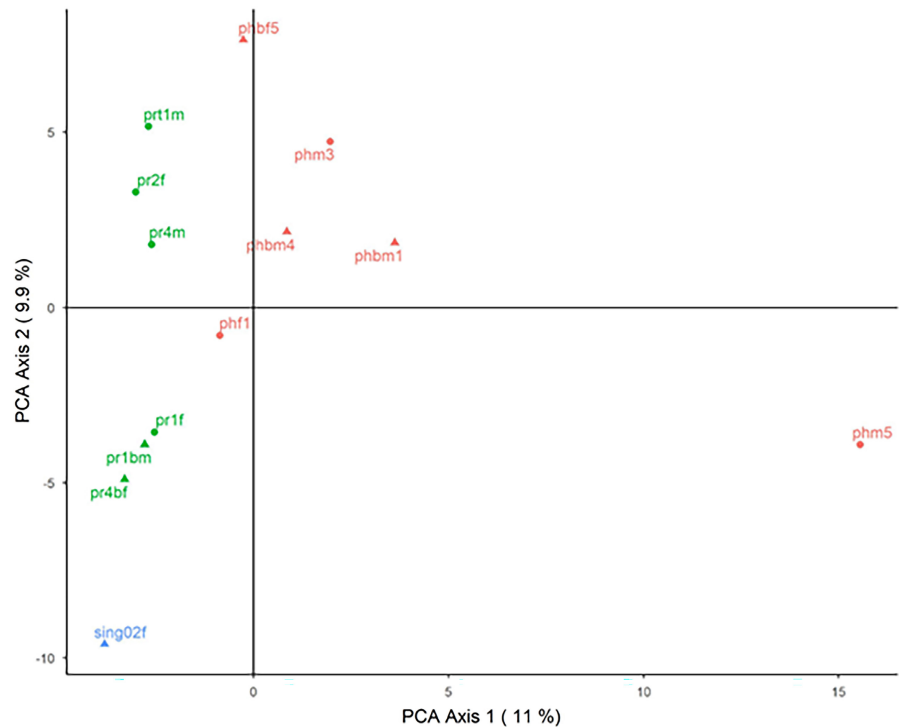
Black aperture individuals were spread along both PCA axes one and two (Figure 3). The two *C. (C.) incisum* shells sampled with black apertures were close to each other in genetic distance, and together with a third orange aperture individual formed a cluster that was distinct from the other three individuals of this species. This cluster was closer to black apertured *C. (C.) urceus* along PCA axis two.

### 4 | DISCUSSION

We found sexual size dimorphism in the axial length of the shell in both species, with females being statistically larger than males. That females were larger than males on average, being 6.81 mm larger in *C. incisum* and 5.03 mm larger in *C. esculentum*, and this is consistent with findings in other stromboideans (Abbott, 1949, 1960, 1961; Reed, 1993a; Mutlu, 2004; Maxwell, Rowell, et al., 2020a; Maxwell, Rymer, et al., 2021b). This evidence, coupled with studies on extinct taxa (Geary & Allmon, 1990), indicates that sexual size dimorphism in favour of females is a symplesiomorphic state in stromboideans.

There was a non-significant bias in favour of one sex in each sample. One of the major problems in determining whether an underlying sex-bias in stromboidean populations is present is not knowing the nature of the population clustering from which the sample is derived. Within congregations of the same taxon, four distinct categories for clustering can be discerned: mixed age; juvenile; mating; and non-mating clusters (Brownell, 1977; Catterall & Poiner, 1983). While female bias is more common (*Laevistrombus vanikorensis* (Quoy & Gaimard, 1834) – Maxwell et al., 2017; *Canarium labiatum* (Röding, 1798) – Maxwell et al., 2020a; *Gibberulus dekkersi* Maxwell, Hernandez Duran, et al., 2021c (not *Gibberulus gibbosus* Röding, 1798) – Maxwell, Rymer, et al., 2021b), and seen here in *C. (C.) esculentum*, studies where males are more frequent, such as with *C. (C.) incisum* in the present study, may

**FIGURE 3** The two most explanatory principal components of a PCA analysis of SNP genotypes, showing distribution of specimens with a black aperture across species: *Canarium (Canarium) esculentum* Maxwell, Rymer, Congdon and Dekkers, 2020b (pink – “Ph”) from Cebu, Philippines; *Canarium (Canarium) incisum* (Wood, 1828) (green – “Pr”), from El Nido, Philippines; and *Canarium (Canarium) urceus* (Linné, 1758) (blue – “Sing”) from Singapore. Individuals with a black aperture are indicated with triangles, and males (m) and females (f) noted in the labelling



be evidence of a spawning event, such as is seen in previous studies in the related *Conomurex luhuanus* (Linné, 1758), which showed a similar female to male ratio of 1 female to 1.42 males (Catterall & Poiner, 1983). As the present sample of specimens did not contain juveniles, this indicates that it was not a mixed-age or juvenile clustering event.

While pseudohermaphroditism is known from *C. (C.) esculentum*, a taxonomically close species also from the Philippines (Ruaza, 2019), we found no evidence for this in the external sex organ morphology of the animals of both populations we examined. There are three possibilities for this (Maxwell, Rowell, et al., 2020a): first, the causal agent tribytkin (TBT) was not in concentrations high enough to negatively affect the organisms from this population; second, the sample was too small to observe this characteristic; third, the phenotype is not naturally present in the population; and fourth, penis-bearing females are misinterpreted as males. Future studies could explore this phenomenon further in these species, as well as others from the same region.

In the *C. (C.) incisum* study, 7.4% of all shells had a black coloured aperture, while in *C. (C.) esculentum*, 50.1% of all shells had a black aperture. This recurrent morphological feature can be explained in one of three ways: first, there could be a lag in the time of genetic divergence, and evidence of this split in the morphology of organisms could be lost when phenotypes are lost (Baum, 2008); second, within a population, there are enough carriers of a mutation for black colouration that genetic drift and selection maintain allele frequencies without leading to either extinction or fixation

(Baum, 2008); or third, there is enough genetic inflow from populations outside of the bioregion, which enables the recurrent introduction of the black colouration within the population to sustain its ongoing recurrence (Delgado et al., 2006; Paris et al., 2006, 2008). There is a high degree of hybridisation within the stromboidean complex and given the ability for veligers to travel hundreds of kilometres, coupled with a year-round spawning habit, this makes the potential for introgression of traits high (Delgado et al., 2006; Paris et al., 2006, 2008; Aldana-Aranda & Perez-Perez, 2007; Maxwell, Bordon, et al., 2019b).

The preliminary DaRTseq data showed no evidence that the black aperture trait is associated with genetic structuring within *C. esculentum*, or across the species complex (Figure 3). The clustering of black apertured *C. incisum* individuals closer to *C. urceus*, a species in which this trait is universal, may indicate historic hybridisation between these species leading to introgression of the black aperture trait into *C. incisum*. However, additional samples are required in order to draw inference about the genetic structuring of black apertured shells in these species. While individual phm5 was an outlier along PCA axis one, it is morphologically similar to phm3 (Figure 3), which is genetically nested within the population.

We do not find the staining of the aperture, which may occur under some environmental conditions, a plausible explanation for black apertured specimens in this case because of the shared habitat of the non-black apertured section of the sample. If an environmental factor were at play to cause this colouration it would have affected the

population equally. Further genetic sampling and analysis is necessary to better understand the genetic structure of these populations and resolve the possible existence of cryptic subspecies.

## 5 | CONCLUSION

The samples examined showed typical stromboidean sexual dimorphism biased in favour of larger females. In addition, we found a non-significant sex ratio bias in favour of males in one sample, and females in another. No pseudohermaphroditism was observed in either species. Within the samples, the black aperture colouration was found to be a phenotype occurred in each population, with higher frequency in *C. esculentum*, but this appeared unrelated to genetic structure of the species complex in general. Understanding population structure of more species of stromboideans enables a better understanding of the extent of the phenomenon of axial-length size dimorphism within the complex, which enables the formulation of models that would seek to explain this.

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