ARTICLE

Analysis of cone snail species in the *Phasmoconus* lineage collected off Aurora, Eastern Luzon

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The marine biodiversity of the Philippines is rich, vast and distinctive making it challenging to design an effective program for systematic scientific investigation. Most studies carried out are either broad surveys, or at the other extreme, highly reductionist studies. The focus of the present study is the specimens in the Superfamily Conoidea collected by a collection trip organized by The Museum of Natural History, Paris (the "Aurora 2007 expedition"). These specimens comprise a biodiverse lineage of cone snails; we focus on the subgenus *Phasmoconus*, (genus *Conus*). There were 10 different morphospecies recovered at the site; 5 were previously reported from the Philippines. Two specimens tentatively assigned to *Phasmoconus* are species not previously documented from the Philippine archipelago (*Conus* c.f. *gabryae* and *Conus* c.f. *grangeri*). Two of the forms collected: *Conus glorialita* and *Conus tayabasensis,* could not be assigned to any previously named taxa in the literature and appear to be undescribed; these new species are described in this article. The most remarkable discovery was *Conus* (*Phasmoconus*) *balerensis*, a new species collected during this expedition. Over 200 specimens of this species were collected; this was by far the most abundant *Conus* species occurring over a wide stratigraphic range. In contrast most *Phasmoconus* specimens collected had a fairly narrow depth distribution. At present, *Conus balerensis* has only been found in deep waters off Aurora. The large fraction of unnamed species and new locality records for *Phasmoconus* recovered during the expedition demonstrate that even for well-studied lineages, a significant fraction of Philippine marine biodiversity remains poorly defined.

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INTRODUCTION

The *Phasmoconus* clade is one of the most species-rich cone snail lineages; a recent monograph on the family Conidae (Monnier et al. 2018) recognized 103 distinct *Phasmoconus* morphospecies. Recent phylogenetic analyses suggest that the ancestral *Phasmoconus* were shallow-water forms that spread over much of the Indo-Pacific, with a subsequent gradual colonization of deeper-water environments in the Western Pacific (Imperial et al. 2007). The deeper water *Phasmoconus* biota includes *Conus mucronatus* and *Conus australis*-type species. We have no direct evidence for the prey of any of these deep-water forms.

Phasmoconus and Asprella are two lineages of venomous cone snails that are poorly characterized with respect to their biology, phylogeny and taxonomy. In recent years, primarily because of the increasing availability of molecular data, these clades have become better defined. *Asprella* was the focus of a previous article (Olivera et al. 2021; Olivera, Saguil, and Bouchet 2019); the present manuscript documents deep-water morphospecies in *Phasmoconus* collected off the eastern coast of Luzon. A brief introduction to these two related groups of venomous cone snails is presented here.

The two subgenera, *Asprella* and *Phasmoconus*, are sister clades within the genus *Conus*, and include a number of species that have been directly observed to be fish-hunting (Olivera et al. 2015). However, most of the published literature generally describes *Asprella* and *Phasmoconus* species as worm-hunting (vermivorous); this is largely due to their radular tooth morphology (Olivera et al. 2015). The classic fish-hunting cone

KEYWORDS

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snails in the subgenera *Chelyconus* and *Pionoconus*, first defined by Alan Kohn (Kohn 1959), have a characteristic radular morphology that allows the radular tooth to be used both to inject venom, as well as to tether the envenomated fish prey. However, most species in *Asprella* and *Phasmoconus* do not have the typical harpoon-like radular tooth morphology of classical fish-hunting *Conus* (Olivera et al. 2015). Despite the widespread assumption that most species in *Asprella* and *Phasmoconus* are vermivorous, direct observations on prey capture are consistent with both being primarily fish hunters (Olivera et al. 2015). In addition, an extensive survey of the venom components of species in these clades is consistent with piscivory (Cordeiro et al. 2019; Chen et al. 2010; Ferber et al. 2004). The latest phylogenetic analysis suggests that the transition from vermivory to fish hunting may have taken place independently in the branch leading to *Phasmoconus* and *Asprella* from the event that led to traditional fish-hunting species such as *Conus striatus* (*Pionoconus*), *Conus bullatus* (*Textilia*) and *Conus geographus* (*Gastridium*) (Puillandre et al. 2014; Kraus et al. 2011; Espiritu et al. 2001).

The present report, using the previous study as a starting point, provides a more comprehensive analysis of the *Phasmoconus* specimens recovered by Aurora 2007 expedition. The deeper-water, poorly-characterized species of *Phasmoconus* collected during the Aurora 2007 expedition are compared to related specimens from other localities (e.g Central Visayas, Sulu Sea, Australia, etc). The results provide a documentation of the range of depths that specimens of *Phasmoconus* inhabit. In general, most species in this group appear to be highly stratified with respect to their habitat at the Aurora 2007 expedition sampling sites.

METHOD

Cone snails belonging to the *Phasmoconus* clade, collected during the Aurora 2007 expedition are described here. Specimens were collected either by dredging/towing at different off shore sites. Global positioning system (GPS) coordinates (Table 1) where specimens were either dredged or trawled as well as when the nets were hauled were recorded (Bouchet and Santos 2007). Specimens were collected using a beam trawl (code CP in Tables 1 and 2) or a Waren dredge (code DW in Tables 1 and 2). Specimens are on an extended loan to the Museum National d'Histoire Naturelle (MNHN), Paris, France until their return to an appropriate Philippine institution.

Table 1: Sampling stations, depths and coordinates where *Phasmononus* specimens were collected during the 2007 Aurora expedition. Data were adapted from the Aurora 2007 cruise report (Bouchet and Santos 2007).

Station	Depth (meters)	Dredging/Towing		Hauling	
		Lat North	Lat East	Lat North	Lat East
DW2726	327-339	15º 20	121º 34	15º 20	121º 34
CP2666	199-307	15º 57	121º 44	15º 58	121º 45
CP2711	184-200	15º 19	121º 32	15º 20	121º 32
CP2742	182-205	16º 03	121º 53	16º 03	121º 52
CP2719	155-160	14º 27	121º 48	14º 26	121º 48
DW2758	151-173	15º 55	121º 50	15º 55	121º 50.15
CP2712	139-140	15º 21	121º 30	15º 20	121º 30
CP2655	125-198	16º 03	121º 54	16º 03	121º 53
CP2747	120-124	15º 55	121º 42	15º 55.53	121º 42
CP2738	111-113	16º 04	121º 55	16º 04	121º 56
CP2760	100	15º 55	121º 40.5	15º 54.2	121º 54.21
CP2654	98-107	16º 04.7	121º 57.5	16º 04.3	121º 57
DW2739	96	16º 05	121º 57	16º 05	121º 58
CP2653	83	16º 06.5	121º 59.7	16º 06.5	121º 59.7
CP2863	246	*na*	*na*	*na*	*na*

The method of specimen collection is indicated in the station codes. CP: beam trawl; DW: Waren dredge. *na:* not available

Table 2: List of *Phasmoconus* specimens collected during the Aurora 2007 expedition. The station code, collection depth and the number of specimens collected are presented.

Station	Depth (meters)	Number of Specimens	Specimens collected
DW2726	327-339	1	*glorialita*, new species
CP2666	199-307	9	*balerensis*
CP2711	184-200	1	*balerensis*
CP2742	182-205	1	c.f. *gabryae*
		3	*balerensis*
CP2719	155-160	1	*australis*
DW2758	151-173	37	*balerensis*
CP2712	139-140	5	*australis* (3 subadult)
		1	*balerensis*
CP2655	125-198	5	*australis* (2 juvenile)
		3	*balerensis*
CP2747*	120-124	2	*australis*
		4	*lynceus* (1 juvenile, 2 subadult)
		1	c.f. *grangeri* (new locality record)
		122	*balerensis*
CP2738	111-113	23	*balerensis*
CP2760	100	1	*balerensis*
CP2654	98-107	2	*laterculatus* (subadult)
		6	*balerensis*
DW2739	96	3	*balerensis*
CP2653	83	2	*laterculatus* (1 subadult)
		1	*mucronatus*
		3	*leobrerai*
		1	*tayabasenis*
		40	*balerensis*
CP2863	246	1	*balerensis*

*In the same dredge haul, 18 specimens of *Conus sulcatus* were also recovered. In column 1, CP: beam trawl; DW: Waren dredge (see Table 1).

Specimens were initially sorted into broad taxonomic groups. Live sorted animals were either preserved in 1% formalin or 80% ethanol. Finally, specimens were cleaned of any lime encrustations and photographed. Otherwise stated, specimens were collected dead. Specimens collected outside the Aurora 2007 expedition are from the personal collection of Prof. Baldomero Olivera. The area covered by the expedition is presented in Figure 1 (Bouchet and Santos 2007).

RESULTS

Larger Species of *Phasmoconus*

In the previous analysis of *Conus* recovered by Aurora 2007 (Olivera, Saguil, and Bouchet 2019), the presence of two smaller species in the *Phasmoconus* lineage (*Conus balerensis* and *Conus leobrerai*) and 3 larger species (*Conus australis*, *Conus lynceus* and *Conus laterculatus*) was documented. Subsequent to the last analysis, all specimens were thoroughly cleaned to remove lime and encrustations and more carefully examined; specimens initially assigned to *Conus australis* proved to be a heterogenous group. The specimens collected at the two deepest stations exhibited clear morphological differences from *C. australis* specimens collected between 120-160 meters. At Station CP2742, a dredge haul from between 182-205 meters, the shell collected was broader in the outline of the body whorl, and more heavily granulated than the *Conus australis* specimens, with some features similar to *C. armadillo*. The specimen recovered at the greatest depth, at Station DW2726 (depth 327-

Figure 1: Map indicating the collection sites (red circles) of the Aurora 2007 expedition. Map adapted from the Aurora 2007 cruise report (Bouchet and Santos 2007).

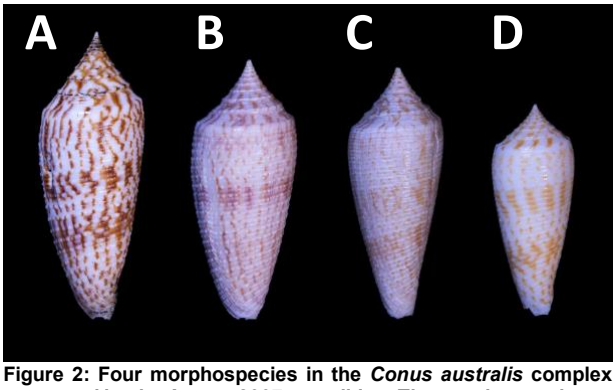

Figure 2: Four morphospecies in the *Conus australis* complex recovered by the Aurora 2007 expedition. The specimens shown were all collected at the Aurora site; two of the morphospecies are specimens of well-known taxa: *Conus australis* (A) and *Conus laterculatus* (D). The other two specimens are distinct from any previous Philippine material; B is tentatively assigned to *Conus gabryae*, while C is a new species that we designate as *Conus glorialita*.

339 meters) also diverged significantly from the typical form: the sculpture of the shell was finer, and the shell more cylindrical with a relatively shorter spire; it seemed morphologically close to *C. laterculatus*. Thus, in the Aurora 2007 material, three similar but distinct morphospecies were assigned to the *Conus australis* complex, with the majority being typical *Conus australis*. We compare the four morphospecies of *Phasmoconus* recovered by Aurora 2007 that are most similar to *Conus australis* (Figure 2). A comparison of the Aurora 2007 material with live-collected specimens from other Philippine localities is shown in Figure 3.

Conus* (*Phasmoconus*) *australis

Except for *Conus balerensis*, most of the *Phasmoconus* species from Aurora 2007 discussed in this study were only found in 1-2 dredge hauls. *Conus australis* and related specimens presented in figures 2 and 3 are notable in that all 15 specimens were recovered from 6 different Aurora 2007 collection stations (see Table II). Notably, none of the stations were shallower than 120 meters in depth, establishing the deep-water habitat of *Conus australis* at this locality. Adult specimens that were harvested at sites between 120-160 meters in depth were quite similar in morphology, and indistinguishable from specimens collected at other sites in the Philippines (Figure 3).

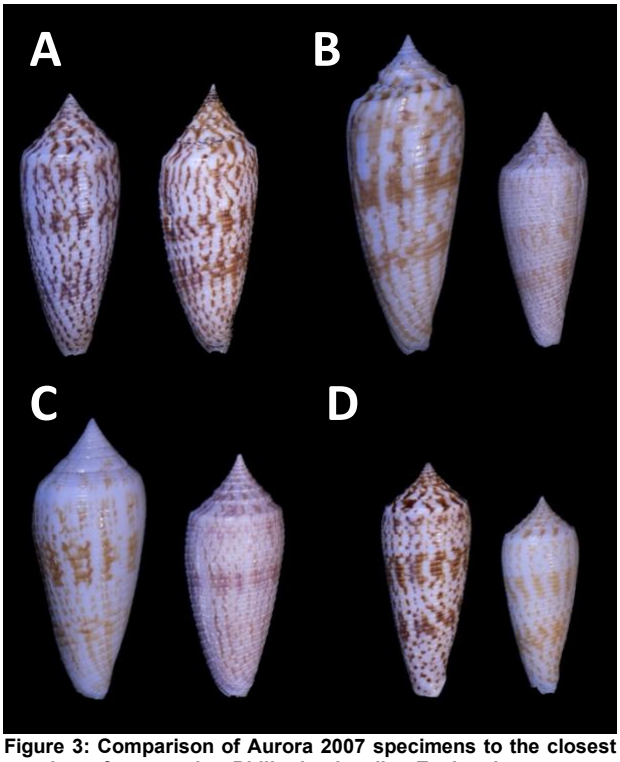

Figure 3: Comparison of Aurora 2007 specimens to the closest specimen from another Philippine locality. Each pair represents the four morphospecies from Aurora 2007 expedition (see Fig 2). The right specimen of each pair was collected during the Aurora 2007 expedition while the left specimen was from another Philippine locality. In the top row are: A) *Conus australis* and B) *Conus glorialita*, a new species. In the bottom row are: C) *Conus* c.f. *gabryae* and D) *Conus laterculatus*. The closest specimen to *Conus* c.f. *gabryae* is probably an unusual variety of *Conus armadillo*. The closest specimen to the holotype of *Conus glorialita* is conspecific, and is regarded as Paratype #1. For *Conus australis*, two live-collected specimens are compared, but for *Conus laterculatus*, the Aurora 2007 specimen is dead collected, while the other *Conus laterculatus* is live taken. Similarly, the Aurora 2007 *Conus glorialita* is an empty shell, while the Paratype was live taken.

***Conus* (*Phasmoconus*) c.f. *gabryae*, Korn and Röckel, 1992**

A single specimen recovered at one of the deepest stations, 182-205 meters is divergent morphologically from the other *Conus australis* collected at the expedition site. The shell appears to have greater similarity to *Conus armadillo*, a species primarily collected in the Central Philippines and Balut Island, off Southern Mindanao, using tangle nets. The Aurora 2007 specimen is somewhat intermediate between *Conus australis* and *Conus armadillo*, but morphologically, differs significantly from both. This specimen seems most similar to *Conus gabryae*, which has been regarded either as a distinctive subspecies of *Conus australis* endemic to the Solomon Islands, and more recently, proposed as a valid species (Monnier et al. 2018). This is the first record for this form in the Philippine Archipelago, and thus would be a new locality record. We illustrate the Aurora 2007 *C. gabryae* specimen with other Philippine specimens of *Conus armadillo* (Figure 4). The assignment to *C. gabryae* is provisional.

***Conus glorialita*, new species**

Holotype: The holotype was dredged off Baler, Aurora, Eastern Luzon (MNHN Station DW2726, 15° 20"N, 121°34"E, using the MV-DA-BFAR vessel. Depth: 327-339 meters and was collected on May 31st, 2007. The holotype is deposited at the MNHN, Paris. This specimen is shown in Figure 5.

Etymology: It is a pleasure for the authors to name this species after our colleagues, Julita (Lita) S. Imperial and Gloria P.

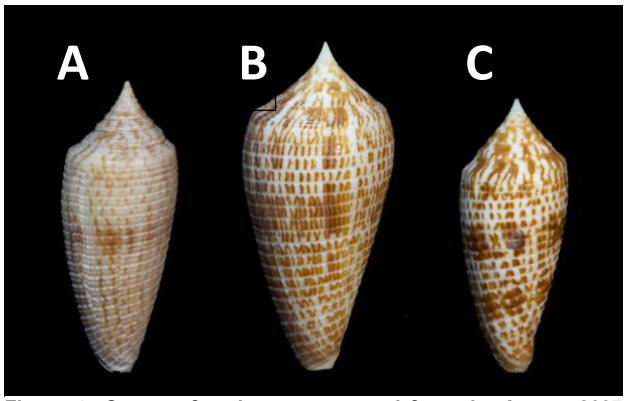

Figure 4: *Conus* c.f. *gabryae*, recovered from the Aurora 2007 expedition (A). This specimen compared to typical Philippine *Conus armadillo* (B and C). As discussed in the text, the new form is tentatively identified as *Conus* c.f. *gabryae*. Note differences in shell morphology between the Aurora specimen and the two typical *Conus armadillo*.

Figure 5: Holotype of *Conus* (*Phasmoconus*) *glorialita*, new species. Collected by the Aurora 2007 expedition.

Description, comparison to *Conus australis*: The holotype, an empty shell, is compared to specimens of *Conus australis*, *Conus laterculatus* and *Conus armadillo* in Figures 2 and 6. Figure 7 illustrates some of the key morphological features that differentiate the new species. Compared to *Conus australis*, the shell of *C. glorialita* is more sharply biconical with a strongly-angled shoulder, and the body whorl is narrower and straighter in outline than *Conus australis*, which is more cylindrical with a less conical body whorl. The ratio of the total length of the spire to the shoulder is smaller in proportion to the length of the body whorl than in *Conus australis*; a diagnostic difference is the much-finer spiral sculpture of the new species; the spiral ribbons

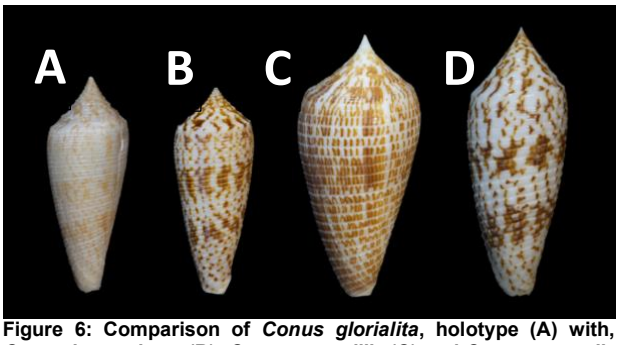

Figure 6: Comparison of *Conus glorialita*, holotype (A) with, *Conus laterculatus* (B); *Conus armadillo* (C) and *Conus australis* (D).

in *Conus australis* are broader, with more defined spaces between ribbons as illustrated in Figure 7. Although in the holotype the shell pattern is faded, it clearly differs from *Conus australis* in being generally finer, with the darker colors more interspersed with lighter background areas. In its general shape, *C. glorialita* is more similar to *Conus laterculatus*, but it differs in the sculpture of the body whorl and the spire whorls, and the higher spire.

Paratype; other related material

The designated paratype (see Figure 8) differs significantly from the holotype in size and condition. The paratype is a large, live-collected specimen purchased from a commercial dealer in July, 2005, said to be from Aliguay Island, off Northern Mindanao, Philippines.

There are a group of albinistic specimens, one of these is approximately the same size as the *C. glorialita* holotype, but with no pattern on the body whorl (shown in Figure 9). This specimen, purchased from a commercial dealer, had the locality "Bohol Island, Philippines, gill nets in deep water" on the label. This is provisionally regarded as an albinistic variety of *Conus* (*Phasmoconus*) *glorialita*. One morphological feature that supports the assignment of the albinistic specimen to the new species is the structural features of the spire. The albinistic specimen has a spire that is much more similar to the holotype than to *C. australis* and *C. laterculatus*. The spire of Paratype 1 of *Conus glorialita* is not shown, because it clearly had been treated with acid by the commercial dealer, a common practice to remove black spots often found on the spires of *Phasmoconus* spp by shell dealers.

We have not included the albinistic specimen in the type series, since we regard the assignment to *Conus glorialita* as provisional, and DNA sequence data for both typical *glorialita* and the albinistic form would be required to confirm this assignment. The albinistic specimen has some similarity to *Conus albellus*, Röckel and Korn (1990), which is now generally regarded as a form of *Conus limpusi*, and believed to be endemic to Queensland, Australia. The typical *Conus limpusi* is morphologically dissimilar to the *Conus glorialita* types. The possibility that *Conus albellus* is not conspecific with *Conus limpusi*, and is a form that extends to the Philippines cannot be eliminated at this time, and is a viable alternative assignment for the albinistic specimen shown in the figure. We note that *Conus limpusi* and *Conus albellus* are not regarded as species in *Phasmoconus*, but are assigned in most of the literature to a different subgenus, *Eremiconus* (Monnier et al. 2018).

Conus* (*Phasmoconus*) *laterculatus

Four specimens of *Conus laterculatus,* one adult (shown in Figures 2 and 3) and three subadult were collected by the Aurora 2007 at depths of 83-107 meters. *Conus laterculatus* has been found at many localities in the Philippines, and was trawled by

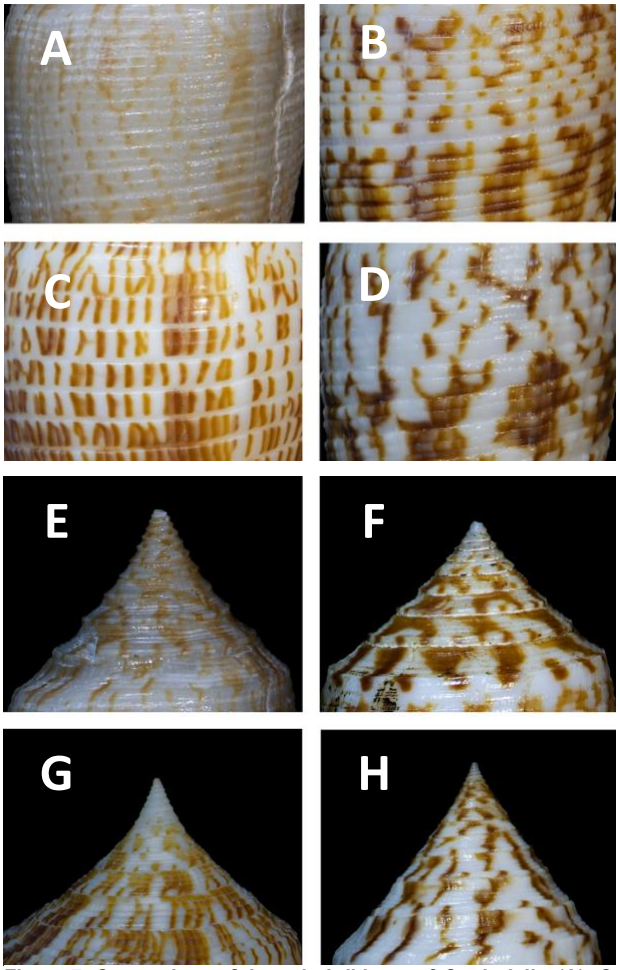

Figure 7: Comparison of the spiral ribbons of *C. glorialita* (A), *C. laterculatus* (B), *C. armadillo* (C) and *C. australis* (D). Comparison of the spiral sculpture of *C. glorialita* (E), *C. laterculatus* (F), *C. armadillo* (G) and *C. australis* (H).

fishing vessels or collected by gill nets. The Aurora 2007 specimens are similar to specimens from other Philippine localities. There has been a morphologically very similar form from Sogod Cebu that was recently named *Conus* (*Phasmoconus*) *sogodensis* (Poppe, Monnier, and Tagaro 2012). The key difference is that the aperture of *Conus laterculatus* is purplish in tone and that of *Conus sogodensis* is white. Because all materials from the Aurora 2007 expedition are dead collected with any interior aperture color faded, we are unable to verify whether this is typical *laterculatus*, or *sogodensis*. In the absence of DNA evidence, it is unclear at this point whether these two species are truly separable.

Conus* (*Phasmoconus*) *lynceus

The Aurora 2007 specimens of *Conus lynceus* were dredged at a depth of 120-124 meters; all were dead-collected, and only one was adult. The majority of specimens of *Conus lynceus* that are in museum collections were a by-catch of fishing vessels, operating in Manila Bay in the 1970s, when fishing trawls still dragged the bottom. The specimens collected by the Aurora 2007 (Figure 10) are not typical of the Manila Bay population; the adult specimen and one juvenile collected off Baler are compared to a series from other localities in Figure 11; although similar specimens have been recovered from other Philippine sites, the dominant morphological variety from Baler is relatively rare elsewhere. The patterns on the shells of *Conus lynceus* vary considerably, as illustrated in Figure 11.

Conus lynceus has been observed by the authors to feed on fish in an aquarium; when presented with a small fish that is tethered,

Figure 8: Paratype of *Conus glorialita*. Collected from Aliguay Island, Philippines.

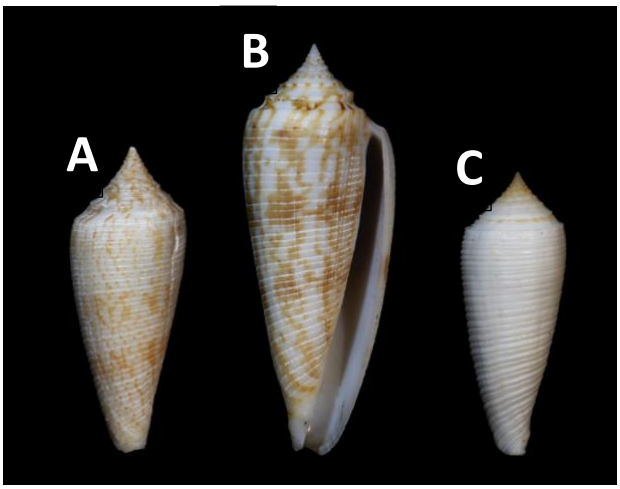

Figure 9: *Conus glorialita* (A), holotype specimen from Aurora 2007 expedition; B) paratype #1 from Aliguay Island; C) albinistic specimen, tentatively assigned to *Conus glorialita* (see Discussion in text).

the snail extends its rostrum, which is surprisingly narrow for the size of the snail. An envenomation event was never observed — the snails clearly recognized and devoured fish (and were much easier to feed in an aquarium than other species of *Phasmoconus*), but how the snail envenomates its natural prey, and what types of fish *C. lynceus* envenomates in the wild remain unknown. The molecular data obtained so far (unpublished) suggest that *Conus lynceus* is in a distinctive branch within *Phasmoconus* that also contains *Conus laterculatus*.

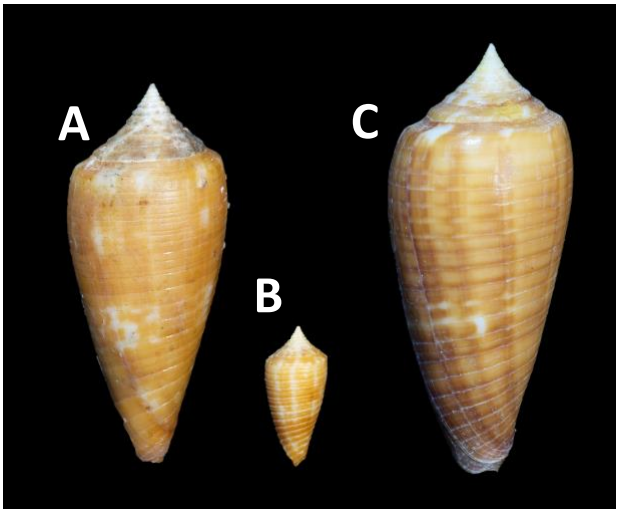

Figure 10: *Conus lynceus* (A and B collected in the Aurora 2007 expedition). Specimen from the Sulu Sea (C) is the morphologically closest variety to the Aurora 2007 specimens.

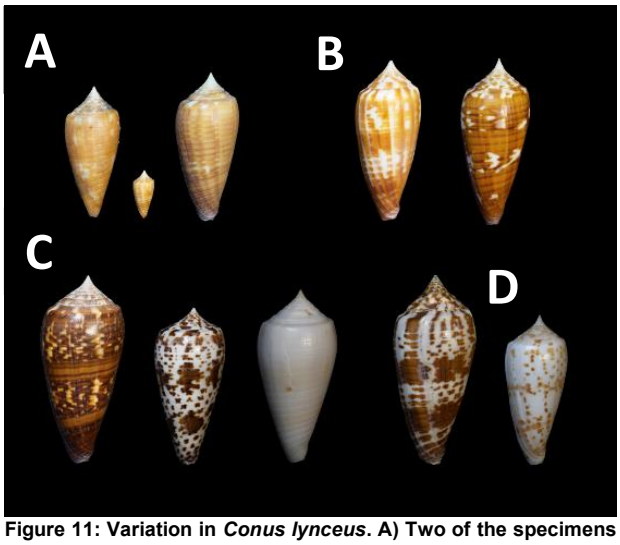

Figure 11: Variation in *Conus lynceus*. A) Two of the specimens from the Aurora 2007 expedition (first two from left) are most similar to the rightmost specimen from the Sulu Sea area (See Fig 10). Other specimens are from Manila Bay (B and C), except for the specimen in D, which is from Swains Reef, Queensland Australia. The series shows the extreme variability that can occur in the shells of *Conus lynceus*; approximately 90% of all specimens in collections are similar to the shell in C, second from right, which is the typical form collected in Manila Bay. This species was regularly collected by fish trawlers that dragged the bottom, but since that trawling method is no longer widely used, *Conus lynceus* has been much more difficult to obtain in recent years.

Smaller *Phasmoconus* Species Collected at Aurora

The five smaller species of *Phasmoconus* recovered at Aurora provide new insights, but also present taxonomic and phylogenetic challenges. In addition to the remarkable harvest of *Conus balerensis*, four other smaller *Phasmoconus* morphospecies can be distinguished, all dead collected, with each represented by only a few specimens. Two of these are species previously recorded from the Philippines, *C. mucronatus* and *C. leobrerai*. Two have not previously been reported from the Philippines, one provisioAnally assigned to *Conus grangeri* and a new undescribed form, *Conus* (*Phasmoconus*) *tayabasensis*, a new species.

***Conus* (*Phasmoconus*) *mucronatus* (Reeve, 1843)**

The single Aurora 2007 specimen of this species was collected at 83 meters, in a trawl haul that also contained *Conus laterculatus*, *Conus leobrerai* and a new unidentified *Phasmoconus*, described below (see Table 2). The *C. mucronatus* specimen from Aurora is typical, resembling *C. mucronatus* from other Philippine sites. *Conus mucronatus* is regularly collected by shell-gathering fishermen at many sites in the Philippines using tangle nets.

***Conus* (*Phasmoconus*) *tayabasensis*, new species**

Type: The holotype was collected at a depth of 83 meters in the same Aurora 2007 trawl that yielded *Conus mucronatus* (Figure 12). The specimen is roughly the same size and shape as *Conus mucronatus*, and was originally assigned to that species; once the shell was cleaned and more closely examined, it became clear that the specimen was not *C. mucronatus* and appears to be an undescribed species in *Phasmoconus*. We cannot eliminate the possibility that this taxon is not a *Phasmoconus*; it has certain characteristics that make an assignment to *Eremiconus*, a proposed lineage of *Conus* species reported only from Australia a viable possibility.

Figure 12: Holotype of *Conus tayabasensis*, new species. Note the fine sculpture on the upper half of the body whorl.

Etymology: The Aurora 2007 expedition was carried out off Baler, now in the province of Aurora. The traditional name for the province covering the Eastern Luzon coast from Baler to the Bicol Peninsula is Tayabas, which was split into two provinces, Aurora and Quezon. Manuel Quezon was the president of the Philippines when it was a commonwealth colony of the U.S.; Aurora Quezon was his wife — they were both from what was then Tayabas province. This name also honors the memory of the parents of the senior author, Carolina Marquez and Baldomero Tañada Olivera, who were from Tayabas Province, from the towns of Lucena and Gumaca, respectively.

Shell Description. The new species is relatively small, conical in outline with a convex spire; the body whorl is white, with brown streaks extending from the sutural ramp and on the spire. The entire shell is decorated with fine spiral ribbons, which become stronger at the anterior, and more widely spaced. Within the interstitial area between the spiral ribbons at the anterior end of the body whorl, small square depressions are present (see Fig 12).

Comparison to other Phasmoconus species. In the general shape and color of the shell, *Conus tayabasensis* is most similar to specimens generally assigned to *Conus lovelreevei* (there is disagreement in the literature whether *lovelreevei* is a separate species (see Monnier et al. 2018) or a subspecies of *Conus asiaticus* see (Rockel, Korn, and Kohn 1995)). The sculpture of *Conus lovelreevei* is distinctly different, in having prominent raised circular ridges that are discontinuous. *Conus tayabasensis* also has some similarities to specimens of *Conus sculpturatus*, but the body whorl of the latter is more cylindrical and elongated, and in general the brown streaks of *Conus suturatus* extend well into the body whorl. Furthermore, the raised ridges that spiral around the body whorl are much more prominent in *Conus sculpturatus*. Comparisons of these species, including a closeup

of the sculptural details that appear to be a diagnostic character are shown in Figure 13.

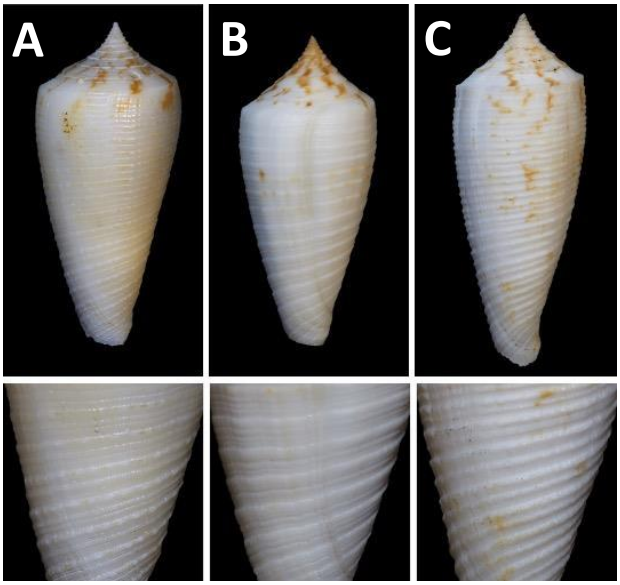

Figure 13: *Conus tayabaensis* (A), a new species compared to *Conus mucronatus lovelreevei* (B) and *Conus sculpturatus* (C). The new species (A) is most similar to *Conus sculpturatus* (C) and specimens generally assigned to *Conus mucronatus lovelreevei* (B), a taxon that is sometimes regarded as a full species. Sculptural differences are illustrated by the close-up of the body whorl shown in the lower panel.

The *Conus leobrerai* complex.

One of the more notable recoveries from Aurora 2007 were three specimens of *Conus leobrerai* (Figure 14). This species is sufficiently morphologically distinct from other *Conus* species and has been widely accepted as a valid, though little-understood taxon. The Aurora 2007 specimens will be discussed together with all specimens assigned to *C. leobrerai* that the authors could access. As a result of the analysis, we have reconfirmed the identity of the Aurora 2007 *Conus leobrerai* specimens. The Aurora 2007 expedition has provided the first detailed collection data for the species. An additional specimen collected during Aurora 2007 originally assigned to *leobrerai* is in fact a different species that we provisionally assign to *Conus grangeri*, a species not previously reported from the Philippines.

This related material, *Conus leobrerai* from the type locality, *Conus leobrerai* collected by the Aurora 2007 expedition, *Conus grangeri* collected by Aurora 2007 and the only other specimen found in the Philippines that we assign to *Conus grangeri* are discussed in the section that follows.

***Conus* (*Phasmoconus*) *leobrerai* (da Motta and Martin, 1982).**

Three specimens of *Conus leobrerai*, all dead collected, were recovered in Aurora at a depth of 83 meters. This poorly-understood species was described from specimens collected in the Visayan Sea, off Northern Cebu Island. The type locality yielded a number of specimens; examples are shown in Figure 14 with the Aurora specimens. Additional specimens that have been assigned to this species that are not from the type locality are also shown. The specimen from Siquijor is clearly similar to the type locality material, although more elongate. Specimens from other localities in Cebu Island and Bohol differ somewhat in the shell pattern, and have a greater similarity to some forms of *Conus mucronatus*, but their overall shape makes an assignment to *Conus leobrerai* likely. The figure documents the potential variation presently known in *Conus leobrerai*.

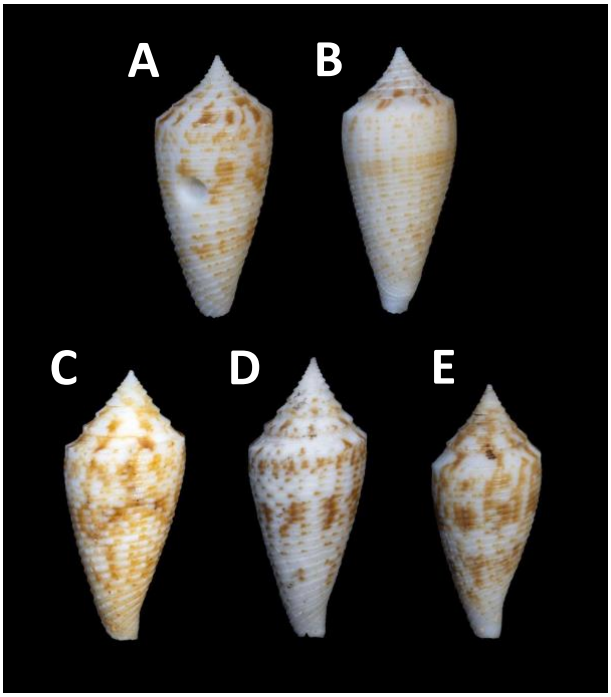

Figure 14: *Conus leobrerai* collected in the Aurora 2007 expedition (A and B) compared to *Conus leobrerai* from the Central Philippines (C - E). C and D are either from Cebu or Bohol and E is from Siquijor.

***Conus* (*Phasmoconus*) c.f. *grangeri* (Sowerby III, 1900)**

A single specimen only provisionally assigned to this poorly-defined species was recovered at a depth of 120-124 meters. The type of *Conus grangeri* comes from an unknown locality (the original description by Sowerby had no locality provided). For this reason, there are different interpretations of what comprises this species. There is one other specimen from the Philippines that we tentatively assign to this species; the two Philippine shells are illustrated in Figure 15. A comparison of these to *Conus leobrerai* is shown in the figure.

Part of the reason for the confusion regarding *Conus grangeri* in the literature is due to the lack of an assigned locality for the holotype. Some workers, notably Röckel et al. (Rockel, Korn, and Kohn 1995) have assigned the type of *Conus grangeri* to a form found in a Red Sea population, which has also been given the name *Conus batheon* (Sturany, 1903). However, Monnier et al. (Monnier et al. 2018) are of the opinion that the type specimen is closer to a Solomon Island population, and these workers separated *Conus grangeri* from *Conus batheon*, while Röckel et al. regard these as synonyms. In any event, this form has not been reported from the Philippines previously, and it seems closest to the Solomon Island specimens illustrated by Monnier and coworkers.

***Conus* (*Phasmoconus*) *balerensis* (Olivera, Saguil and Bouchet, 2019)**

The most remarkable discovery made by the Aurora 2007 expedition is this small new species of *Phasmoconus*, the most common cone snail at the site, which to date, has not been found anywhere else except at the original collection locality off Baler, Aurora Province, Eastern Luzon Island. The holotype is shown in Figure 16. Compared to other small species of *Phasmoconus* recovered at Aurora 2007, *Conus balerensis* had an extremely wide depth range, including several stations where specimens were collected alive. The DNA sequence obtained established that it belonged to *Phasmoconus*, and its position on the phylogenetic tree suggested that among the species for which molecular data had been obtained, it was on the same branch as

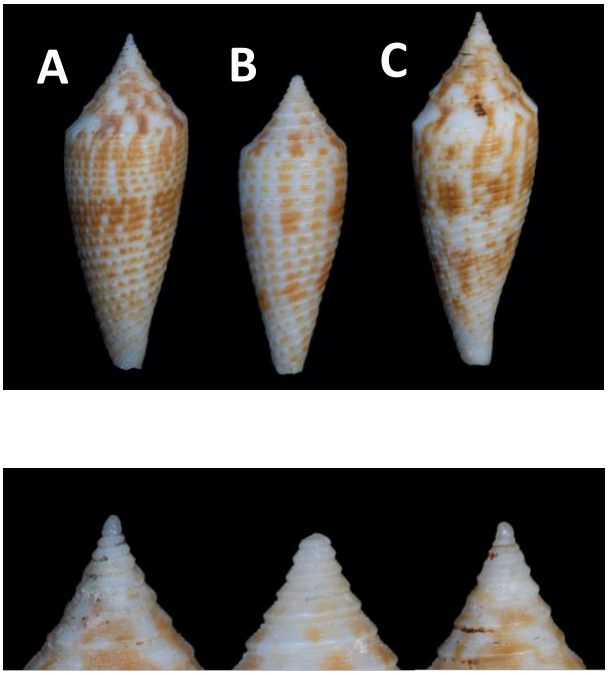

Figure 15: Comparison of *Conus* c.f. *grangeri* from Aurora 2007 (B) compared to *Conus leobrerai* (C). A second specimen (A), not previously recognized, appears to be conspecific with the Aurora 2007 *Conus grangeri.* Bottom panel is a close up of the spire of each specimen.

Conus mucronatus. As was pointed out in the original it seems closest to *Conus* (*Phasmoconus*) *asiaticus* and to *Conus* (*Phasmoconus*) *alabaster*, for which no DNA sequences are presently available; it remains to be seen whether these morphological affinities translate into closer phylogenetic relationships than can be established using the presently available data.

DISCUSSION

The present study has focused on the species in the subgenus *Phasmoconus* collected by the Aurora 2007 expedition. This group of *Conus* has generally been poorly characterized. The Aurora 2007 expedition, organized by the MNHN, was carried out off Baler, Aurora, Eastern Luzon, at a site that proved to be unique in terms of the distribution of the putative fish-hunting cone snail species recovered. We identified morphospecies of *Phasmoconus* that have not previously been recognized as occurring in the Philippines, and/or not previously described in the scientific literature. A summary of all of the *Phasmoconus* found during the Aurora 2007 expedition is provided (Table 2), including the number of specimens of each, and the depth range in which each specimen was collected. This has provideed the most detailed field-collecting data available for this set of deeper-water *Phasmoconus*, revealing the relative stratigraphy of many of the off-shore species for the first time. The accurate field data, and careful sorting carried out under the direction of Philippe Bouchet, Muséum National d'Histoire Naturelle (MNHN) in Paris provides a rich trove of correlative data; we present an overview of general insights gained regarding *Phasmoconus* based on the specimens collected during the expedition, and from a comparative analysis of additional related material collected at other sites.

The hauls from trawls and dredges that led to the recovery of specimens of *Phasmoconus* spp varied in depth at Aurora from 66 to 380 meters, a broad stratigraphic range. Some species of *Phasmoconus* recovered were represented by a single specimen; for most species, less than 5 specimens were found.

Figure 16: *Conus balerensis* holotype collected during the Aurora 2007 expedition showing the dorsal (left) and ventral (right) views of the shell.

Nevertheless, it is clear that there appears to be a characteristic depth at which the individual species were collected. The most abundant *Conus* species at the site, *Conus balerensis*, was recovered at many stations over an extremely broad stratigraphic range. Of the 9 other morphospecies of *Phasmoconus* found, 4 were recovered in the 66-100 meter depth range: *laterculatus*, *leobrerai*, *mucronatus* and *tayabasensis*. At somewhat deeper sites stratigraphically, two additional species were found, *C. lynceus* and *C.* c.f. *grangeri*. Three species were recovered only at depths greater than 120 meters — *C. australis*, *C.* c.f. *gabryae* and *C. glorialita*.

This analysis of *Phasmoconus* based on specimens from the Aurora 2007 expedition and related material has resulted in the definition of 10 different morphospecies. Of the species defined by the Aurora 2007 material and related specimens analyzed in this study, 5 have not previously been recorded from the Philippines — two of these, *Conus* c.f. *grangeri* and *Conus* c.f. *gabryae* are tentatively assigned to poorly understood species and the other 3 were apparently undescribed and have been named in this and the previous article: *Conus balerensis*, *glorialita* and *tayabasensis*. This is an enormously-skewed distribution of new records for cone snails in the Philippines. Given that the Philippine archipelago is arguably the most intensively-sampled locality in the world for *Conus*, such a high proportion of species previously unrecorded in a single study has broad implications. One rationale for the high proportion of new records is the nature of the Aurora 2007 expedition. The ability to collect systematically in deeper water and at a new locality not sampled previously certainly was one key factor.

However, these results suggest a significant undiscovered biodiversity of deep-water *Phasmoconus*. The fact that the most common species recovered has not been found in any other locality indicates that the discovery of *Conus balerensis* may be the harbinger for the future discovery of other deep-water *Phasmoconus* that are geographically highly localized. The subgenus *Phasmoconus* can be roughly divided into shallow-water species, accessible through standard scuba diving, and the deep-water *Phasmoconus* biota, found at depths greater than 50 meters. In recent years, there has been an explosion of new forms of *Phasmoconus* described, largely from the shallow-water biota. In their monograph of living *Conus* species, Monnier and coworkers define 103 potential morphospecies in *Phasmoconus*, one of the largest groups of cone snails recognized (Monnier et al. 2018). Of these, 57 are either still undescribed or were

described after 1970. A very high proportion is small, shallow-water forms discovered by collectors using scuba or hookah. Of the new forms recorded in this analysis, 4 are relatively-small species of *Phasmoconus*, but from the deep-water biota. Thus, a clear implication is that there is a radiation of deep-water, small *Phasmoconus* species that remain to be defined. Among fish-hunting cone snail lineages, these may be a significant sector of the total biodiversity of living *Phasmoconus*.

The authors have undertaken this analysis as part of a larger effort to understand speciation in *Phasmoconus*, which has one of the largest numbers of putative species proposed for any lineage of cone snails. The venom components of this group of cone snails have generally been uncharacterized; only one species has been examined in some detail, the type species of *Phasmoconus*, *Conus radiatus*. The analysis of this first *Phasmoconus* venom has already demonstrated significant biomedical potential. One characterized conopeptide from *Conus raaiatus*, κM-RIIIJ, has proven to be an important pharmacological tool ,both for understanding different classes of neurons, as well as for defining the voltage-gated ion channels present in each type of excitable cell (Cordeiro et al. 2019; Chen et al. 2010) — thus, the potential of *Phasmoconus* venom components for basic research in neuroscience, and for addressing pathologies of the nervous system provide a strong incentive for prioritizing the characterization of this poorly-understood, biodiverse group of cone snails.

Investigating biodiversity has traditionally been carried out in two sharply divided modes: 1) a broad survey of a taxonomic group, or at the other extreme; 2) reductionist studies at the organism level. This will almost certainly change radically in the near future, since recent technological advances (genomics, transcriptomics, proteomics, molecular phylogenetics) should lead to an integration between different biological levels and the reductionist and the whole organism/taxonomic data can become increasingly linked. The types of studies described in this report will be one approach to be able to forge these connections. By analyzing taxonomic/ecological data that is focused both with respect to the taxonomic group and the specific site, insight into speciation and biological differences between lineages can be gained. Because it is our intention to collect molecular/biochemical data on *Phasmoconus*, the present study serves as a starting point for clarifying how different species may be adapted to their differing physical environments and biotic interactions.

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