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The Molecular Phylogeny and Biogeography of the Trochomorphidae in Belau (Republic of Palau, Oceania)

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THE MOLECULAR PHYLOGENY AND BIOGEOGRAPHY OF THE TROCHOMORPHIDAE IN BELAU (REPUBLIC OF PALAU, OCEANIA)

By:

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Abstract

E.B. Clark. The Molecular Phylogeny And Biogeography Of Trochomorphidae In Belau (Republic of Palau, Oceania), 83 pages, 6 tables, 22 figures, 2020. CSE style.

The Trochomorphidae is an understudied family of terrestrial pulmonate gastropods. The genera of this family are found throughout Southeast Asia and in western Pacific islands. Belau (Republic of Palau, Oceania) is home to five species of trochomorphids: *Videna electra*, *Videna oleacina*, *Videna pagodula*, *Videna pumila*, and *Liravidena lacerata*. While these species were previously described nearly 100 years ago, detailed research on the relationships between these species has yet to be studied. At the same time, these species are facing an extinction crisis due to humans, in the form of habitat loss and the introduction of invasive predators. This research presents the first phylogenetic analyses of the Belau trochomorphids, the first photographs of each of the five species, updated species descriptions, and current geographic range maps. Conservation suggestions for Belau trochomorphids were made based on the results of this research, including the continuation of rat eradication efforts across the archipelago.

Keywords: Trochomorphidae, *Videna*, land snails, Palau, phylogenetics, biogeography

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1. Introduction

1.1. Taxonomy of Belau trochomorphids

Alan Solem's 1959 work, *Systematics of the Land and Freshwater Mollusca of the New Hebrides*, makes a short observation on the neighboring Belau archipelago: "The Palaus… are worth mentioning because of the remarkable radiation of the trochomorphid genus *Videna*, which occurred there" (p. 303). While this was just a quick observation on Solem's part, it beautifully describes the diversification of these trochomorphid *ngetmakl* (land snails) on Belau (the accepted indigenous name for the archipelago that encompasses the country of the Republic of Palau; Motteler 2006).

The genus *Videna* was first described in 1855 by Henry and Arthur Adams as a subgenus of *Trochomorpha* (Albers 1850). *Videna* comprises over 60 described species from Southeast Asia and the western Pacific (E.B. Clark 2020, unpublished data). The type species of the genus is *Videna metcalfei* (Baker 1941).

It was during this time of Pacific exploration in the 1800s that Carl Semper described the Belau *Videna* species of *V. electra*, *V. pagodula,* and *V. oleacina* in 1873, and considered these species not as *Videna* but as *Trochomorpha*. By 1890, a subfamily within the Zonitidae had been assigned for *Videna* and related species, the Trochomorphinae (Mollendorf 1890), and so the Belau species were moved into this subfamily. *Videna* continued to be used as a genus throughout this time, acquiring and losing species as more were described and as our understanding of land snail taxonomy grew. In 1941, H.B. Baker had published his *Zonitid Snails of the Pacific* and included updated illustrations of the known Belau *Videna* species, and described a new *Videna* as well, *Videna pumila*. He also reassigned *V. pagodula* and *V. oleacina* to the genera *Peleliua* and *Periryua*, respectively, based on shell morphology and reproductive tract characteristics. *Peleliua* is named after the Anglicized spelling of the southern Belau island of Beliliou. *Periryua* is named after the Japanese translation of Beliliou, Periryū. The specimens Baker dissected were initially collected by Yoshio Kondo in 1935-1936.

The fifth trochomorphid species found on Belau, *Liravidena lacerata*, was initially identified as an endodontid land snail, *Endodonta lacerata*, and this taxonomy did not change until Solem in 1959. Since then, little else has been done to further understand the taxonomy of *Liravidena*.

Much of the taxonomic assessment of Trochomorphidae and *Videna* has been based on morphological characteristics, including external and internal shell characters, radulae, and genitalia. Little has been done in recent years to reexamine the relationships within both the Trochomorphidae and *Videna* at the molecular level. The most current taxonomy (Bouchet et al. 2017) places *Videna* as follows: Pulmonata (the monophyletic group that includes the largest group of land snail species), Clade Stylommatophora (land snails united by the presence of retractile tentacles and a pedal gland), Infraorder Limacoidea (which includes the Helicarionidae, Limacoid clade; Batsch 1789), superfamily Zonititoidea (Mörch 1864), Superfamily Trochomorphoidea (including the Euconulidae and Chronidae), family Trochomorphidae (Mollendorf 1890), Genus *Videna* (Adams and Adams 1855).

1.2 Belau geology and geography

Belau (Republic of Palau, Oceania; Figure 1) is located at the southern end of the Palau-Kyushu ridge on the Philippine plate near the eastern edge of the Pacific plate (Rundell 2008). More recent research on the plate boundaries in this region of the Pacific has found that a microplate, the Caroline plate, makes up the plate boundary where the Palau trench is formed (Figure 2; Wu et al. 2016). Belau has never been associated with any mainland continent and was formed through the submarine rifting and uplift of limestone beds and volcanic rock along the ridge (Colin 2009). It is categorized as an arc-trench system archipelago (cf. hot spot archipelagos). The archipelago is approximately 800 km from Mindanao (Philippines), Moluccas and New Guinea, and 1500 km from Borneo (Crombie and Pregill 1999, Rundell 2008). It comprises 586 islands, the largest being Babeldaob, which makes up over 80% of the land mass of Belau (Crombie and Pregill 1999). Babeldaob and several smaller, nearby islands are made up of volcanic rock of late Eocene to early Miocene in age (33.9-23 mya, Neall and Trewick 2008, Colin 2009). Belau's volcanic rock was the result of ancient submarine volcanism, subsequent uplift, and accumulation of scleractinian coral reefs on top of the volcanic substrate, which have subsequently also been uplifted. The remaining islands are biogenic limestone rock islands, low platform islands, and atolls, ranging in age from the Miocene through the Pleistocene (23 mya-18,000 years ago; Neall and Trewick 2008, Colin 2009). At the time of the last Glacial Maximum (approximately 20,000 years ago), Belau was one large land mass (Paleo-Palau). Rising sea levels following the glacial melt isolated higher points and created the archipelago as it is today (Colin 2009).

Belau has one of the largest intact tracts of lowland rainforest in Micronesia, a unique feature of the archipelago (Rundell 2008). Temperatures stay around 27° C with a high humidity and rainfall averaging almost 400 cm/year (Colin 2009). These factors, coupled with the large quantities of limestone habitat found on the rock islands and in the karst outcrops on the southern end of Babeldaob, make for ideal terrestrial snail habitat. Calcium availability, in particular, typically leads to higher species richness and endemicity within land snails (Emberton et al.

1997). This pattern can be seen in Belau through the high levels of endemism found on the limestone Rock Islands within the middle of the archipelago between Beliliou and Babeldaob, which includes many species of single and few island endemic land snails.

1.3 Past phylogenetic work on trochomorphid land snails and the Belau trochomorphid fauna

There has been little molecular work done on the relationships of Trochomorphidae to other pulmonate land snail families, and little research done on relationships among species of trochomorphids. The work that has been done has involved sampling only one or two species, both at the molecular level and morphologically in order to better understand the placement of the Trochomorphidae within the greater stylommatophoran phylogeny (Haudorf 1998, Wade et al. 2006, Hyman et al. 2007).

Previous taxonomic research has resulted in the genus *Videna* being kept squarely within the Trochomorphidae, but workers have not agreed on the placement of Trochomorphidae within the Stylommatophora (Nordsiek 1986, Tillier 1989, Hausdorf 1998). Most, if not all, of the old descriptions were heavily based on shell and reproductive morphologies, which do not give a full picture of the species relationships, since cryptic speciation occurs frequently among the genera within Trochomorphidae (Schileyko 2002). Many species are difficult to tell apart by looking at external morphological characteristics, such as *V. metcalfei* and *V. electra*, which require dissection of the genitalia and a detailed examination of shell characters to distinguish species (Baker 1941, Schileyko 2002).

The initial placement of the family, now Trochomorphidae, was as a subfamily (Trochomorphinae) within the Zonitidae. This positioning in hindsight makes little sense given that nearly all true zonitid snails are found in Palearctic regions, such as Europe and North

America. This system did not change until the 20th century, when new methods to understand morphology were applied and when molecular systematics research blossomed. Baker (1941) and Solem (1978) considered Trochomorphidae to be a subfamily within Zonitidae, following older taxonomies. Nordsieck used shell morphology and geographic distribution to establish the relationships of the stylommatophoran land snails and placed Trochomorphidae within the Helicarionidae (Nordsieck 1986). Tillier (1989) moved Trochomorphidae back to the Zonitidae, basing this choice on the morphological characteristics of the pallial complex, digestive tract, and central nervous system. Hausdorf provided a more updated morphological phylogeny in 1998, using a series of character traits, including reproductive morphology, radulae, lung, and shell characters, and generated a phylogeny based on these traits. He placed Trochomorphidae within the Gastrodontoidea (which includes *Zonitoide*s, *Gastrodonta*, and *Vitrinizonites* land snails). Molecular work on the family did not occur until the early 2000s, with Wade et al.'s (2006) use of the large ribosomal subunit internal transcribed spacer 2 (ITS2), 28S rDNA (28S), and 5.8S rDNA (5.8S) nuclear gene regions and Hyman et al.'s (2007) addition of 16S ribosomal RNA (16S) and mitochondrial cytochrome C oxidase subunit I (COI) gene regions, identifying Trochomorphidae as its own family, but moving it within the superfamily Gastrodontoidea. Again, the extent of these studies was to compare the relationships among larger taxonomic units, and only a few trochomorphid species were sampled.

The most recent phylogenetic work done suggests that Trochomorphidae: 1) does not form a clade with Palearctic groups in Gastrodontoidea, but rather with more closely related Pacific families such as Euconulidae; 2) is distinct from the Helicarionoidea; and 3) is therefore part of its own superfamily, the Trochomorphoidea (Hausdorf 1998, Wade et al. 2006, Hyman et al. 2007, Bouchet et al. 2017, Teasdale 2017). Members of this superfamily include the

Trochomorphidae, Euconulidae, Dyakiidae, Chronidae, and potentially Staffordiidae (Bouchet et al. 2017). It should also be noted that Microcystinae is a sister group to Trochomorphidae, as is the Euconulidae (Bouchet et al. 2017).

Few *Videna* land snails have been studied at the molecular level, and the relationships of this genus and other trochomorphids are still unknown within the Trochomorphidae. Many species that were initially described as *Videna* have since had their taxonomies reassessed and are now considered members of other genera within Trochomorphidae based mostly on morphological features, particularly the reproductive morphology.

Belau *Videna* have seen little taxonomic scrutiny since they were first described. Initial placement of the five trochomorphid species within *Trochomorpha* was based upon these species' descriptions by Semper (1873). These Belau species were then moved to *Videna*. Baker (1941) considered three of the four *Videna* to be contained within two separate genera, *Peleliua pagodula*, *Peleliua pumila,* and *Periryua oleacina*.

1.4 Aims of this study: Phylogenetics, shell morphology and current geographic ranges

The aims of this study are to attain better understand the relationship among species of Belau *Videna*, and to start to provide a clearer picture of the relationships of Belau *Videna* to their fellow members of the genus and to the Trochomorphidae as a whole. Gene regions commonly used in genetic barcoding methods for other metazoans were applied to Belau trochomorphid species to assess these relationships. Specimens collected from the years 2003 to 2019 were photographed and identified to species based on their shell characteristics. These represent the first published photos of the Belau trochomorphids. Species descriptions for each Belau trochomorphid have been compiled and revised. Current geographic range maps have also been drawn for each species to provide an accurate representation of which islands each species is found on. These are the most complete representations of these species' geographic distributions that have ever been compiled. Belau trochomorphid specimens were also assessed for any potential damage from rats found in Belau that are known to predate on these snails, and possible suggestions for conservation with respect to rat predation are given. Black rats (Rattus rattus) and Norway rats (Rattus norvegicus) were introduced by Spanish colonizers in 1710 and are invasive in Belau (Crombie and Pregill 1999). (The only native terrestrial mammals in Belau are: *chesisualik*, the Polynesian sheath-tailed bat (*Emballonura semicaudata*), *olik*, the Palau fruit bat, and a second fruit bat, the large Palau fruit bat (*Pteropus pilosus*), which has been extinct since the late 1800s.) Finally, further research on Belau *Videna* is suggested to provide a path forward in our understanding of this genus and other genera found on Belau.

1.5 Belau trochomorphid taxonomy changes in 2020

MolluscaBase is the modern online clearinghouse for mollusc taxonomic information, and the editors there aim to record the latest reasonable published opinion on mollusc taxa. The process of reviewing the taxonomy of all Recent snails and assessing the validity of names has now caught up to the Trochomorphidae. Despite the long history of ignoring the taxonomy of Belau trochomorphids, this effort has now included *Videna*, which also includes Belau species. Suggested genus-level changes by the editors have oddly coincided with the completion of this thesis and include three of the Belau trochomorphid species: *V. oleacina, V. pumila and V. pagodula*, which will likely no longer be accepted as valid names. Rather, the newly accepted taxonomy indicates that these three species should be part of the genus *Peleliua* as described by Baker (1941). *Peleliua* is united by the geographic distribution of the genus and genital and shell characters. For the purposes of this thesis, I have elected to keep the name *Videna* for these species throughout, since *Videna* in Belau is still in common usage, and currently still adopted by the IUCN Red List, where Belau trochomorphids are formally listed. The new genus status also provides an opportunity to potentially explore the validity of *Peleliua* with respect to molecular phylogeny. I plan to make changes in names of genera, as appropriate, for future publications.

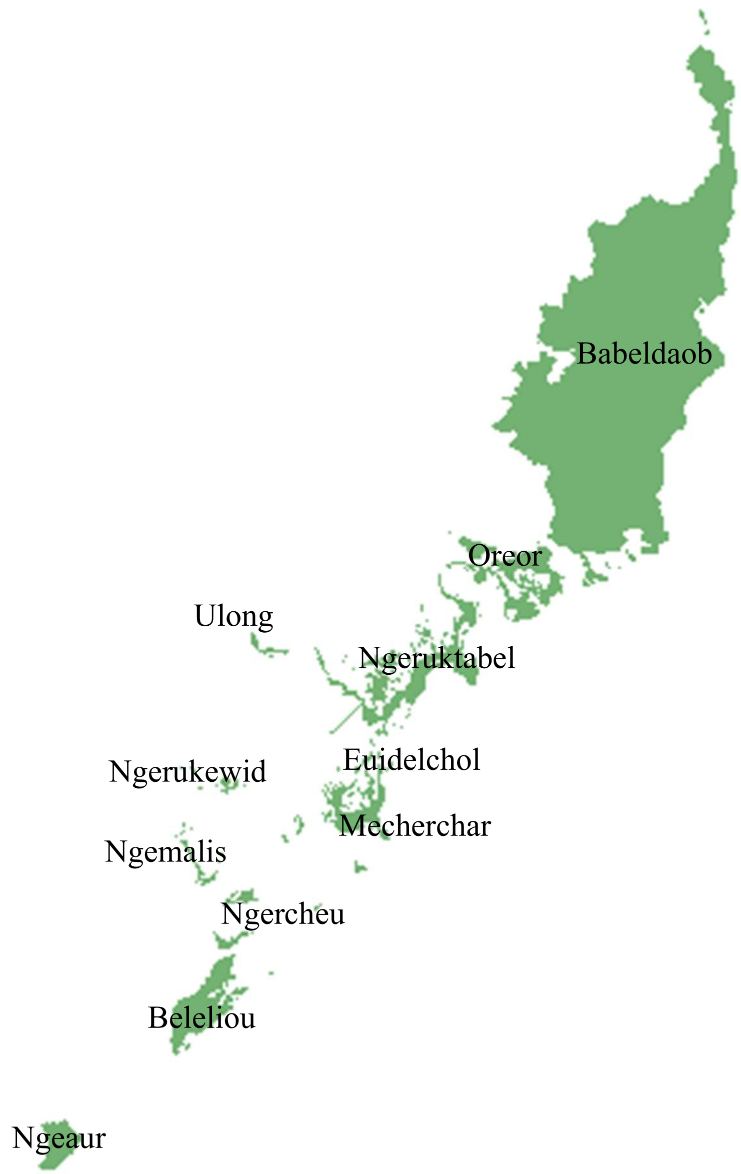


Figure 1.1 Map of Belau, 2020. Major islands and groups of islands are identified according to the accepted indigenous names of the islands, according to Motteler (2006). The islands of Oreor, Ngeruktabel, Ulong, Euidelchol, Mecherchar, Ngerukewid, Ngemalis, and Ngercheu, as well as the small islands associated with these islands, are considered Rock Islands. Babeldaob is volcanic, and Beliliou is a low limestone island.

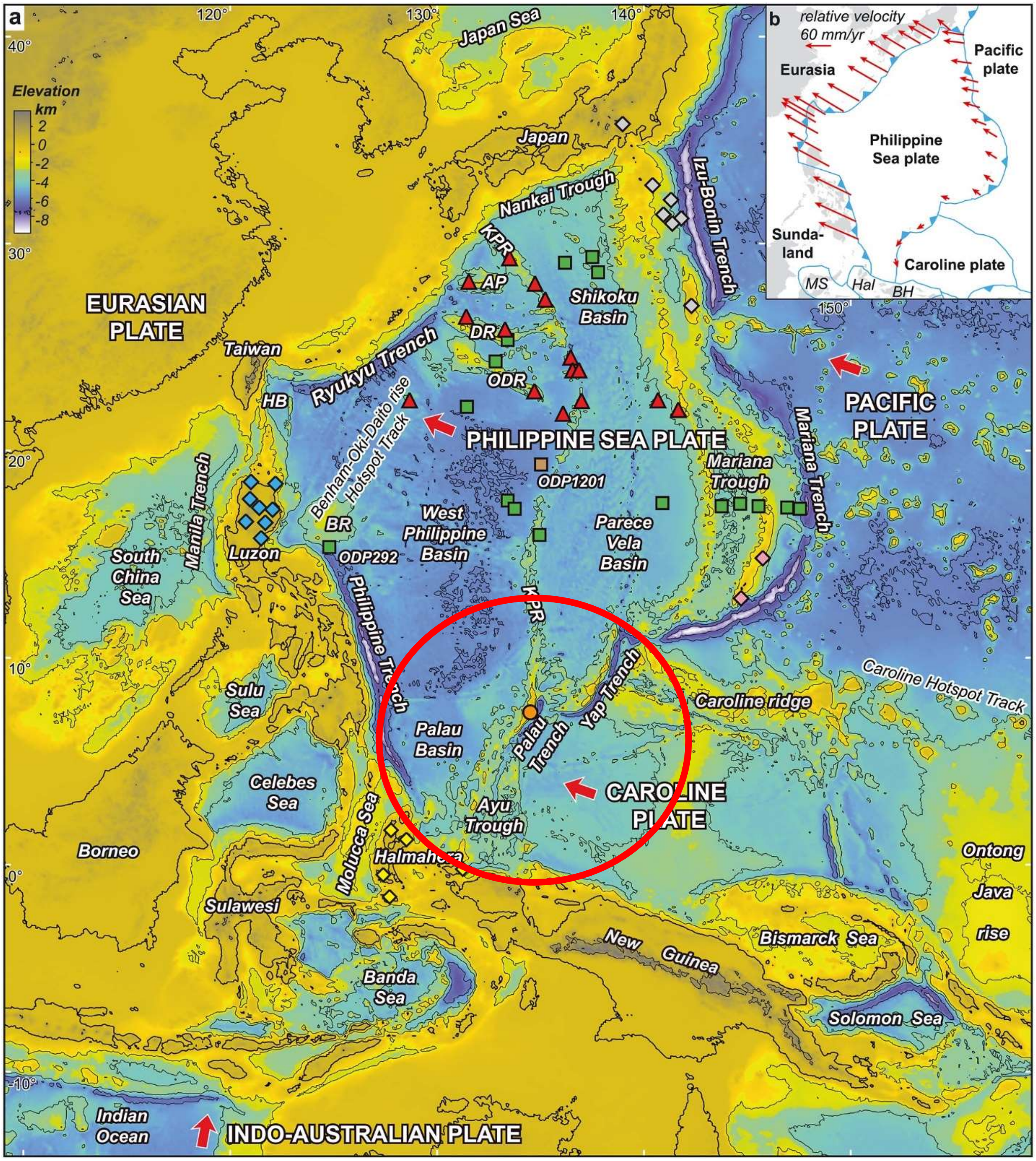


Figure 1.2 Map depicting Belau's location within the Pacific and its geologic position. Belau sits on the edge of the Philippine plate and the Caroline plate, a microplate of the Pacific plate. Reproduced from Wu et al. 2016.

2. Shell morphology of Belau trochomorphids: Updates on species descriptions

2.1 Introduction

The original *Videna* generic description by Henry and Arthur Adams (1855) in *Genera of Recent Mollusca* is as follows: "Shell widely umbilicated, discoidal, keeled, flat or slightly elevated above, convex at the base, last whorl slightly deflexed at the aperture; peristome simple, acute or slightly marginate, the margins arcuated. The species of *Videna* are from the Indian and Western Australian islands, the Philippines, New Guinea, Java, and China. Their usual habitat is under fallen leaves and among decaying vegetable matter" (pp. 114-115). The specimens that the Adams brothers examined were collected by Arthur Adams during his time as assistant surgeon on a survey of the Philippines and Indonesia and deposited in the British Museum of Natural History (British Museum 1904).

This description of the genus has not been changed since it was written, in spite of the fact that species have been added and removed from the genus and geographic ranges have been updated. We now also have the potential to add new or updated character sets through the addition of technologies and molecular phylogenetics research, which in some cases might enhance future species descriptions (e.g., DNA barcodes). Such updates are useful not only in deepening our understanding of these species, but in aiding in species' diagnoses, which are particularly important in facilitating the conservation and further study of the species.

The descriptions for the Belau trochomorphid species have also not been updated in almost 80 years. The last time that the species were evaluated was in H. B. Baker's (1941) *Zonitid Snails of the Pacific Islands*. Baker provided the first drawings depicting genital morphology, radulae, and shell characteristics of each species, but no images depicting the body colors of the animals were shown.

2.2 Materials and methods

Specimen collection, preservation, and sorting

Specimens were collected across the Belau archipelago (Republic of Palau) from leaf litter, rocks, and emergent vegetation from 2003 to 2019. Collections were made by hand, and included timed searches, according to methods described in Rundell (2010). Collections from 2018 and 2019 also included sifting of leaf litter. The relatively large size of Belau trochomorphids, compared to most other Belau land snail species, increased the likelihood that, if a trochomorphid species was present at a particular sampling site, the species would be found. However, at the same time, trochomorphids in Belau also seem to be present in low abundance where they are found and are cryptic. All five species of described Belau trochomorphids (*Videna electra*, *V. oleacina*, *V. pagodula*, *V. pumila*, and *L. lacerata*) were sampled during the collection years above, along with the full diversity of Belau land snails, as part of Rundell's Belau Land Snail Project, begun in 2003. Both live and dead shells were collected. All Belau trochomorphid species were found alive in Belau between 2003 and 2019. Live snails were killed and preserved in 95% ethanol. Specimen sorting and preservation procedure also follows Rundell (2010). Some trochomorphid specimens were sorted out of the mixed-species collections, according to morphospecies, in the Division of Invertebrates at the Field Museum of Natural History (Chicago, Illinois, USA). Sorting continued and species identity was confirmed or discovered by the current author (EC) using shell characteristics and a dissecting microscope at SUNY-ESF, including in the Roosevelt Wild Life Collections lab at SUNY-ESF.

Specimen imaging

Specimens were selected for imaging based on the completeness of the shell. Specimens selected showed no cracks, holes, or breaks, and the body of the animal was still present inside. Each shell was photographed on black clay submerged in 95% ethanol, using a Nikon Ds-Vi1 microscope camera (Nikon Instruments Inc., Melville, NY, USA) mounted to a dissection microscope, using the program NIS-elements (Nikon Instruments Inc., Melville, NY, USA). Shells were manually imaged using the Z-series setting, and then aligned and focused in NIS-elements. Shells were photographed from the shell's aperture, apex, and umbilicus for each species. Images were edited using Adobe Photoshop CS6 (Adobe, San Jose, CA, USA) to provide a solid background and create a sharper image.

Shell measurements

Approximately 50 specimens of each of the Belau trochomorphids were selected to be measured in order to represent an even distribution among localities. Only adult specimens were measured. Shells were measured using digital calipers. Diameter was measured across the widest point of the shell (across the body whorl to the farthest side of the aperture), shell height was measured from the base of the shell to the penultimate whorl for height. The umbilicus was measured across its widest extent. Whorls were counted starting at the edge of the aperture and an approximate average number of whorls was given for each species. The whorl count was averaged to incorporate the uncertainty of age, as adult Belau trochomorphids do not typically possess a lip around the aperture that would have enabled denoting an adult stage. Specimens with height and diameter under 3 mm were not included in the study and assumed to be juveniles.

2.3 Updates on Belau trochomorphid descriptions

The following updates improve upon historical data provided in species descriptions that were written by systematists who did not collect the specimens in the wild in Belau themselves, and who relied on few specimens on which to base their descriptions. Here I treat Belau trochomorphids as a cohesive fauna, with the aim of both improving our understanding of these species, and to assist Belau field biologists and conservation managers in species' diagnoses and comparisons. Examining the Belau fauna as a unit is important because citizens and biologists encountering these species are likely only to require comparison between other Belau species, rather than between *Videna* from elsewhere on Earth. They will also likely only be able to identify the species by eye, unassisted by dissection or a microscope. Relevant descriptive information will also be used to update IUCN Red List species assessment entries, in order to provide free and easy access to species information.

Most Belau endemic land snail species are less than 5 mm in greatest shell length. In contrast, Belau trochomorphids range in maximum shell length from ~7 to ~16 mm in diameter. They are all helicoid in shape. The species vary from one another in terms of the degree of shell keeling (sharp edge of the last body whorl), body color and color patterns, umbilicus width, umbilicus depth, and shell pattern. Below I describe features of each species that assist in their diagnosis, that expand our knowledge of species' shell morphology.

2.3.1 *Videna electra* Semper, 1873

Videna electra's most notable feature is the chestnut band that runs along the outer edge of the shell that extends inward following the whorls to the apex of the shell and is visible both apically and ventrally (Figure 2.1 a. b., Figure 2.2). This spiral is about 0.2 mm thick on average. The shell is flattened dorsally, more than any other Belau *Videna* species, although the apical whorl comes to a slight point. The shell is planispiral with a very sharp keel angling downward. The ventral side of the shell is flatter than *V. pumila*, helping to distinguish the two species from each other. The umbilicus is deep but not as wide as that of *V. pumila* (Figure 2.1 c). *Videna electra* is also the species that best resembles the original description of *Videna* among the four described Belau species, which may have been why Baker (1941) assigned new genera to *V. pumila, V. pagodula* and *V. oleacina* when he incorporated these generic changes into his publication. Baker mentions that *V. electra* looks nearly identical to another *Videna* species, *V. metcalfei* (A species from Cebu island in the Philippines) at first glance but has a slightly different reproductive morphology upon dissection. The oviduct on *V. electra* is situated behind the spermathecal stalk and the stimulator is thicker (Baker 1941).

Videna electra is the most widespread of the Belau *Videna*. It occurs throughout the Rock Islands, including the southeastern end of Airai and the Airai State Rock Islands, Beliliou, and Ngeaur. Several color morphs of this species have been found in recent surveys where the band color and thickness vary from thin to extremely wide and dark, although further assessment is required to determine whether these are truly a color morph or potentially a different cryptic trochomorphid species. The average whorl count is about 5.5 whorls. The average shell diameter is 16.5 mm, making it the widest species of Belau *Videna*. *Videna electra's* shell height average is 7.0 mm. The umbilicus diameter average is about 2.0 mm (Table 2.1).

2.3.2 *Videna oleacina* Semper, 1873

Videna oleacina's shell is the tallest of the Belau trochomorphids. The shell overall is bulbous and round with a flattened apical whorl with a rounded ventral side (Figure 2.3 a, b).

The shell is uniquely shiny apically, but the ventral side is duller. The body is visible through the tan shell (Figure 2.4). The body is a light tan color with irregular black splotches that vary in size across the body. The head and tentacles are a mottled dark grey to black and are lighter at the eyes. A short, broken stripe runs dorsally between the tentacles towards the aperture. It has the smallest and shallowest umbilicus of the Belau trochomorphids, and the interior edge of the aperture nearly runs into the center of the umbilicus (Figure 2.3 c). Despite its rounded appearance, *V. oleacina* has a sharp keel angling downward toward the umbilicus. Baker (1941) notes that the lamellar thickenings in the aperture are unique to *V. oleacina*, but its other morphological features reaffirm the relationship of this species to the other Belau species. *V. oleacina* has an average whorl count of 5.5 whorls. The shell diameter average is 13.0 mm. The shell height average is around 8.0 mm, the tallest of the trochomorphid species on Belau. The umbilicus width average is 0.8 mm (Table 2.1).

2.3.3 *Videna pagodula* Semper, 1873

Videna pagodula has one of the most distinctive shells of any trochomorphid. While the shell is helicoid or planispiral like its fellow trochomorphids, the spire is much higher in relation and steeped on the sides, reminiscent of a pagoda roof (Figure 2.5 c). The apical whorl is flattened (Figure 2.5 a). The shell is a pale yellow, and like the rest of the trochomorphids on Belau, the body is visible through the shell (Figure 2.6). The umbilicus is very wide and shallow and takes up most of the ventral side of the shell (Figure 2.5 b), causing the interior edge of the aperture to start at the umbilicus. There is a very sharp keel on the shell. Baker (1941) noted that *V. pagodula* and *V. pumila* have a similar shell shape, however *V. pagodula*'s shell is significantly taller. *V. pagodula's* body is a light tan with distinctly round black spots. The tentacles are dark gray. A short dorsal stripe sits between the tentacles and extends from the mouth to the base of the tentacles towards the aperture. The eyes are visible at the ends of the tentacles. The average number of whorls is 5. The average diameter of the shell is 7.3 mm, and the average height it 3.7 mm. The umbilicus diameter average is 3.9 mm (Table 2.1).

2.3.4 *Videna pumila* Baker, 1941

Videna pumila's shell is slightly convex, and the shape is planispiral. The apical whorl is flattened (Figure 2.7 a). Overall, the coloration of *V. pumila's* shell is a dull light amber; in contrast to *V. oleacina*, in which the shell is brighter and glossier on the apical side or to *V. pagodula*, in which the shell is very light to clear colored. The umbilicus is shallow and wide, with the interior edge of the aperture makes up the edge of the umbilicus (Figure 2.7 b). *Videna pumila* has a sharply keeled shell and has a slight dome shape, almost like a halfway point between *V. oleacina* and *V. pagodula* (Figure 2.7 c). The ventral side of the shell is rounder than *V. electra*, which is considerably flatter. Baker (1941)'s definition of *V. pumila* notes that this species also bears a great resemblance to another trochomorphid species, *Trochomorpha swainsoni,* but the top of the shell is far rounder. The average number of whorls on *V. pumila* is 5. The average shell diameter is 8.2 mm, and the average height is 4.7 mm. The umbilicus diameter average is 2.2 mm wide (Table 2.1).

2.3.5 *Liravidena lacerata* Semper, 1874

Liravidena lacerata is one of the more unique Belau trochomorphids. The shell has a scalloped edge following the whorls that nearly hides the keel (Figure 2.8 a, b, c). This pattern covers the entire shell. The apical whorl is flattened, as is the ventral side of the shell. The umbilicus is very wide and shallow, and the interior edge of the aperture makes up the outer edge of the umbilicus. The shell can be dark brown to tan and the body is visible through it. Of the Belau trochomorphids, *L. lacerata* is the only one to have a distinct lip on the aperture (Figure 2.8 b). The body of the snail is pale tan with irregular black splotches that are much larger under the shell than on the foot or near the head (Figure 2.9). These splotches are relatively uniform in size underneath the shell. The tentacles are solid dark grey to black. A black stripe runs dorsally from the snail's head to the opening of the aperture. The eyes are very visible at the ends of the tentacles. The average whorl count of *L. lacerata* is 4.5 whorls. The average diameter of the shell is 9.8 mm, with an average height of 3.7 mm. The umbilicus diameter average is 3.5 mm (Table 2.1).

2.4 Further research

It is not always ideal to use shell characteristics and other morphological features alone in reconstructing phylogeny, for a variety of reasons. One of these reasons is that there may be cryptic species, i.e., those that are morphologically nearly identical, but that constitute distinct species. In this case, we risk not analyzing an important component of species diversity if species are only pulled into an analysis based on morphological differences (which, of course, is unavoidable in the case of fossils). Another reason is that in some cases we wish to ask questions about the shell shape (or other morphological features) and its relationship to the ecology of the species, and so it would be considered circular logic to use the same characters for reconstructing phylogeny that one wishes to question and understand. For these reasons, the addition of molecular tools can be helpful in adding a character-rich dataset for understanding phylogenetic relationships as well as providing an independent source of data for asking questions about the evolution of species' morphology.

It would also be beneficial to produce new descriptions of other morphological features of these species, especially of the radulae and genitalia, since these are the two most utilized character sets in older taxonomies of trochomorphids and other species (Baker 1941). It would also be useful to photograph these radular and genital characteristics, either using photography or SEM imaging, since there are no images of these structures for the Belau trochomorphids. Trochomorphids, like most stylommatophorans, are hermaphroditic, and the size, shape, thickness, and position of such structures as the spermathecal stalk and oviduct are strong morphological characters for species identification. The extent of the current knowledge of the ecology of Belau trochomorphids is that they possess love darts like others within their genus and family (Baker 1941).

Finally, the size range for Belau trochomorphids make them among the largest-bodied endemic land snails in Belau. Since most of the endemic land snails found on Belau are 5 mm and under, such a massive body size makes the trochomorphids far more noticeable, not only to people but to potential predators. Belau trochomorphids have unique and interesting shell colors and patterns that are very visible and potentially obvious to see within their forest habitat, much like the partulid tree snails. Previous sampling in French Polynesia has found that trochomorphids there are endangered, and conservation actions plans have been ongoing (Coote et al. 2005). Since the Belau trochomorphids are so large and unique in appearance as well as considered endangered by the IUCN, they would make ideal candidates to monitor for future Belau island conservation plans.

Species	Whorls	Diameter (mm)	Height (mm)	Umbilicus (mm)
V. electra	5.5	16.52	7	1.96
V. oleacina	5.5	13.01	8.02	0.8
V. pagodula	5	7.25	3.7	3.88
V. pumila	5	8.2	4.66	2.19
L. lacerata	4.5	9.79	3.7	3.49

Table 2.1 Belau trochomorphid shell measurements (n=50 adult specimens). Whorls were counted starting at the final body whorl at the aperture, and each successive whorl was counted as 1. Height was measured from the penultimate whorl to the lowest point on the ventral side (bottom of aperture). Diameter was measured at the widest point across the shell (across from the final body whorl, aperture side).

Figure 2.1 *Videna electra* a) Apical, b) Umbilical and c) Aperturial views. This particular specimen possessed a lighter brown band than others, but it is noticeable through the shell to the ventral side. Specimen was collected in Belau within Ngerukewid.

Figure 2.2 *Videna electra* in the wild. Photo by R.J. Rundell.

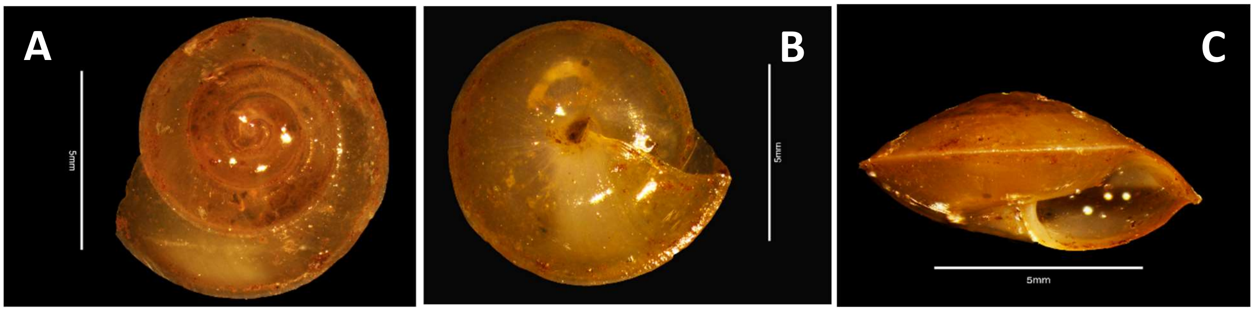


Figure 2.3 *Videna oleacina* a) Apical, b) Umbilical and c) Aperturial views. This specimen was slightly smaller than the average *V. oleacina*. Specimen was collected in Belau on Beleliou.

Figure 2.4 A live *Videna oleacina* from Belau 2019. Photo by R.J. Rundell.

Figure 2.5 *Videna pagodula* a) Apical, b) Umbilical and c) Aperturial views. Specimen collected in Belau on Beleliou

Figure 2.6 A live *Videna pagodula* from Belau 2019. Photo by R.J. Rundell.

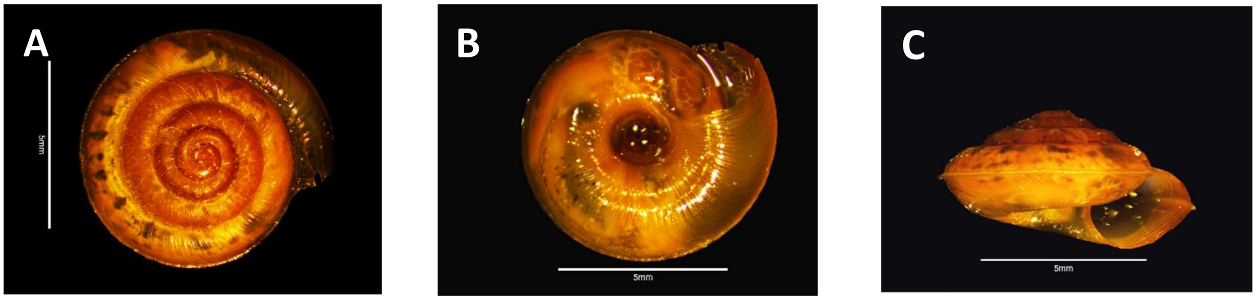


Figure 2.7 *Videna pumila* a) Apical, b) Umbilical and c) Aperturial views. *Videna pumila* bears a close resemblance to *V. electra* but lacks the characteristic banding and is much rounder through the body whorls. Specimen collected in Belau on Euidelchol.

Figure 2.8 *Liravidena lacerata* a) Apical, b) Umbilical and c) Aperturial views. Specimen collected in Belau on Ngeruktabel

Figure 2.9 A live *Liravidena lacerata* from Belau 2019. Photo by R.J. Rundell.

3. Phylogenetic analyses of Belau trochomorphids

3.1 Abstract

Videna (Trochomorphidae: Pulmonata) land snails are an understudied genus from the tropical Pacific and Southeast Asia. A modern molecular phylogenetic study of this genus has not previously been undertaken and would improve our understanding of the evolution of this genus and the family to which it belongs. Four endemic *Videna* species are currently recognized on Belau (Republic of Palau, Oceania): *Videna pagodula*, *V. oleacina*, *V. pumila* and *V. electra*. For the first time, the diversification of the *Videna* species of Belau, along with a fellow trochomorphid relative from Belau, *Liravidena lacerata*, were studied using maximum likelihood (ML) and Bayesian inference (BI) methods on nuclear (5.8S, ITS2 and 28S) and mitochondrial (COI) gene regions. As is the case in inter-specific phylogenetic reconstruction of other pulmonate genera, COI was found to provide the most useful information for phylogenetic reconstruction, however nuclear gene regions were also explored for future use. Phylogenetic reconstruction based on COI DNA sequences shows that Belau *Videna* form a monophyletic group that is distinct from previously sequenced DNA from *Videna* specimens outside of Belau and other trochomorphids. The addition of other gene regions might provide a more robust analysis of the relationships between these species and other members of their genera and family. For example, slower-evolving gene regions might assist in the reconstruction of phylogeny at deeper nodes.

3.2 Introduction

Mollusca is the second largest phylum of animals, and within molluscs, Gastropoda is the most species-rich clade, comprising more than 60,000-80,000 described species (Wade et al. 2001). In particular, the pulmonate order Stylommatophora comprises some 30,000-35,000 described species of land snails (Wade et al. 2001). Much of this diversity can be observed on Pacific islands, which have high levels of species endemism and diversity. This is particularly true in Belau, where there are an estimated 200 identified endemic land snails, many of which are restricted to only a few islands (Rundell 2008).

Considerable efforts have been made to resolve relationships within the stylommatophoran clades. Early studies of different families within Stylommatophora utilized morphological characteristics such as shell characteristics, genitalia, central nervous system, pallial cavity, and excretory and renal morphology to define the relationships between species and genera in families (Baker 1941, Nordsiek 1986, Tillier 1989, Hausdorf 1998). The addition of molecular phylogenetics to the taxonomic toolbox has allowed for a greater understanding of the relationships of families within Stylommatophora, and these relationships continue to be refined (Wade et al. 2001, Wade et al. 2006, Saadi and Wade 2019). However, many families, including Trochomorphidae and therefore the genus *Videna*, have yet to be studied in detail. The few molecular and morphological phylogenetic hypotheses that exist and incorporate trochomorphids have only sequenced a handful of species, and the studies have been focused on the broader Stylommatophora as opposed to just the Trochomorphidae (Hausdorf 1998, Wade et al. 2006).

This study sought to explore the subset of trochomorphid snails that are endemic to Belau through molecular means for the first time. DNA sequences from mitochondrial (COI) and nuclear (5.8S, 28S and ITS2) gene regions were explored for their utility in contributing to trochomorphid phylogenetic reconstruction and were used to help resolve the relationships among Belau *Videna* and *Liravidena* species, within the genus *Videna,* and between *Videna* species and other members of the family Trochomorphidae.

3.3 Materials and methods

Specimen collection, identification, and imaging

Specimens were collected across the Belau archipelago (Republic of Palau) from leaf litter, rocks, and emergent vegetation from 2003 to 2019. Collections were made by hand, and included timed searches, according to methods described in Rundell (2010). Collections from 2018 and 2019 also included sifting of leaf litter. The relatively large size of Belau trochomorphids, compared to most other Belau land snail species, increased the likelihood that if a trochomorphid species was present at a particular sampling site, that the species would be found. However, at the same time, trochomorphids in Belau also seem to be present in low abundance where they are found and are cryptic. All species of described Belau trochomorphids were sampled during the collection years above, along with the full diversity of Belau land snails, as part of Rundell's Belau Land Snail Project, begun in 2003. Both live and dead shells were collected. All trochomorphid species were found alive in Belau between 2003 and 2019 at the collection localities. Live snails were killed and preserved in 95% ethanol. The specimen sorting and preservation procedure also follows Rundell (2010). Some trochomorphid specimens were sorted out of the mixed-species collections, according to morphospecies, in the Division of Invertebrates at the Field Museum of Natural History (Chicago, Illinois, USA). Sorting continued and species identity was confirmed or discovered by the author (EC) using shell characteristics and a dissecting microscope at SUNY-ESF, including the Roosevelt Wild Life Collections lab at SUNY-ESF.

Specimen imaging

Specimens were selected for imaging based on the completeness of the shell. Specimens selected showed no cracks, holes, or breaks, and the body of the animal was still present inside. Each shell was photographed on black clay submerged in 95% ethanol, using a Nikon Ds-Vi1 microscope camera (Nikon Instruments Inc., Melville, NY, USA) mounted to a dissection microscope, using the program NIS-elements (Nikon Instruments Inc., Melville, NY, USA). Shells were manually imaged using the Z-series setting, and then aligned and focused in NIS-elements. Shells were photographed from the shell's aperture, apex, and umbilicus for each species. Images were edited using Adobe Photoshop CS6 (Adobe, San Jose, CA, USA).

DNA isolation and PCR

Foot tissue for DNA isolations was chosen from the 2018 collection year trochomorphid specimens when possible since this was the freshest material and thus most likely to yield high-quality genomic DNA. Pieces of foot tissue approximately 1 mm^3 in volume were dissected from specimens for all DNA isolations using sterile forceps and scalpel blades. For each trochomorphid species, at least two individuals were sampled that best represented the different island localities where these species are found. DNA was extracted using a DNeasy kit, according to the manufacturer's instructions (Qiagen, Valcenia, CA). Samples were digested in 18 microliters buffer ATL and 20 microliters proteinase K overnight at 56°C. An analytical gel was run to determine that the DNA isolation procedure resulted in high quality (fragments of long length) genomic DNA, as evidenced by a bright and relatively clear band nearest the longest length indicator band on the DNA reference ladder.

Universal primers for the COI mitochondrial gene region (Folmer et al. 1994), LCO1490 5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3' and HCO2198 5'-TAC TTC AGG GTG ACC AAA AAA TCA-3', were used to amplify the target strand of mtDNA, along with primers LSU1 5'-CTA GCT GCG AGA ATT AAT GTG A-3' and LSU3 5'-ACT TTC CCT CAC GGT ACT TG-3' and LSU2 5'-GGG TTG TTT GGG AAT GCA GC-3' and LSU4 5'-GTT AGA CTC CTT GGT CCG TG-3' for internal transcribed spacers of rRNA (ITS 1 and 2), which encompass 5.8S and 28S flanking regions (Wade and Mordan 2000). These were amplified for each species. A 700 bp region of COI was amplified according to the profile used by Folmer et al. (1994). The large ribosomal subunit internal transcribed spacer 2 (ITS2), 28S rDNA nuclear gene regions comprised a 580 bp region and the partial 5.8S comprised a 935 bp region. Both were amplified according to the profile used by Wade and Mordan (2000). The PCR recipe used PuReTaq Ready-to-Go PCR beads (GE Healthcare Biosciences, Pittsburg, PA) along with the following for each gene region: 1 microliter of forward primer, 1 microliter of reverse primer, 2 microliters of DNA sample, and 21 microliters of deionized water. PCR products were cleaned with a modified protocol for ExoSAP-It (USB Corp., Cleveland, OH): 1 microliter of ExoSAP-It was added to 10 microliters of sample and incubated at 37° C for 30 minutes. PCR products were then incubated at 80° C to deactivate ExoSAP-It. PCR products were visualized on a 1.5% agarose gel with GelRed, then sent to the Cornell University Institute of Biotechnology (Ithaca, New York) for sequencing according to their Sanger sequencing protocols on an Applied Biosystems automated 3730xl DNA analyzer (Applied Biosystems, Waltham, MA).

3.4 Phylogenetic analyses

Outgroups were selected from previously sequenced and GenBank-accessioned specimens from other authors, both from Trochomorphidae and Euconulidae. Representative outgroups were chosen based on their close relationship to the ingroup, while still being suspected to be outside of the ingroup clades. Euconulidae is a sister family to Trochomorphidae, and the additions of other trochomorphids was included to show the relationship of the Belau trochomorphids within the family. Choices were limited to the species with published DNA sequences from the desired families. Previously sampled *Videna* species were also included as ingroup members (*Videna planorbis*, Genbank accession no. EF015429.1 and *Videna gouldiana*, Genbank accession no. AY841313.1 and AY841314.1). Since its addition to Genbank, the name *V. planorbis* is no longer accepted and is now considered to be *Trochomorpha froggatti*, however it will be kept as *V. planorbis* for the purposes of this thesis. Further research and publications will note the name change. Outgroup taxa are as follows: *Euconulus fulvus* (GenBank accession no. MN022736.1 and MK299738.1) and *Trochomorpha rhysa* (GenBank accession no. MK779478.1).

Raw chromatogram files were assembled and ends trimmed using Geneious Prime 20.2.4 (Biomatters LTD. Auckland, New Zealand). Sequences were also edited and aligned using Geneious Prime and its built-in features for MUSCLE (EMBL-EBI Hinxton, UK), ClustalX (Dublin, Ireland) and MAAFT (CBRC AIST Osaka, Japan). Aligned sequences were corrected for ambiguities and concatenated (all gene regions linked together) in Geneious Prime.

Maximum likelihood (ML) analysis was performed on the concatenated sequence alignments and individual gene alignments using the RAxML function in Geneious. Several substitution models were assessed using MEGA (MEGA-X, State College, PA), with the

HKY+G DNA substitution model being selected as the most appropriate for the dataset based on Akaike Information Criterion (Akaike, 1974) derived from the MEGA model test function. The HKY+G bootstrap model was selected using the rapid bootstrapping algorithm, searching for the best scoring ML tree for 100 iterations. The best scoring ML tree was assembled with associated bootstrap values was then visualized using the tree builder function in Geneious. Bayesian inference (BI) was also performed using the MrBayes plugin function in Geneious. Four independent chains of a Markov Chain Monte Carlo (MCMC) algorithm were run to explore tree space. Each chain was run for 1,100,00 generations sampling every 200 generations.

3.5 Results

The maximum likelihood (ML) and Bayesian inference (BI) trees for the concatenated sequences, ITS2, 28S and 5.8S and the BI tree for COI are given in Appendix 1.1 through 1.4. Results from both ML and BI analyses on alignments composed of concatenated sequences showed poor resolution or unresolved relationships between the Belau trochomorphid species in either the ML or BI trees from any of the concatenated sequences or ITS-2, 28S or 5.8S individual gene regions. Due to the lack of resolution from ITS-2, 28S and 5.8S genes and the concatenated sequences with COI, they have been excluded from the resulting discussions, but kept as appendices. Only the gene region COI was included and assessed, with only the ML tree providing resolution of the relationships among Belau trochomorphids. While this decreases our ability to draw certain conclusions from the phylogenetic trees generated, for the time being, it does provide a better position from which to understand some of the relationships of the Belau trochomorphids, as well as a starting point for future research.

Genetic distances between pairs of Belau trochomorphid species are: 11% between all *Videna* species and *L. lacerata*, and 10-11% between *V. oleacina* and *V. pumila*. Greatest within-species genetic distances for *V. electra* are 5.5% difference between individuals from Euidelchol and Oreor islands (Table 3.1, 3.2).

Phylogenetic reconstructions based on ML and BI analyses of data from the COI mtDNA gene region resolved relationships among trochomorphid species with relatively high nodal support (n=84). The ML tree supports a monophyletic origin of Belau trochomorphids (Fig. 3.1). A polyphyletic origin of *V. pumila* is supported with nodal support (n=90).

3.6 Discussion

The Belau trochomorphids are monophyletic, based on the ML phylogenetic reconstruction using COI mtDNA data (Figure 3.1). Based on this tree it is also possible that there was one colonization event to the Belau archipelago that resulted in the evolution of these and perhaps other trochomorphid species in Belau, however, without additional sampling of trochomorphid species outside of Belau included in the phylogenetic analyses, it is impossible to draw any firm conclusions with respect to Pacific-wide or regional biogeography. Furthermore, certain species of Belau trochomorphids, particularly *Videna electra*, have shells that bear strong resemblance to other members of *Videna* and other trochomorphids across the western Pacific. The lack of available sequence data for nearly all known trochomorphid species means that the monophyletic origin of Belau trochomorphids may not be completely true, as it is possible that there is a closely related species on another archipelago or island that was not included, and thus the results show an incomplete picture. Acquiring gene region sequences from trochomorphids found in regions like Indonesia, the Philippines, Guam, and New Guinea would create a significantly more robust tree and to better resolve the monophyly of Belau trochomorphids if true. The success of COI as a gene region in this analysis suggests that it would be a more useful region when looking at other relationships within Trochomorphidae in the future.

It is interesting to note the suggested polyphyly of *V. pumila*. While the morphospecies suggests the validity of a single species, two distinct clades with good nodal support (bootstrap 77%; Figure 3.1). Specimens collected from islands in and around Oreor at the northern end of the Rock Islands (*V. pumila* 1-5) formed one clade while those collected in and around Euidelchol (*V. pumila* 6-7) formed a second clade. It is possible that there are two cryptic species, or that there is evidence of phylogeographic structure within *V. pumila*.

Videna pagodula is similarly shown as polyphyletic, however the strong similarity among specimens identified to this species does not support this (Figure 3.1). The bootstrap value indicated in the COI tree for the polyphyletic clades of *V. pagodula* (bootstrap 45%) is below the threshold of 70%, which decreases confidence in the support at this node, and depiction of polyphyly in the trees is most likely due to sampling error (Figure 3.1).

Liravidena lacerata and *V. oleacina* appear to be sister to each other, although the support there is not strong (bootstrap 47%). Interestingly, *L. lacerata* is found within *Videna*¸ which could suggest that the taxonomy for this species should be updated; or perhaps that the taxonomy for *V. oleacina* needs greater review, as it may be a member of a different trochomorphid genus rather than *Videna*. It is possible that long branch attraction, which is the occurrence of distantly related lineages are incorrectly shown to be closely related, might explain relationship resolution issues within certain genes. This may be the cause behind the relationship shown between *V. oleacina* and *L. lacerata*.

Videna electra is of special interest based on the trees generated. Sixteen individuals were sampled, comprising eight of the larger rock islands and covering as many localities as possible. The COI phylogenies suggest that specimens collected from nearby localities share a closer relationship than those found farther away. Particularly interesting is the grouping of the *V. electra* individuals from the islands of Euideichol and Ngeanges, islands that are just under 2 km apart. The ML tree suggests that there may be polyphyletic, however the nodal support is lacking. Further research into these relationships, incorporating more gene regions and sequences from more individuals across the archipelago would help to solidify this observation and provide more concrete evidence of any phylogeographic patterns.

It is interesting to note that *V. planorbis* and *T. rhysa* cluster more closely together on both trees, suggesting that the newly accepted name *T. froggatti* is valid. Further research would provide a much clearer answer as to the validity of the taxonomic change.

ITS2, 28S and 5.8S are powerful gene regions for exploring higher-order taxonomic relationships (i.e., evolution at deeper nodes), but due to their slow evolutionary rate, data from these gene regions might not be as successful in reconstructing relationships among relatively closely related species, such as relationships below the family level. Further research should include other commonly sequenced gene regions for gastropods, particularly 16S and 18S rRNA (Winnepenninckx et al. 1998, Thacker and Hadfield 2000, Teasdale 2017). These regions, particularly 16S, have been shown to help resolve relationships among closely related species (Thacker and Hadfield 2000).

Sampling problems are likely to have occurred as well, limiting the results of the selected gene regions. Tissue was taken from specimens that were one year old and the DNA may have already started degrading. Fresh tissue samples would make isolations cleaner and provide more information, so further field sampling and additional isolations would provide more information and allow for a more robust tree. Increasing the number of individuals per species would also provide greater resolution of the relationships among Belau trochomorphids, as only a few samples of *V. oleacina* were extracted due to the limited number of specimens with tissue available. A stronger, more robust tree would result from these additions and provide more information on the relationships observed in this research.

Species	**Code**	**Locality**	**Genbank Accession no.**	**COI**	**LSU2**	**28S**	**5.8S**
Videna electra	Velectra1	Palau	not yet added	X	X	X	X
Videna electra	Velectra2	Palau	not yet added	X	X	X	X
Videna electra	Velectra3	Palau	not yet added	X	X	X	
Videna electra	Velectra4	Palau	not yet added	X			
Videna electra	Velectra5	Palau	not yet added	X	X	X	X
Videna electra	Velectra6	Palau	not yet added	X	X	X	
Videna electra	Velectra7	Palau	not yet added	X			
Videna electra	Velectra8	Palau	not yet added	X	X	X	
Videna electra	Velectra9	Palau	not yet added	X			X
Videna electra	Velectra10	Palau	not yet added	X	X	X	
Videna electra	Velectra11	Palau	not yet added				
Videna electra	Velectra12	Palau	not yet added	X			X
Videna electra	Velectra13	Palau	not yet added	X			
Videna electra	Velectra14	Palau	not yet added	X			
Videna electra	Velectra15	Palau	not yet added				
Videna electra	Velectra16	Palau	not yet added				
Videna oleacina	Voleacina1	Palau	not yet added				
Videna oleacina	Voleacina2	Palau	not yet added				
Videna oleacina	Voleacina3	Palau	not yet added	X			
Videna pagodula	Vpagodula1	Palau	not yet added		X	X	X
Videna pagodula	Vpagodula2	Palau	not yet added		X	X	X
Videna pagodula	Vpagodula3	Palau	not yet added	X			X
Videna pagodula	Vpagodula4	Palau	not yet added	X			X
Videna pagodula	Vpagodula5	Palau	not yet added	X	X	X	
Videna pagodula	Vpagodula6	Palau	not yet added	X			X
Videna pagodula	Vpagodula7	Palau	not yet added		X	X	X
Videna pagodula	Vpagodula8	Palau	not yet added				
Videna pagodula	Vpagodula9	Palau	not yet added	X	X	X	X
Videna pumila	Vpumila1	Palau	not yet added	X	X	X	X
Videna pumila	Vpumila2	Palau	not yet added	X	X	X	
Videna pumila	Vpumila3	Palau	not yet added	X	X	X	
Videna pumila	Vpumila4	Palau	not yet added	X	X	X	X
Videna pumila	Vpumila5	Palau	not yet added	X	X	X	X
Videna pumila	Vpumila6	Palau	not yet added				X
Videna pumila	Vpumila7	Palau	not yet added	X	X	X	
Liravidena lacerata	Llacerata1	Palau	not yet added	X			
Liravidena lacerata	Llacerata2	Palau	not yet added		X	X	X
Liravidena lacerata	Llacerata3	Palau	not yet added				
Liravidena lacerata	Llacerata4	Palau	not yet added				
Liravidena lacerata	Llacerata5	Palau	not yet added				
Videna gouldiana		Japan	AY841313.1				X
Videna gouldiana		Japan	AY841314.1		X	X	
Videna planorbis		New Guinea	EF015429.1	X			
Trochomorpha rhysa		Borneo	MK779478.1	X			
Euconulus fulvus		Europe	MN022736.1	X			
Euconulus fulvus		Europe	MK299738.1		X	X	X

Table 3.1 Sampled Belau trochomorphids and trochomorphids from GenBank. X denotes which gene regions were successfully sequenced from each individual. COI=Cytochrome C oxidase subunit 1 (mitochondrial), LSU2=large ribosomal subunit 2 (nuclear), 28S gene region (nuclear), 5.8S (nuclear).

	E. fulvus	V. electra 1	V. electra 11	V. electra 8	V. electra 10	V. electra12	V. electra 2	V. electra 3	V. electra 14	V. electra 13	V. electra 16	V. electra 4	V. electra 7	V. electra 9	V. pagodula 3	V. pagodula 6	V. pagodula 9	V. pumila 2	V. pumila 4	V. pumila 7	V. pagodula 4	V. pagodula 5	V. pumila 1	V. pumila 3	V. pumila 5	V. electra 6	V. oleacina 3	V. electra 5	T. rhysa	L. lacerata 1	V. planorbis
E. fulvus		87.1	87.3	87	87	86.9	87	87	87.2	87.1	87	87	86.3	86.9	85.4	86.4	86.5	85.2	85.1	85.2	84.8	84	84.5	85.7	85.7	84.5	86.1	84.4	84.5	80.2	84.9
V. electra 1	87.1		97.7	97.3	97.3	97.3	97.4	97.5	97.7	97.8	97.1	97.8	97.1	96.9	94.5	94.5	94.8	94.8	94.8	94.5	94.8	93.6	93	93.2	93	94.8	92.3	93.8	85.2	86.3	83.5
V. electra 11	87.3	97.7		97.3	97.4	97.5	97.5	97.5	97.4	96.8	97.1	96.3	96.2	96.7	94.8	94.7	95	94.6	94.6	94.1	95	93.5	93	93.3	93.3	94.5	92.2	93.4	85.4	86	82.9
V. electra8	87	97.3	97.3		97.6	97.5	97.4	97.5	97.4	96.8	97	96.1	96.2	97.2	94.4	94.4	94.7	94.2	94.4	93.9	94.6	93.3	93.1	93.7	93.4	94.5	91.8	93.2	85.2	85.7	82.9
V. electra 10	87	97.3	97.4	97.6		97.6	97.3	97.4	97.2	96.7	96.9	96.1	96	97.1	94.5	94.5	94.8	94.2	94.3	93.9	94.7	93.3	93.2	93.6	93.5	94.4	91.8	93.3	85.2	85.9	82.8
V. electra 12	86.9	97.3	97.5	97.5	97.6		97.2	97.3	97.1	96.6	96.8	96	95.9	97.2	94.6	94.5	94.8	94.2	94.2	93.8	94.7	93.3	93.1	93.6	93.5	94.3	91.8	93.1	85.1	85.6	82.4
V. electra 2	87	97.4	97.5	97.4	97.3	97.2		99.4	99.4	99.1	98.8	98.7	98.1	95.3	94.3	94.4	94.7	94.3	94.6	93.9	94.6	93.6	92.7	93.1	92.7	96.1	92.5	94	84.9	86.1	83.1
V. electra 3	87	97.5	97.5	97.5	97.4	97.3	99.4		99.5	99.2	98.9	98.8	98.2	95.3	94.4	94.5	94.7	94.4	94.7	94	94.7	93.7	92.7	93.1	92.7	96.2	92.6	94	84.9	86.2	83.1
V. electra 14	87.2	97.7	97.4	97.4	97.2	97.1	99.4	99.5		98.9	98.6	98.5	98.3	95.7	94.4	94.3	94.5	94.8	94.6	94.4	94.5	94	92.6	92.9	92.6	96.3	92.9	94.2	85.2	86.4	83.3
V. electra 13	87.1	97.8	96.8	96.8	96.7	96.6	99.1	99.2	98.9		98.2	98.7	98.5	94.7	93.8	93.8	94	93.9	94	93.4	94.1	93	91.9	92.4	92	95.9	91.9	93.9	85	85.3	82.2
V. electra 16	87	97.1	97.1	97	96.9	96.8	98.8	98.9	98.6	98.2		97.4	97.5	94.6	94.2	94.6	94.8	93.9	94.1	93.8	94.4	92.9	92.5	93	92.7	95.6	92	93.5	85	85.6	82.3
V. electra 4	87	97.8	96.3	96.1	96.1	96	98.7	98.8	98.5	98.7	97.4		98.2	94.5	93.2	93.3	93.5	93.6	93.4	93.3	93.5	92.8	91.5	91.7	91.5	95.2	91.7	93.9	84.9	85.4	82
V. electra 7	86.3	97.1	96.2	96.2	96	95.9	98.1	98.2	98.3	98.5	97.5	98.2		94.1	93.3	93.3	93.6	93.3	93.5	93.1	93.4	92.4	91.5	91.9	91.5	95.6	91.4	93.2	84.2	85.3	82
V. electra 9	86.9	96.9	96.7	97.2	97.1	97.2	95.3	95.3	95.7	94.7	94.6	94.5	94.1		94.2	94.1	94.2	95	94.4	94.4	94.1	93.7	93	93.4	93.5	92.5	92.2	92.1	85.4	86.2	83.8
V. pagodula 3	85.4	94.5	94.8	94.4	94.5	94.6	94.3	94.4	94.4	93.8	94.2	93.2	93.3	94.2		95.1	95.7	94.7	94.7	94.7	97.4	96.3	93	92.8	92.8	91.4	91.2	91.2	84.3	85.2	82.7
V. pagodula 6	86.4	94.5	94.7	94.4	94.5	94.5	94.4	94.5	94.3	93.8	94.6	93.3	93.3	94.1	95.1		99.4	94.7	94.4	95.2	95.2	93.6	92.9	93.2	93.5	91.4	92.1	91.1	84.7	85	82.5
V. pagodula 9	86.5	94.8	95	94.7	94.8	94.8	94.7	94.7	94.5	94	94.8	93.5	93.6	94.2	95.7	99.4		94.9	94.9	95.7	95.7	94.1	93.3	93.5	93.6	91.6	92.2	91.4	85	85.6	82.7
V. pumila 2	85.2	94.8	94.6	94.2	94.2	94.2	94.3	94.4	94.8	93.9	93.9	93.6	93.3	95	94.7	94.7	94.9		99.2	96.5	94.8	94.2	94.5	92	91.9	91.3	91.8	91	84.3	85.9	82.1
V. pumila 4	85.1	94.8	94.6	94.4	94.3	94.2	94.6	94.7	94.6	94	94.1	93.4	93.5	94.4	94.7	94.4	94.9	99.2		96.1	94.7	93.8	94.5	92.1	91.8	91.6	91.3	91.1	84.2	85.6	81.7
V. pumila 7	85.2	94.5	94.1	93.9	93.9	93.8	93.9	94	94.4	93.4	93.8	93.3	93.1	94.4	94.7	95.2	95.7	96.5	96.1		94.5	94	93.1	92.2	92	91.2	91.9	91	84	86.1	81.8
V. pagodula 4	84.8	94.8	95	94.6	94.7	94.7	94.6	94.7	94.5	94.1	94.4	93.5	93.4	94.1	97.4	95.2	95.7	94.8	94.7	94.5		96.9	92.9	92.6	92.7	91.7	91.3	91.7	84.4	85.5	81.9
V. pagodula 5	84	93.6	93.5	93.3	93.3	93.3	93.6	93.7	94	93	92.9	92.8	92.4	93.7	96.3	93.6	94.1	94.2	93.8	94	96.9		92	91.2	91.1	90.5	91	91.2	83.4	85.4	81.6
V. pumila 1	84.5	93	93	93.1	93.2	93.1	92.7	92.7	92.6	91.9	92.5	91.5	91.5	93	93	92.9	93.3	94.5	94.5	93.1	92.9	92		95.2	94.9	89.9	89.8	90.3	84.3	84.9	81
V. pumila 3	85.7	93.2	93.3	93.7	93.6	93.6	93.1	93.1	92.9	92.4	93	91.7	91.9	93.4	92.8	93.2	93.5	92	92.1	92.2	92.6	91.2	95.2		99.1	90.3	90.1	90	86	84.8	82.4
V. pumila 5	85.7	93	93.3	93.4	93.5	93.5	92.7	92.7	92.6	92	92.7	91.5	91.5	93.5	92.8	93.5	93.6	91.9	91.8	92	92.7	91.1	94.9	99.1		90	90.3	89.8	85.9	84.6	82.2
V. electra 6	84.5	94.8	94.5	94.5	94.4	94.3	96.1	96.2	96.3	95.9	95.6	95.2	95.6	92.5	91.4	91.4	91.6	91.3	91.6	91.2	91.7	90.5	89.9	90.3	90		89.8	91.2	82.3	83.4	80.5
V. oleacina 3	86.1	92.3	92.2	91.8	91.8	91.8	92.5	92.6	92.9	91.9	92	91.7	91.4	92.2	91.2	92.1	92.2	91.8	91.3	91.9	91.3	91	89.8	90.1	90.3	89.8		89.6	84	85.7	82.6
V. electra 5	84.4	93.8	93.4	93.2	93.3	93.1	94	94	94.2	93.9	93.5	93.9	93.2	92.1	91.2	91.1	91.4	91	91.1	91	91.7	91.2	90.3	90	89.8	91.2	89.6		82.8	84	81.2
T. rhysa	84.5	85.2	85.4	85.2	85.2	85.1	84.9	84.9	85.2	85	85	84.9	84.2	85.4	84.3	84.7	85	84.3	84.2	84	84.4	83.4	84.3	86	85.9	82.3	84	82.8		78.9	82.5
L. lacerata 1	80.2	86.3	86	85.7	85.9	85.6	86.1	86.2	86.4	85.3	85.6	85.4	85.3	86.2	85.2	85	85.6	85.9	85.6	86.1	85.5	85.4	84.9	84.8	84.6	83.4	85.7	84	78.9		77.6
V. planorbis	84.9	83.5	82.9	82.9	82.8	82.4	83.1	83.1	83.3	82.2	82.3	82	82	83.8	82.7	82.5	82.7	82.1	81.7	81.8	81.9	81.6	81	82.4	82.2	80.5	82.6	81.2	82.5	77.6	

Table 3.2 COI gene matrix of pairwise distance (%) for the MAAFT alignment of the Belau trochomorphids and outgroups.

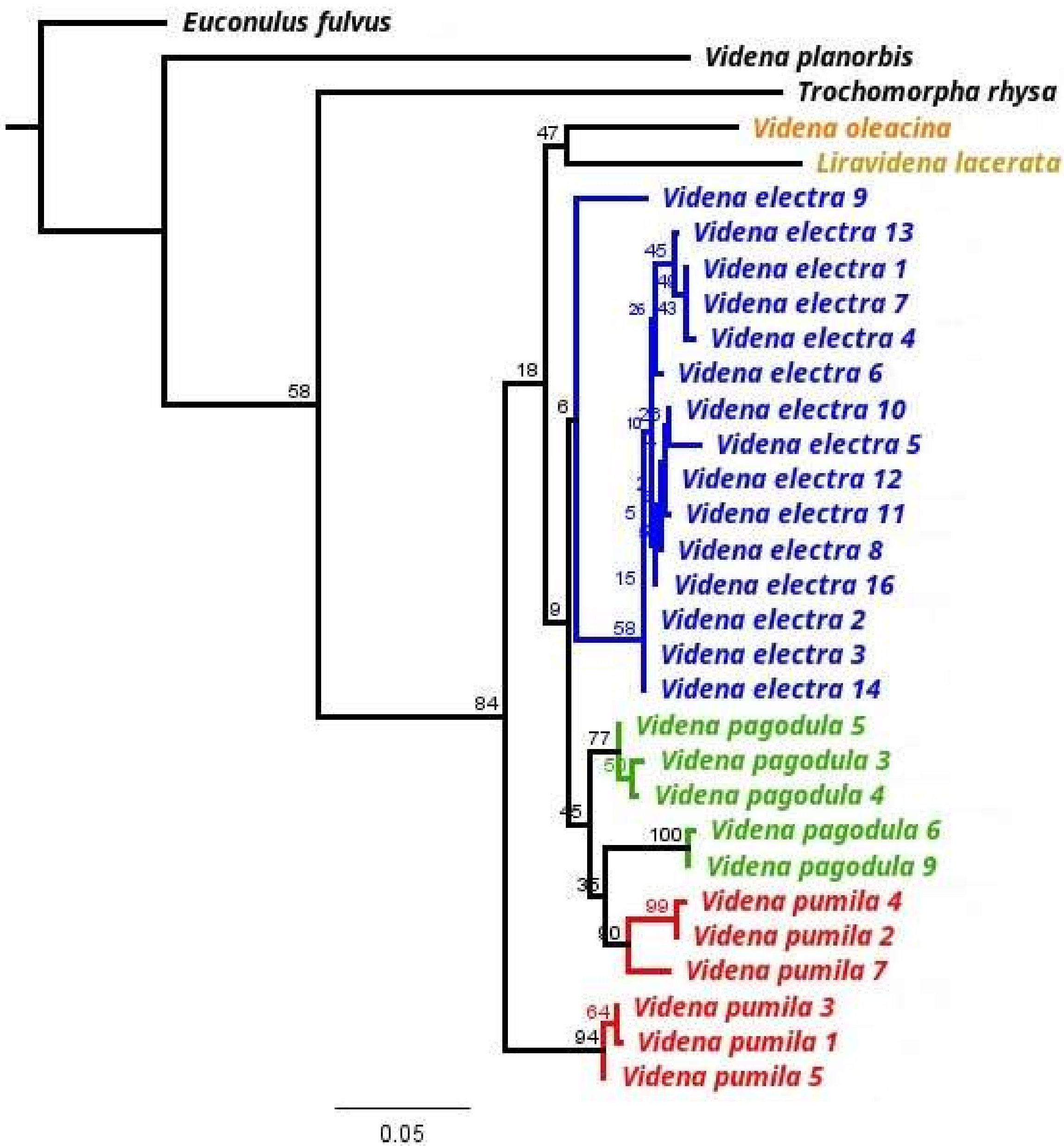


Figure 3.1 Maximum likelihood tree of the 700 bp COI gene region with boostrapping for nodal support. Outgroup *E. fulvus*. Results tentatively indicate a monophyletic origin of Belau trochomorpid species, with potential polyphyly of both *V. pumila* and *V. pagodula*. It is interesting to note that *L. lacerata* falls within the *Videna* clade and is sister to *V. oleacina*.

4. The current geographic ranges of Belau *Videna* species and their implications for conservation

4.1 Insular biogeography: Hindering large-bodied land snails for millions of years

Insular biogeography focuses on the immigration of species to islands and the extinction of species found therein. Factors such as the degree of isolation, island size, isolation time, and habitat suitability affect a species' ability to reach an island and to successfully survive and eventually undergo speciation. For terrestrial snails, dispersing to islands is not possible without something accidentally interfering in their favor. There have been several suggested theories as to the passive dispersal of snails to islands: rafting on debris, being blown by wind or storms, being carried by birds both through predation (Wada et al. 2012), and becoming stuck to birds' feathers or legs (Vagvolgyi 1975). However, some of these methods are better suited for minute snail species. Larger snails, such as those found in the genus *Videna* are more likely to be carried in such a manner as juveniles (Vagvolgyi 1975). However, the juvenile stage is not permanent and limits mating potential, especially when compared to an adult, gravid minute snail (Vagvolgyi 1975). Because terrestrial snails have low vagility, they often have high endemicity in the areas where they are found (Schilthuizen et al. 2002). This, particularly in the tropics where land snail diversity is already high, often leads to extensive speciation, especially on limestone karsts (Schilthuizen et al. 2002).

Belau's geographic location in the Pacific is remote, and it has had no contact with any mainland continent in its geologic history (Crombie and Pregill 1999). The closest continent is over 3,000 km away. However, there are multiple islands between Belau and mainland Asia, and it is possible that the Belau *Videna* species arrived via "island hopping" while undergoing passive dispersal, possibly via rafting. It is also possible that a *Videna* ancestor had already reached Belau prior to the last glacial maximum (20,000 years ago) when sea levels were significantly lower than they are currently. Belau would have been a solid land mass (Paleo-Palau), and would have been submerged as sea levels increased, effectively isolating higher points into islands, and decreasing dispersal capabilities of the fauna that remained (Rundell 2008, Colin 2009). Separation between pockets of habitat, such as limestone karst ridges, could allow for allopatric speciation to occur on the various islands within Belau, however the deep divergences among many species suggest that this diversification pre-dated the time when much of Belau was a solid land mass (Rundell 2008, Colin 2009).

4.2 Current range of the family Trochomorphidae and the genus *Videna*

Members of *Videna* have been described throughout Southeast Asia and into the western Pacific. This includes India, Laos, Vietnam, Japan, the Philippines, Indonesia, Micronesia, New Guinea and Belau (Table 4.1). Even though no extensive survey of the genus alone has been conducted, general surveys of localities across these regions have found *Videna* species present. However, there is a lack of consistent taxonomic information on *Videna*, as it is possible that many species that are currently considered *Videna* belong to other genera related to *Videna*. Currently there are over 60 described *Videna* species (Clark 2020, unpublished data).

Members of the Trochomorphidae have been found throughout Southeast Asia and into the western Pacific as well. There is a concentration of documented trochomorphids from the Philippines and Indonesia. No trochomorphids have been recorded in the Hawaiian archipelago in Polynesia, however five trochomorphid species are known from the Samoan archipelago (Cowie 1998, Cowie et al. 2017). All of these species are endemic to Samoa and are rare, and all but a few are poorly known. *Trochomorpha apia* (Hombron and Jacquinot 1853), the best-known

Samoa trochomorphid species, is listed as Endangered on the IUCN Red List (Mollusc Specialist Group, 1996). This species was seen alive in 2008 but was extremely rare at this time (Cowie et al. 2017).

The Belau trochomorphids (*Videna electra, Videna oleacina, Videna pagodula, Videna pumila, Liravidena lacerata)* are endemic to the archipelago, and older surveys have found them ranging from Bloody Nose Ridge on the island of Beliliou (Peleliu State) north into the limestone outcrops in Airai State on Babeldaob, but they do not extend much farther into the island (Baker 1941). Airai is a combination of volcanic rock and organic limestone, which is preferred by these species.

4.3 Conservation and Belau trochomorphids: What could we lose?

Pacific island land snails are among the most species rich taxa in the Pacific, with over 5,000 described species and more awaiting discovery (Chiba and Cowie 2016). Many are endemic to the archipelagos where they are found, often to individual islands and even single localities on those islands. Their low dispersal abilities facilitated these isolation and diversification events. However, Pacific island land snails are still an understudied group of animals, particularly when compared to all vertebrate groups. Relatively little is known regarding their conservation, despite nearly 10% of known land snail species potentially having gone extinct (Chiba and Cowie 2016). Terrestrial gastropods have made up over 40% of extinctions since 1500, and of those 70% have been oceanic island-dwelling snails (Chiba and Cowie 2016). Fewer than 10% of all Pacific island land snail species have had their conservation status formally assessed. Oceanic island land snails are particularly vulnerable to human induced extirpation, especially from invasive predators. This is due in part to the lack of natural predators found on islands, which would influence a need to evolve predatory defenses over the evolution of traits that favor interspecific competition (Chiba and Cowie 2016). Much land snail diversity exists on Pacific Islands, in part due to their isolation, and Belau is no exception. Belau is home to over 200 endemic species, many being single island endemics (Rundell 2008).

Unfortunately for land snails, predators abound on remote Pacific islands, especially those that were introduced to islands from the mainland. The rosy wolf snail (*Euglandina rosea*) is one such predator. Originally from Florida, the rosy wolf snail was introduced to islands as an attempt to control the spread of the giant African snail (GAS; *Achatina fulica*), which had become a pest. This biocontrol was a failure, as the rosy wolf snail did not feed on juvenile GAS as thought but preyed upon many native species of land snail instead. These have been devastating to partulid species, especially in Hawaii (Cowie 2000). A predatory flatworm, *Platydemus manokwari*, was also introduced as a form of GAS control and has also proven to be a threat to many Pacific island land snail species (Sherley 2000). Unlike other invasive predators, the rosy wolf snail and *P. manokwari* are not easily removed.

Rats in particular pose a large threat to Belau trochomorphids because they are larger bodied, ground-dwelling snails. At least three species of rat and one mouse species have been recorded on Belau: the Polynesian rat (*Rattus exulans*), the black/roof/ship rat (*Rattus rattus*), the brown or Norway rat *(Rattus norvegicus*), and the house mouse (*Mus musculus*). Rats made their way to the archipelago in the 18th and 19th centuries through stowing away aboard canoes and ships from Spain that traveled to and among the islands (Crombie and Pregill 1999). Shells bearing rat predation marks are often broken into from the side, top or aperture, and chew marks are sometimes visible (Figure 4.2). Rats are not just a threat to the endemic land snails—they have also been found preying on the eggs and young of the endangered Micronesian megapode

(*Megapodius laperouse*) and other bird species found in Belau, and are considered agricultural and domestic pests across the archipelago (Hall 2017). Rats are also disease vectors, particularly for scrub typhus in Belau (Demma et al. 2006).

Currently, all four species of Belau *Videna* are listed within Threatened categories (i.e., are listed as VU, EN, or CR) on the IUCN Red List (Rundell 2012 a-d). *Liravidena lacerata* has not yet been assessed by the IUCN. *Videna electra* is considered Vulnerable (VU), *V. oleacina* is Endangered (EN) and both *V. pumila* and *V. pagodula* are considered Critically Endangered (CR), the highest threat category.

Despite the severe threat of extinction, there has not been a significant effort to generate geographic range maps for Belau trochomorphids. Past species descriptions and surveys have indicated islands within the archipelago generically, and often only listed one or two islands of the hundreds that make up Belau. This makes the creation of conservation plans for Belau trochomorphids difficult, for if the actual geographic range is unknown conservation areas cannot be readily established. The goals of this mapping project were to provide more accurate and updated range maps for the Belau trochomorphids, create a map of areas of rat predation, and use the data to inform potential conservation management plans for each of the five species.

4.4 Materials and Methods

Specimen and data collection

Specimens were collected across the Belau archipelago (Republic of Palau) from leaf litter, rocks, and emergent vegetation from 2003 to 2019 (2003, 2005, 2007, 2013, 2018, 2019). Collections were made by hand, and included timed searches, according to methods described in Rundell (2010). Collections from 2018 and 2019 also included sifting of leaf litter. The large size of Belau trochomorphids, compared to most other Belau land snail species, increased the likelihood that if a trochomorphid species was present at a particular sampling site, the species would be found. However, at the same time, trochomorphids in Belau also seem to be present in low abundance where they are found and are cryptic. All five species of described Belau trochomorphids were sampled during the collection years above, along with the full diversity of Belau land snails, as part of Rundell's Belau Land Snail Project, begun in 2003. Both live and dead shells were collected. All trochomorphid species were found alive in Belau between 2003 and 2019 at collection localities. Live snails were killed and preserved in 95% ethanol. Specimen sorting and preservation procedure also follows Rundell (2010). Some trochomorphid specimens were sorted out of the mixed-species collections, according to morphospecies, in the Division of Invertebrates at the Field Museum of Natural History (Chicago, Illinois, USA). Sorting continued and species identity was confirmed or discovered by the author (EC) using shell characteristics and a dissecting microscope at SUNY-ESF, including the Roosevelt Wild Life Collections lab at SUNY-ESF.

Locality information was collected during specimen collection using GPS data stored in the WGS 1984 coordinate system for each field season. The conditions of the specimens were identified by how they were found at each site, with bleached, and/or empty shells being counted as dead. Shells with visible rat chewing were noted by locality as well.

Mapping ranges

Maps were built using ArcMAP 10.8 (Esri, Boston, MA, USA). A shapefile for the Belau shoreline was accessed and downloaded through the National Centers for Coastal Ocean Science (Silver Spring, MD, USA). GPS coordinates were transformed into shapefiles by year, species, live/dead, and rat predation using ArcMAP.

4.5 Results

The current geographic ranges of the Belau trochomorphids situates all five species within the Rock Islands, verifying some of the previous range information provided in the initial descriptions by Semper and Baker's assessment (Semper 1873, Baker 1941). However, the ranges are much larger than previously described, encompassing more island groups in the archipelago. *Videna electra* is the most widespread species, being found on most islands throughout Belau, including Beliliou, Euideichol, Ngeanges, Mecherchar, Ngermalk, Oreor, and the southern end of Babeldaob, which is predominantly limestone (Figure 4.3). *Videna oleacina* is found towards the southern end of the archipelago and is not found any farther north than Ngeruktabel (Figure 4.4). *Videna pagodula* is concentrated at the southern end of the archipelago, particularly on Beliliou and is not found any farther north than Euidelchol and Mecherchar (Figure 4.5). *Videna pumila* and *Liravidena lacerata* share a similar range to *V. electr*a, although neither are found on the limestone islands in southern Babeldaob (Figure 4.6, 4.7). *Videna electra* occurs in sympatry with every other trochomorphid species found on Belau (Table 4.2). Many of the trochomorphids also occur in sympatry, particularly on Koror where all five species were found (Table 4.2). This may be unique to Belau trochomorphids, as such levels of sympatry are not regularly observed in other land snail species.

The number of trochomorphids found during each survey year varies greatly, partly due to the number of people available to assist in surveying (e.g., years such as 2005 saw several field technicians available and 2018 a field course on Belau was taught), but also in part because they are cryptic and more difficult to find during surveys than other species. In certain years, some species were not found (e.g., *V. pagodula* was not collected in 2013, but this was a solo trip with just Rundell and involved visiting a very limited number of localities, relative to 2003, 2005, and 2007). Of the collected specimens of trochomorphids, *V. oleacina* and *V. electra* have the most empty shells collected in the field. *V. electra*'s larger numbers are due to it being the most common trochomorphid in Belau, but it is very concerning that most of the *V. oleacina* specimens were dead prior to collection (Table 4.3). Efforts involved in collecting shells differed between sites due to the habitat searchability of each site.

Videna oleacina was found to have the most rat predation damage on dead shells, with 22% of collected *V. oleacina* specimens since 2003 bearing chew marks (Table 4.3). *Videna pumila* specimens had 21% of *V. pumila* dead shells with rat predation evidence, while *L. lacerata* had the lowest percentage of rat damaged shells at 8% of all *L. lacerata* specimens collected (Table 4.3). This may be due to the shell sculpture, which has the most texture of any Belau trochomorphids and may make the snail a less desirable prey item.

4.6 Discussion

Conservation recommendations

Rat predation does not seem to be restricted to certain islands, nor does it appear to be growing worse or lessening over time (Figure 4.8). This is consistent with the current knowledge of rat invasions found in the archipelago, where rats have been found on many of the islands. Rats were not restricted to areas of increased human activity such as towns or popular tourist spots, but rather were found in all areas where the Belau trochomorphids were surveyed. The trochomorphid most preyed upon by these invasive rodents is *V. oleacina*, which is the largest bodied trochomorphid in Belau. Since 2003, 22% of the dead *V. oleacina* collected bore evidence of rat predation (Table 4.3).

Rat eradication is an ongoing effort in Belau, with a recent successful attempt having happened on the northern atoll of Ngcheangel, and another recent rat eradication project on the Rock Island of Ngeanges in the main lagoon since rats were causing a severe decline in megapode numbers and other native birds and were ruining crop harvests on some inhabited islands. Rats were killed using poison bait pellets and an increase in the number of megapode eggs and chicks was observed on Ngeanges (Hall 2017). Rat eradication efforts such as this not only protect the endangered megapode, but can protect other endemic, endangered species found in Belau. It can be assumed that the removal of rats from Ngeanges might benefit the Belau trochomorphids found there, given the extent to which trochomorphids are preyed on by rats elsewhere, however without surveys for these species before and after rat eradication it would be hard to tell for certain.

Treating the megapode as an "umbrella species" on islands where all five Belau trochomorphids and the megapode are found may be a useful tool for land snail conservation management. By protecting these areas for the birds, the snails would also be safe from further habitat encroachment, and this would provide more focused areas for rat eradication efforts. However, this should be taken with great consideration, as species should have overlapping habitats to provide more ideal protection for more species (Fontaine et al. 2007). Megapodes and Belau trochomorphids both utilize leaf litter for food, so with further research it is likely that the megapode would be an ideal candidate for an umbrella species for these snails, and provide them with some much needed protections.

Genus	Species	Described	Location	Code
Videna	abbasi	Thach 2020	Sumatra	U
Videna	albocincta/albocineta	Pfeiffer	Philippines	U
Videna	alticola	Mollendorf 1894	Philippines	U
Videna	andamanica	Godwin-Austen 1895	India	U
Videna	beckiana	Pfeiffer 1842	Philippines	T
Videna	belmorei	Cox 1868	Solomon Islands	U
Videna	bicolor	Martens 1864	Sumatra, Indonesia, Malaysia, Borneo	N Geotrochus bicolor
Videna	boettgeri	Mollendorf 1890	Philippines	U
Videna	boholensis	Semper 1873	Philippines	U
Videna	cantoriana	Benson 1861	Malaysia	U
Videna	castra	Benson 1852	India, Bangladesh	N Sivella castra
Videna	crassula	Mollendorf 1898	crassula	U
Videna	crassicarinata	Fulton 1907	Indonesia	U
Videna	dohertyi	Aldrich 1898	Indonesia	U
Videna	electra	Semper 1873	Palau	V
Videna	frauenfeldi	Pfeiffer and Zelebor 1867	India	U
Videna	frogatti	Iredale 1941	Malaysia	T
Videna	gouldiana	Pilsbury 1901	Japan	V
Videna	gracilis	Mollendorf 1894	Philippines	U
Videna	granulosa	Mollendorf 1888	Philippines	N Sivella granulosa
Videna	grubauri	Moellendorf 1902	Malaysia	U
Videna	harmtanni	Pfeiffer 1845	Java	U
Videna	horiomphala	Pfeiffer 1845	Japan	N Videnoida horiomphala
Videna	infanda	Semper 1873	Philippines	V
Videna	intermedia	Mollendorf 1894	Philippines	U
Videna	iopharynx	Moerch 1876	India	U
Videna	kelantanensis	Moellendorf 1902	Malaysia	U
Videna	lacerata	Semper	Palau	N Liravidena lacerata Semper 1873
Videna	lardea	Martens 1864	India	U
Videna	latior	Blanford 1863	India	N Sivella latior
Videna	marginata	Mollendorf 1890	Philippines	U
Videna	metcalfei	Pfeiffer 1845	Philippines, Malaysia	V
Videna	minahasse	Sarasin and Sarasin 1899	Indonesia	U
Videna	modesta	Fulton 1907	Malacca	U
Videna	neglecta	Pilsbry 1892	Philippines	V
Videna	niasensis	Fulton 1907	Indonesia	U
Videna	nitidella	Mollendorf 1898	Philippines	U
Videna	oleacina	Semper 1873	Palau	Periyua subgenus? Baker 1941
Videna	pagodula	Sepmer 1873	Palau	Peleliua pagodula Baker 1941 subgenus?
Videna	papua	Lesson 1831	New Guinea	T
Videna	paviei	Morlet 1885	French Indonesia	T
Videna	planorbis	Lesson 1830	Philippines, New Guinea, Java, Indonesia	N Trochomorpha froggatti
Videna	pseudosanis	Fulton 1897	India	U
Videna	pseudosericina	Mollendorf 1898	Philippines	N Sivella pseudosercina
Videna	pumila	Semper 1873	Palau	Peleliua pumila Baker 1941 subgenus?
Videna	quadrasi	Hidalgo 1890	Philippines	V
Videna	repanda	Mollendorf 1890	Philippines	V
Videna	rufa	Mollendorf 1888	Philippines	N Sivella rufa
Videna	saigonensis	Crosse 1867	French Indochina	T
Videna	sanis	Benson 1861	India	U
Videna	sapeca	Heude 1890	Vietnam, Philippines	T
Videna	schmakeri	Mollendorf 1894	Philippines	U
Videna	sculpticarina	Martens 1883	Malaysia	U
Videna	sibuyanica	Hidalgo 1887	Philippines	U
Videna	splendens	Sepmer 1889	Philippines	V
Videna	splendidula	Mollendorf 1890	Philippines	U
Videna	strubelli	Boettger 1890	Indonesia	U
Videna	subnigritella	Beddome 1891	India	U
Videna	sulcipes	Moerch 1872	India	U
Videna	suturalis	Mollendorf 1894	Philippines	N Sivella suturalis
Videna	swainsoni	Pfeiffer 1846	Palau	T
Videna	sylvana	Dohrn and Semper 1862	Philippines	N Geotrochus sylvana
Videna	ternatana	Le Guillou 1842	Philippines	T
Videna	timorensis	Martens 1867	Timor	V
Videna	tricolor	Martens	Indonesia	T
Videna	trilineata	Moerch 1876	India	U
Videna	trochiformis	Pfeiffer 1842	Vietnam	T

Table 4.1 All currently described *Videna* species with localities. Name changes have been noted, and the current accepted name is listed where possible. V-Known *Videna*¸ T-Changed to *Trochomorpha,* U-Unknown status, N-No longer accepted.

Island	Type	2019					2018					2013					2007					2005					2003				
		V. electra	*V. oleacina*	*V. pumila*	*V. pagodula*	*L. lacerata*	*V. electra*	*V. oleacina*	*V. pumila*	*V. pagodula*	*L. lacerata*	*V. electra*	*V. oleacina*	*V. pumila*	*V. pagodula*	*L. lacerta*	*V. electra*	*V. oleacina*	*V. pumila*	*V. pagodula*	*L. lacerata*	*V. electra*	*V. oleacina*	*V. pumila*	*V. pagodula*	*L. lacerata*	*V. electra*	*V. oleacina*	*V. pumila*	*V. pagodula*	*L. lacerarata*
Angaur	Low											X	X	X								X		X							
Babeldaob	Volcanic																					X	X	X	X		X	X			X
Babeldaob	Volcanic	X		X																											
Babeldaob	Volcanic											X				X						X									
Babelomekang	Rock									X																					
Carp	Rock																		X												
Chemoi	Rock																														
Chief's Rock	Volcanic																										X				
Chouwid	Coral																														
Eil Malk	Rock																X	X													
Euideichol	Rock						X	X	X	X												X		X	X						
Homer	Rock																														
Ioulomekong	Rock																														
Kltaltebechel	Rock																														
Klouklubed	Low																X														
Kmekumer	Rock						X																		X						
Koror	Volcanic/Rock	X				X	X	X	X		X						X										X	X	X		X
Malakal	Volcanic																											X		X	
Mecherchar	Rock						X			X							X	X		X	X	X			X	X	X				
Metukriikull	Low				X																										
Ncheangel	Atoll																														
Neco	Rock																X														
Ngchus	Rock							X											X	X		X	X	X	X	X					
Ngeanges	Rock						X	X																							
Ngebedangel	Rock																	X	X												
Ngemelis	Rock																					X			X						
Ngerchaol	Rock	X	X																							X					
Ngerchong	Low																														
Ngerkebesan	Volcanic						X	X	X	X																					
Ngerkeuid	Low				X	X																									
Ngermalk	Rock						X															X	X	X	X	*X*					
Ngermeaus	Rock																					X									
Ngermeuangel	Rock																											X		X	
Ngermid	Rock																					X	X				X				
Ngersomel	Rock						X		X	X	X																				
Ngerukewid	Rock																				X										
Ngeruktabel	Rock		X		X	X	X	X	X	X	X								X	X	X	X	X	X	X	X					
Ngeskill	Rock	X	X	X																											
Ngeteklou	Rock																														
Ngkesill	Rock																										X				
Omekang	Rock																					X		X							
Onangel	Rock						X	X		X																					
Peleliu	Low						X	X		X		X	X	X								X	X	X	X	X	X	X	X	X	
Pkuluklim	Rock																										X				
Techakl	Low																														
Ulebsechel	Volcanic/Rock						X															X	X		X	X					
Ulong	Rock						X	X	X		X	X	X	X		X	X	X	X			X	X				X		X		

Table 4.2 Collection localities of Belau trochomorphids from 2003-2019. Island type is listed along with island name.

Species	Live	Dead	Rat Chew	Total	% Live	% Dead	% Rat Chew
V. electra	105	165	36	270	39	61	13
V. oleacina	14	90	23	104	13	87	22
V. pagodula	35	34	11	69	51	49	16
V. pumila	17	155	32	172	10	90	21
L. lacerata	40	113	13	153	26	74	8

Table 4.3 Totals of the five Belau trochomorphid species, collected as live, dead, and rat predated from 2003-2019. *Videna oleacina* showed the most instances of rat predation of all the trochomorphid species for the collection periods.

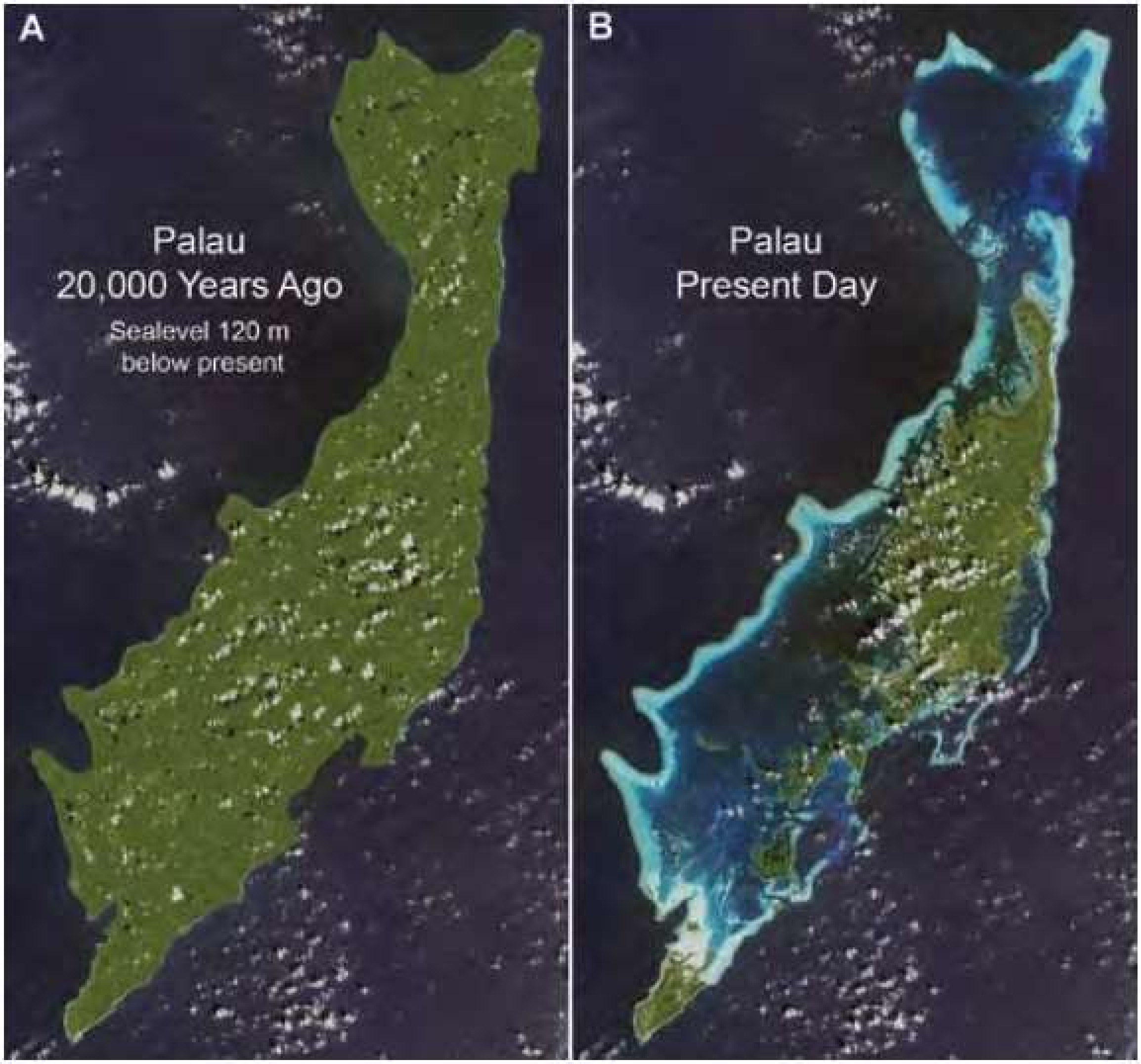


Figure 4.1 Paleo-Palau and present-day Belau. Sea levels were 120 m below present-day levels during the Pleistocene, and the rising sea level could have caused allopatric speciation of Belau *Videna* species. Photo reproduced from Colin's (2009) *The Marine Environments of Palau*.

Figure 4.2 Two specimens of *Videna oleacina* bearing telltale rat predation markings. Rat species will often break into the shells through the sides or tops, and the shells will bear uneven or jagged chew marks around the periphery of the holes the rats have made in the shells.

Figure 4.3 *Videna electra* (blue) current geographic range, based on collection localities from 2003-2019. *Videna electra* has the widest range of the Belau trochomorphids. Islands were colored in when specimens were found at localities, and do not indicate that a species can be found throughout the island (i.e., Beliliou).

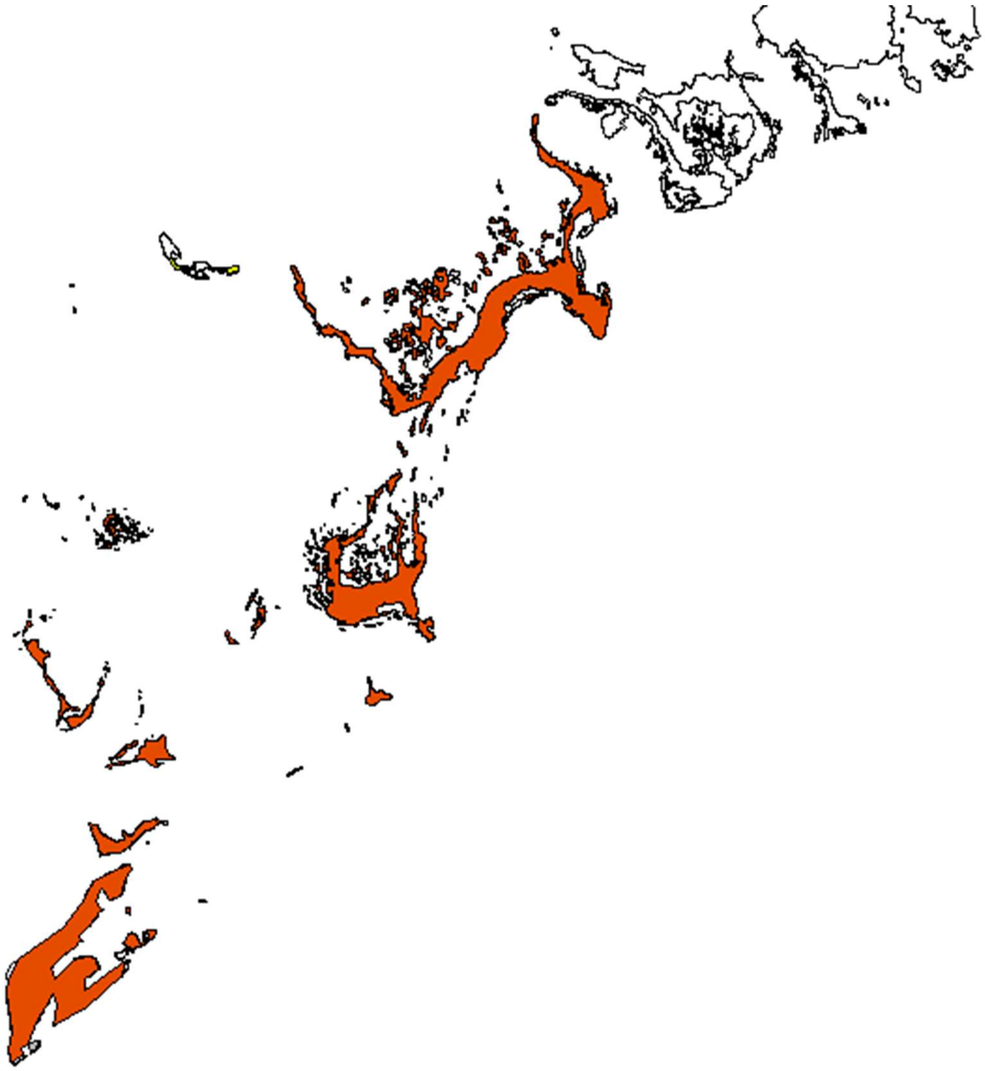


Figure 4.4 *Videna oleacina* (orange) current geographic range, based on collection localities from 2003-2019. Islands were colored in when specimens were found at localities, and do not indicate that a species can be found throughout the island (i.e., Beliliou).

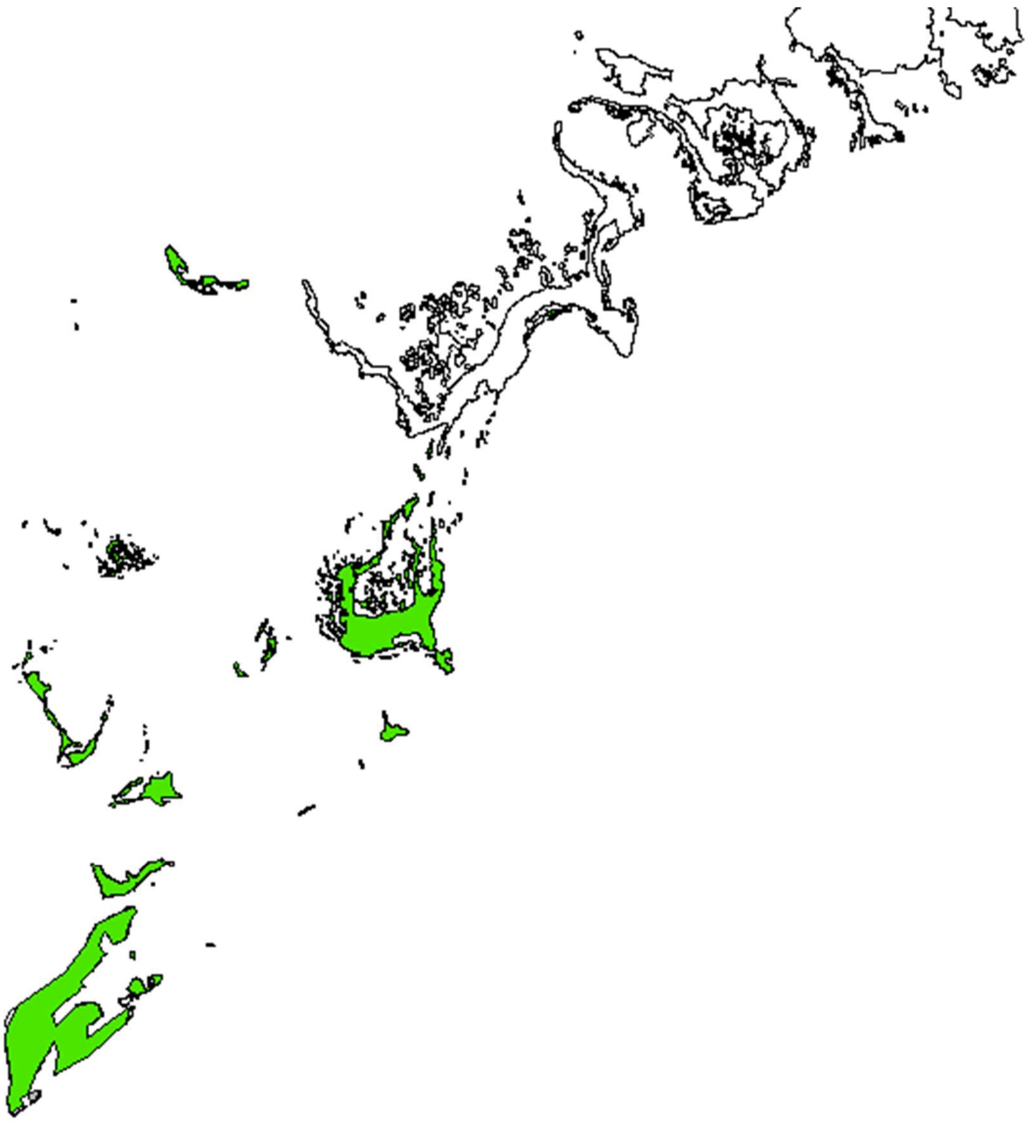


Figure 4.5 *Videna pagodula* (green) current range based on collection localities from 2003-2019. *Videna pagodula* has a considerably more limited range than the other Belau trochomorphids, mainly being found on Beliliou and the southernmost Rock Islands. Islands were colored in when specimens were found at localities, and do not indicate that a species can be found throughout the island (i.e., Beliliou).

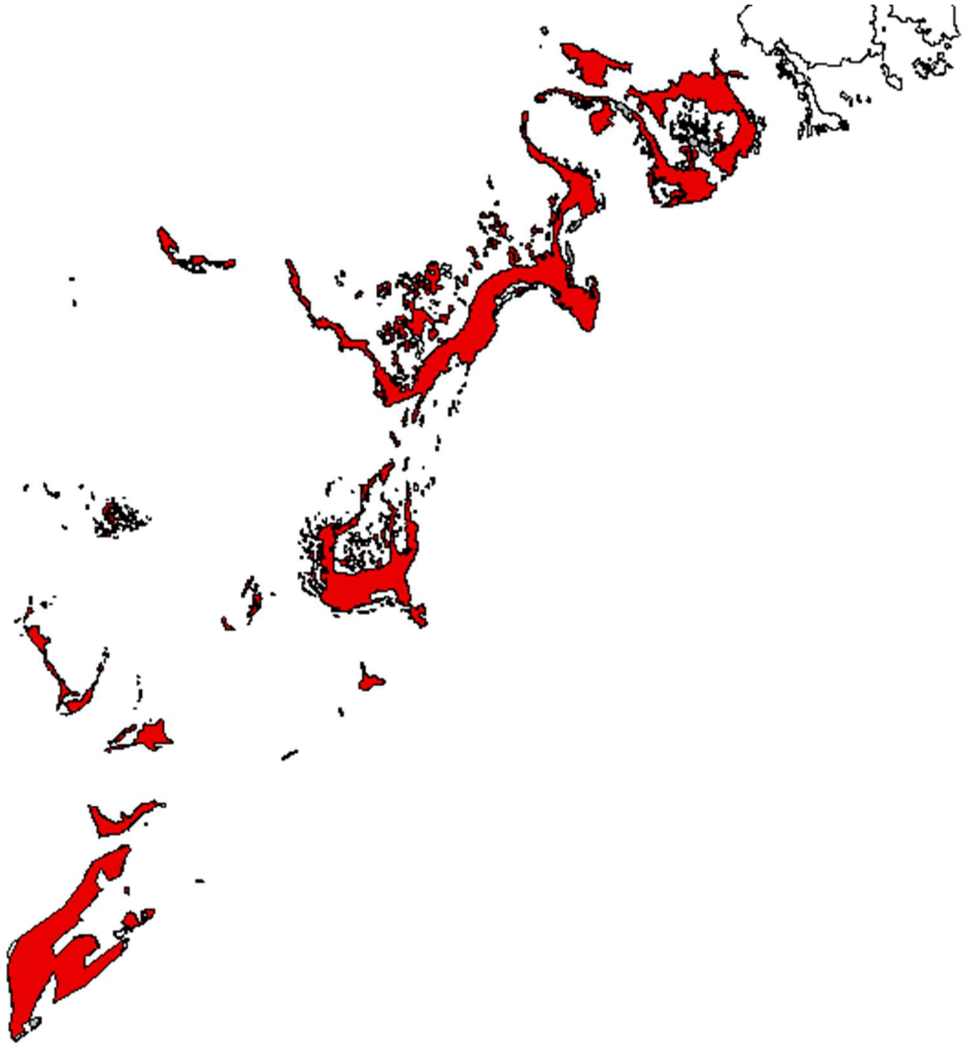


Figure 4.6 *Videna pumila* (red) current range based on collection localities from 2003-2019. *Videna pumila* is found throughout the Rock Islands and Beliliou but was not found in the limestone outcrops of southern Babeldaob. Islands were colored in when specimens were found at localities, and do not indicate that a species can be found throughout the island (i.e., Beliliou).

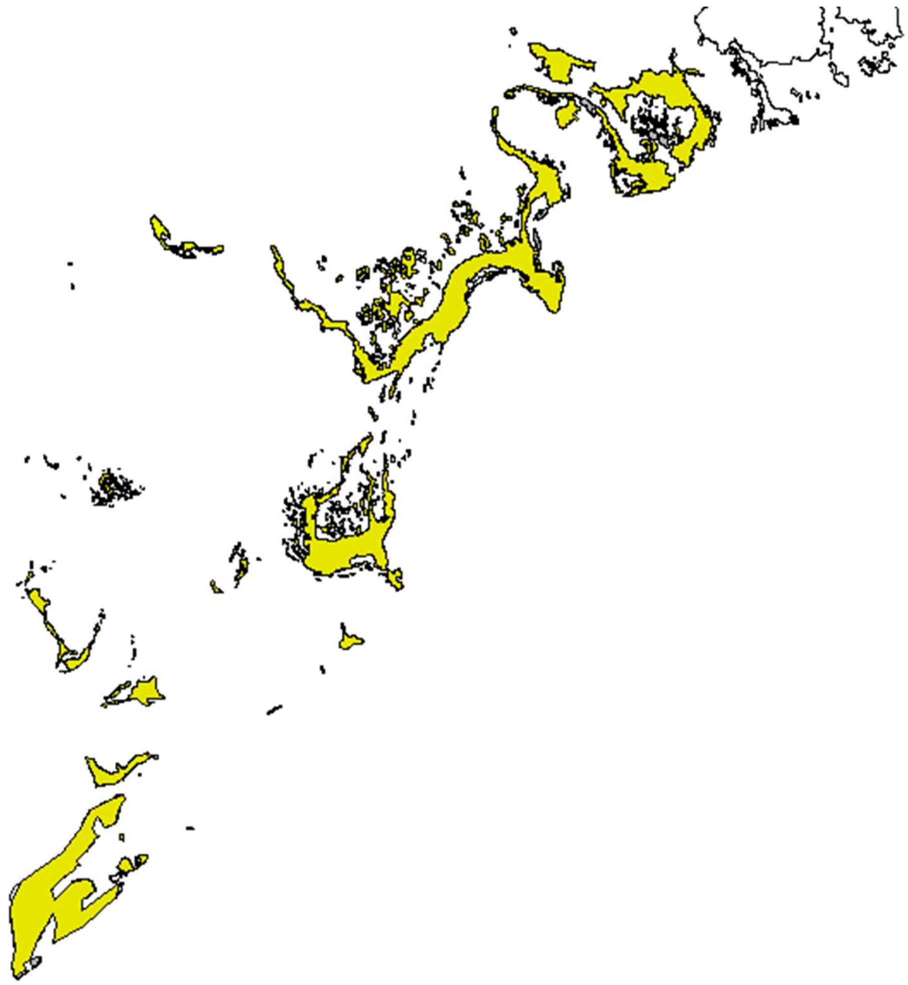


Figure 4.7 *Liravidena lacerata* (yellow) current range based on collection localities from 2003-2019. *Liravidena lacerata* is found across the Rock Islands and Beliliou but was not found on the limestone islands of southern Babeldaob. Islands were colored in when specimens were found at localities, and do not ndicate that a species can be found throughout the island (i.e., Beliliou).

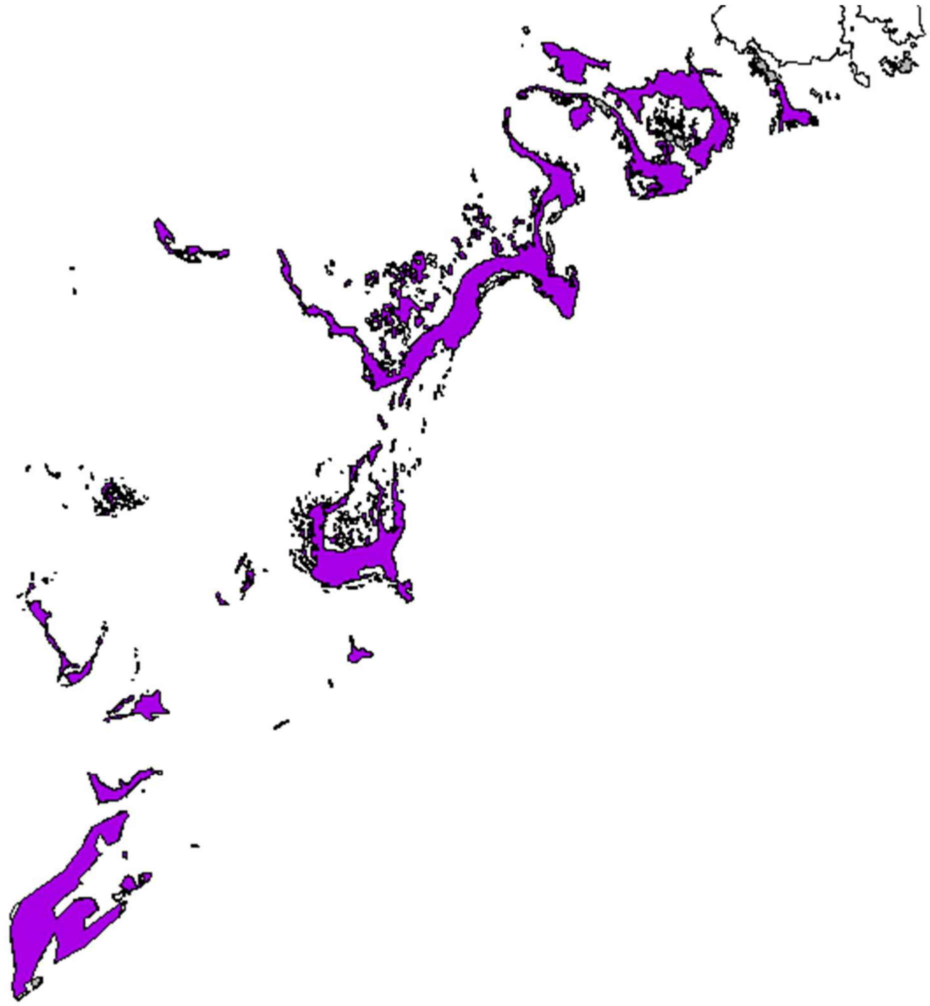


Figure 4.8 Instances of rat predation on collected trochomorphid shells collected from 2003-2019 (purple). Rat predation in the forms of chewing on shells was found across the Rock Islands, Beliliou and the limestone islands on the southern end of Babeldaob and was not limited to areas with higher human populations, such as popular tourist areas or inhabited islands. Rat predation on the main island of Babeldaob is not depicted.

5. Conclusions and further research

5.1 Conclusions of this study

The trochomorphids of Belau are unique, not just because they are endemic to the archipelago, but because they are a monophyletic group which appears genetically distinct from other trochomorphids. A reinstated genus, *Peleliua*, has been suggested earlier this year (Molluscabase 2020), and the monophyly of the clade reconstructed using species' sequences from the gene region COI for Belau trochomorphids partially supports the decision (Figure 3.1). However further research and the inclusion of additional gene regions and taxa outside of Belau will likely be useful in increasing the resolution of future phylogenetic reconstructions. Based on my research, the following gene regions might be less useful, e.g. IT2, 28S and 5.8S (Table 3.1), but it is suggested that 16S and 18S gene regions might be employed, since they have been successful in several species-level studies of pulmonate land snails.

Belau trochomorphids possess beautiful, charismatic shells that attract not only researchers but invasive predators, and as such these species are facing declines in their populations, particularly from rats. Habitat loss from human encroachment is also a danger to these snails, and steps to limit deforestation and limestone mining will help to slow decline. Eradications of invasive rats have shown success, but are not permanent solutions for the problem, since rats are able to swim between islands, and could return to islands where rat eradication had previously taken place. They can also still be transported via stowing away in boats from islands where rat eradication has not yet occurred, and be reintroduced to rat eradicated islands.

With revised species descriptions and the first photographs, researchers involved in conservation efforts across the archipelago will be able to readily identify the Belau trochomorphids, which will in turn provide more conclusive data to add to the newly reconstructed current geographic ranges.

5.2 Phylogeographic assessment of *Videna electra*

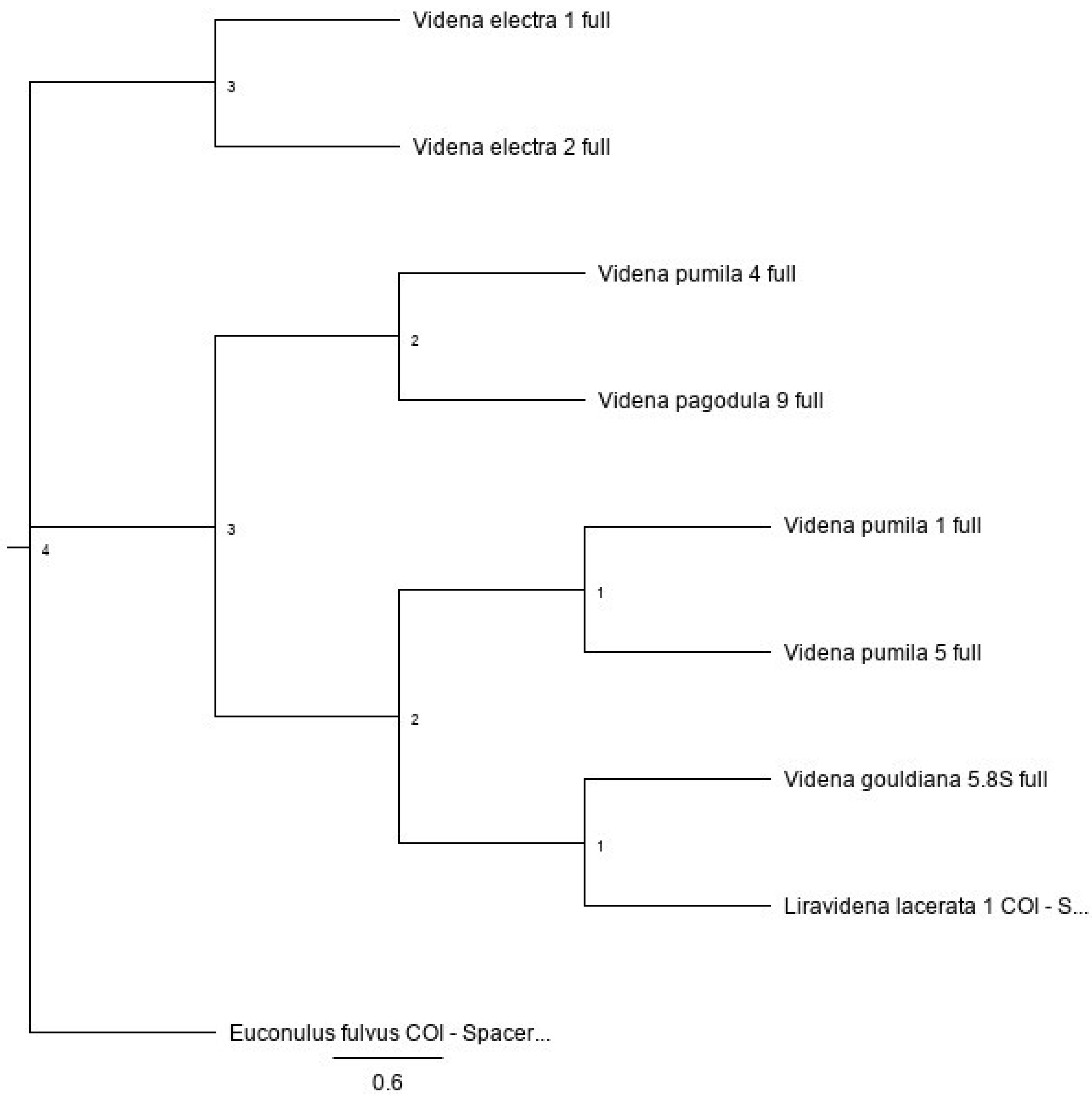
Videna electra is of particular interest phylogenetically and phylogeographically. Several unique shell characters have been noted in *V. electra.* The size and color of the characteristic amber band varies from very thin to extremely wide, and in some cases the band is almost nonexistent while other morphological characters remain the same. These color “Morphs” of *V. electra* also form a pattern across the Rock Islands, with the thin amber banded *V. electra* being found more in the southern end of the archipelago and the thicker, darker banded *V. electra* being found towards the middle of the Rock Islands around Ngeruktabel (Figure 5.1). Specimens that most resemble the type specimen for *Videna electra* can be found throughout the Rock Islands. Sampling these specimens and adding them to the current trees to observe the relationships and any patterns that occur would be the next step in a deeper understanding of *V. electra*.

5.3 Potential new trochomorphid species found on Belau, summer 2019

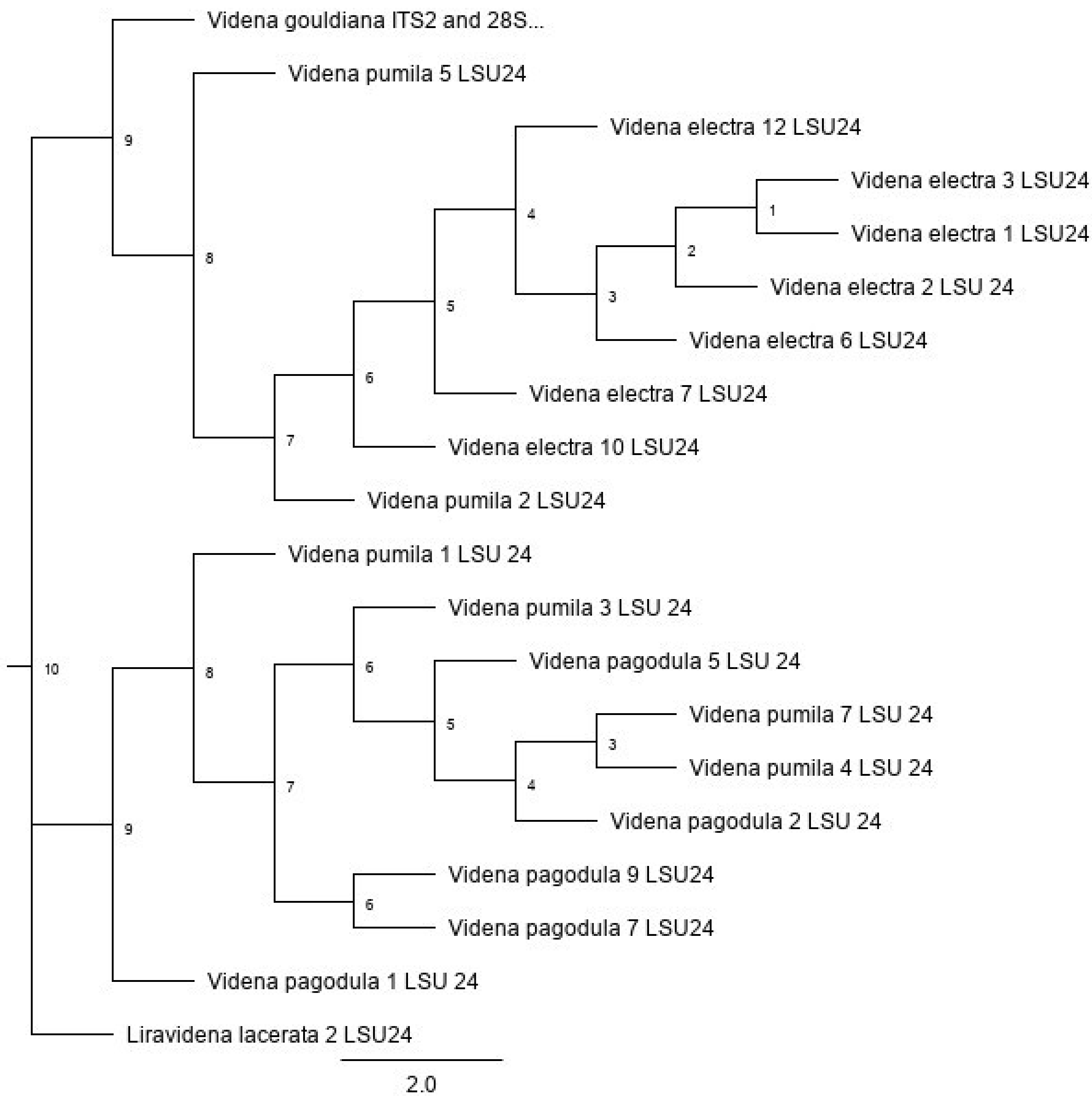
During the field season of 2019, a potential new trochomorphid was found (Figure 5.1). It was collected near the Ngardmau falls in the northwestern side of Babeldaob, which would be a newly discovered location for Belau trochomorphids to inhabit, as trochomorphids have yet to be collected from non-limestone sections of Babeldaob, although the entirety of the island has yet to be surveyed in extensive detail specifically for trochomorphids. This specimen would need to be added to the existing phylogenetic trees once its DNA has been isolated. There is only one specimen of this trochomorphid currently in the Rundell lab, so great care must be taken when removing foot tissue for DNA analysis so that the shell will remain unbroken. A detailed morphological description is also required, including a full assessment of the shell characters and reproductive morphology. Further survey efforts around Ngardmau falls for this trochomorphid would provide more tissue for DNA isolation and allow for a more detailed analysis of its morphological characters. However, given the lack of available genetic data for trochomorphids, especially for members of the genus *Videna*, it cannot be said with certainty that this trochomorphid is a new species, or rather a new species arrival to Belau.

Figure 5.1 Map of Belau depicting collection locations for the color "Morphs" of *Videna electra*. Lighter banded specimens predominantly came from the southern end of the archipelago, while darker banded specimens were collected towards the center around Ngeruktabel. Those specimens most like the type specimen of *V. electra* are found throughout the surveyed islands.

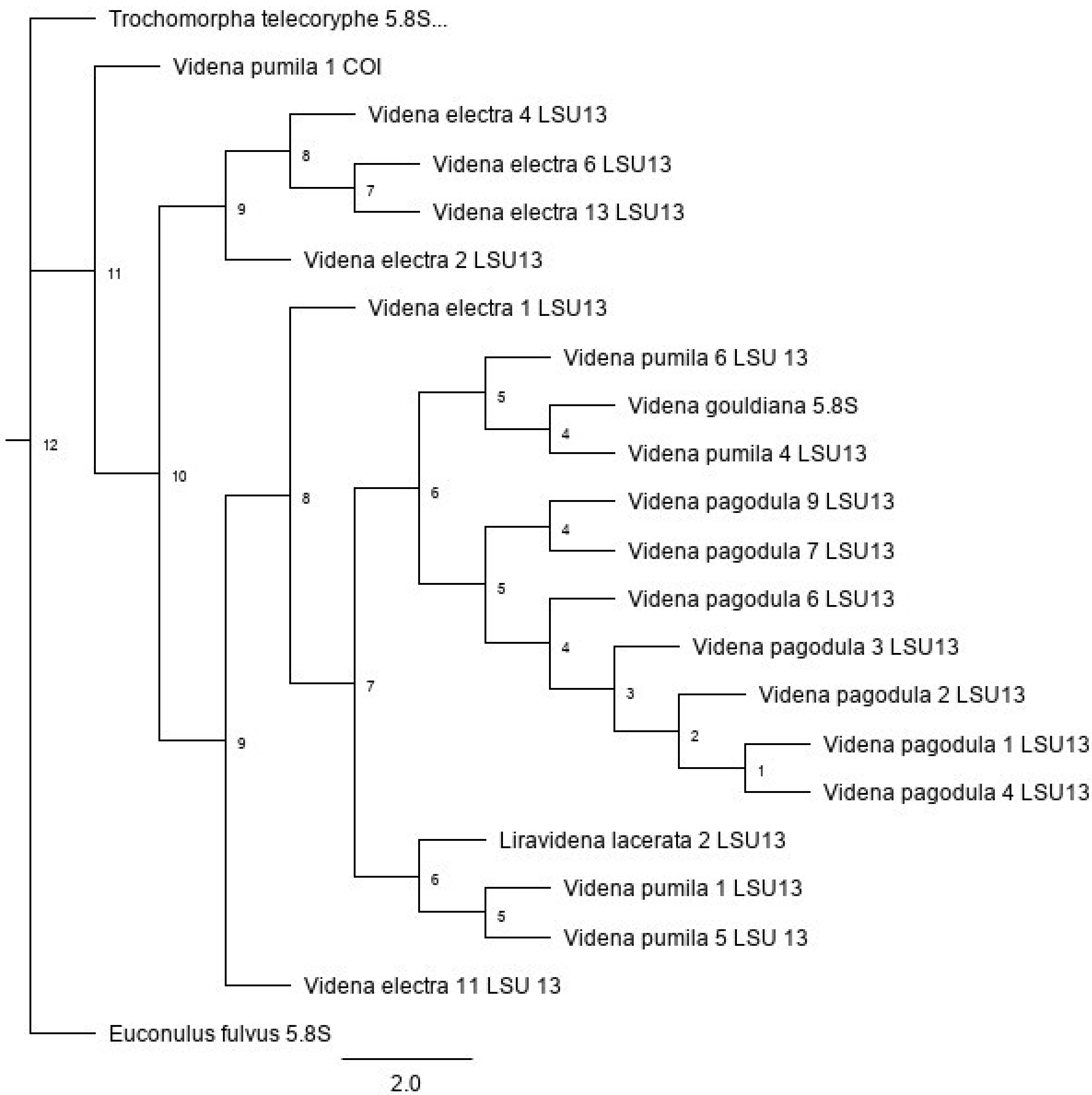
Figure 5.2 The new possible trochomorphid found in Belau 2019 in northwestern Babeldaob near Ngardmau falls. Further research, including surveys, dissections, DNA isolation and placement in the existing Belau trochomorphid phylogenetic tree is needed before any conclusive results can be made about this species.



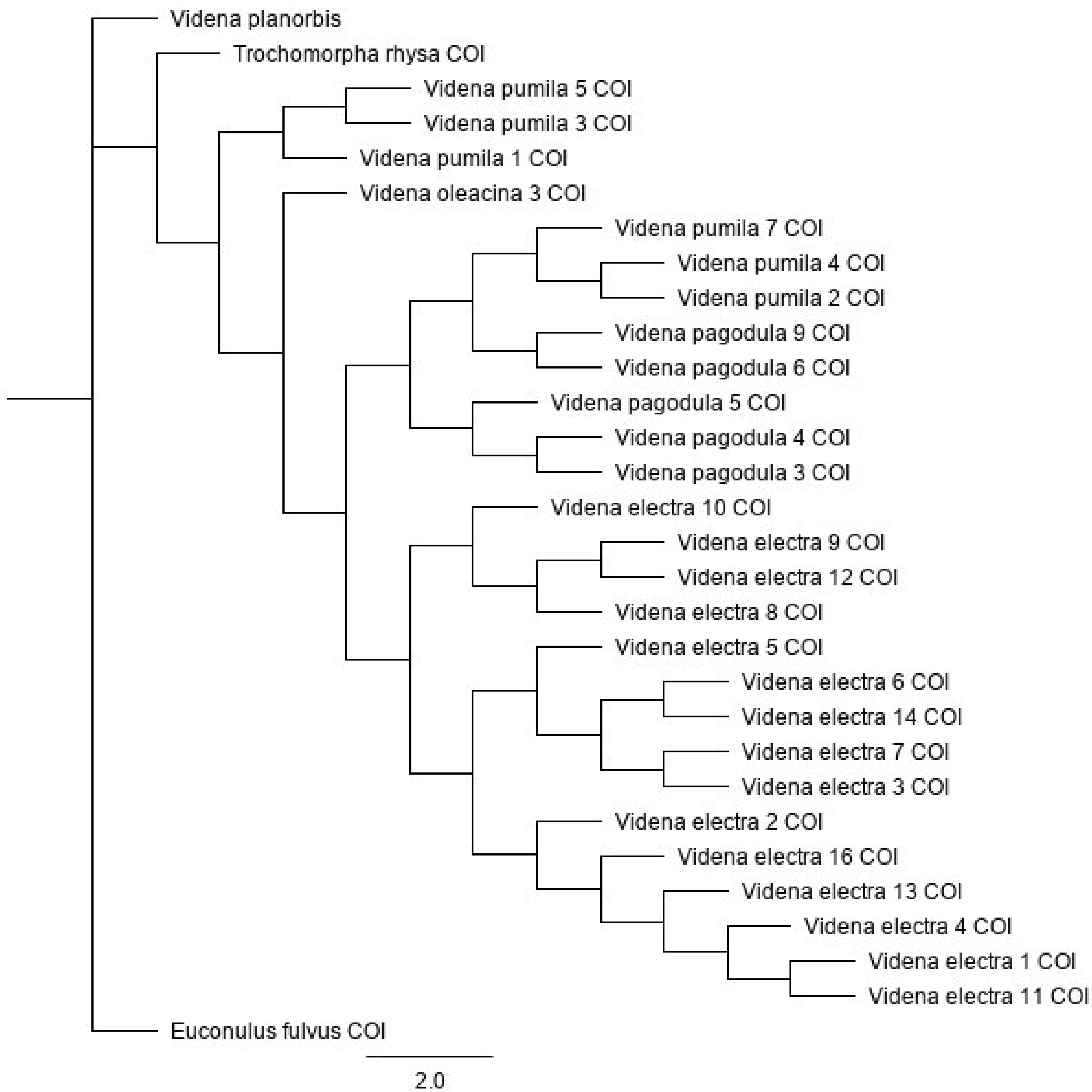
Appendix 1.1 Phylogenetic tree generated using RAxML applied to concatenated COI, 28S and 5.8S gene regions of Belau trochomorphids, with additional trochomorphids *Videna planorbis, V. gouldiana* and *Trochomorpha rhysa,* and *Euconulus fulvus* outgroup.



Appendix 1.2 Phylogenetic tree generated using RAxML applied to the 28S gene region of Belau trochomorphids, with additional trochomorphids *Videna gouldiana* and *Euconulus fulvus* outgroup.



Appendix 1.3 Phylogenetic tree generated using RAxML applied to the 5.8S gene region of Belau trochomorphids, with additional trochomorphids *Videna gouldiana* and *Euconulus fulvus* outgroup.



Appendix 1.4 Phylogenetic tree generated using MrBayes applied to COI gene regions of Belau trochomorphids, with additional trochomorphids *Videna planorbis*, *Trochomorpha rhysa* and *Euconulus fulvus* outgroup.

Literature Cited

Adams H and A 1858. Genera of Recent Mollusca. 114-116 pp.

Baker HB 1941. Zonitid snails from Pacific Islands. Part 3 and 4. Genera other than Microcystinae and distribution and indexes. 203–370 pp.

Barker, G. M. 2001. Gastropods on land: phylogeny, diversity and adaptive morphology. IN: Barker, G. M. (ed.) The Biology of Terrestrial Molluscs. CAB International, Wallingford, UK, pp. 1-146.

Bouchet, P., Rocroi, J. P., Hausdorf, B., Kaim, A., Kano, Y., Nützel, A., Parkhaev, P., Schrödl, M. & Strong, E. E. 2017. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. Malacologia, 61(1-2), 1-526.

British Museum 1904. The History of the Collections Contained in the Natural History Departments of the British Museum. Elibron Classics. 462 pp.

Chiba S & Cowie RH 2016. Evolution and Extinction of Land Snails on Oceanic Islands. Annu. Rev. Ecol. Evol. Syst. 47: 123–41.

Colin PL 2009. Marine environments of Palau. Mutual Publishing, LLC, Honolulu, Hawai'i. 416
Crombie RI, Pregill GK, & Monographs H 2007. A Checklist of the herpetofauna of the Palau Islands (Republic of Belau), Oceania. 13: 29–80.

Fiorentino V, Salomone N, Manganelli G, & Giusti F 2008. Phylogeography and morphological variability in land snails: The Sicilian Marmorana (Pulmonata, Helicidae). Biol. J. Linn. Soc. 94: 809–823.

Folmer O, Black M, Hoeh W, Lutz R, & Vrijenhoek R 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. 3: 294–299.
Hall T 2017. Megapodes Return Home. Isl. Conserv.: 1.

Hausdorf B. 1998. Phylogeny of the Limacoidea sensu lato (Gastropoda: Stylommatophora). J. Molluscan Stud. 64: 35–66.

Hausdorf B 2000. Biogeography of the Limacoidea sensu lato (Gastropoda: Stylommatophora): vicariance events and long-distance dispersal. J. Biogeogr. 27: 379–390.

Holland BS & Cowie RH 2009. Land snail models in island biogeography: A tale of two snails. Am. Malacol. Bull. 27: 59–68.

Hyman IT, Ho SYW, & Jermiin LS 2007. Molecular phylogeny of Australian Helicarionidae, Euconulidae and related groups (Gastropoda: Pulmonata: Stylommatophora) based on mitochondrial DNA. Mol. Phylogenet. Evol. 45: 792–812.

Kobayashi K 2004. Origin of the Palau and Yap trench-arc systems. Geophys. J. Int. 157: 1303–1315.

MolluscaBase eds. 2020. MolluscaBase. *Peleliua* H. B. Baker, 1941. Accessed at: http://www.molluscabase.org/aphia.php?p=taxdetails&id=995246 on 2020-11-01.

Mollusc Specialist Group 1996. *Trochomorpha apia*. 2006 IUCN Red List of Threatened Species. Downloaded on 10 October 2020.

Motteler LS 2006. Pacific island names. Second Edition. Bishop Museum Bulletin in Cultural and Environmental Studies 2. Bishop Museum Press. Honolulu, Hawaii. 95 p.

Nordsieck H 1992. Phylogeny and system of the Pulmonata (Gastropoda). Arch. für Molluskenkd. 121: 31–52.

Pippard H, Oceania I, & Office R The current status and distribution of land snails in the Pacific Islands of Oceania.: 1–24.

Rundell RJ, Holland BS, & Cowie RH 2004. Molecular phylogeny and biogeography of the endemic Hawaiian Succineidae (Gastropoda:Pulmonata). Mol. Phylogenet. Evol. 31: 246–255.

Rundell RJ 2010. Diversity and conservation of the land snail fauna of the western Pacific islands of Belau (Republic of Palau, Oceania). Am. Malacol. Bull. 90: 81–90.

Rundell RJ 2005. The land snails of Belau: survey of the 16 States. East: 20.

Rundell RJ 2008. Cryptic diversity, molecular phylogeny and biogeography of the rock- and leaf litter-dwelling land snails of Belau (Republic of Palau, Oceania). Philos. Trans. R. Soc. B Biol. Sci. 363: 3401–3412.

Rundell RJ 2010. Diversity and conservation of the land snail fauna of the western Pacifi c islands of Belau (Republic of Palau, Oceania). Am. Malacol. Bull. 90: 81–90.

Rundell, R.J. 2012a. *Videna pagodula*. *The IUCN Red List of Threatened Species* 2012: e.T22961A2783172. http://dx.doi.org/10.2305/IUCN.UK.2012.RLTS.T22961A2783172.en. Downloaded on 25 February 2019.

Rundell, R.J. 2012b. *Videna pumila*. *The IUCN Red List of Threatened Species* 2012: e.T22962A2783240. http://dx.doi.org/10.2305/IUCN.UK.2012.RLTS.T22962A2783240.en. Downloaded on 25 February 2019.

Rundell, R.J. 2012c. *Videna oleacina*. *The IUCN Red List of Threatened Species* 2012: e.T22960A2783057. http://dx.doi.org/10.2305/IUCN.UK.2012.RLTS.T22960A2783057.en. Downloaded on 25 February 2019.

Rundell, R.J. 2012d. *Videna electra*. *The IUCN Red List of Threatened Species* 2012: e.T22959A2782947. http://dx.doi.org/10.2305/IUCN.UK.2012.RLTS.T22959A2782947.en. Downloaded on 25 February 2019.

Schileyko, A.A. 2003. Treatise on recent terrestrial pulmonate molluscs. Part 8. Punctidae, Helicodiscidae, Discidae, Cystopeltidae, Euconulidae, Trochomorphidae. Ruthenica,

Smith BD 1993. Working list of the terrestrial gastropods of Palau, Caroline Islands.

Solem A 1959. Zoogeography of the land and freshwater mollusca of the New Hebrides. Fieldlandia Zool. 43: 303.

Sosa BO, Batomalaque GA, & Fontanilla IKC 2014. An updated survey and biodiversity assessment of the terrestrial snail (Mollusca: Gastropoda) species in Marinduque, Philippines. Philipp. J. Sci. 143: 199–210.

Thacker RW & Hadfield MG 2000. Mitochondrial phylogeny of extant Hawaiian tree snails (Achatinellinae). Mol. Phylogenet. Evol. 16: 263–270.

Tillier, S. 1989. Comparative morphology, phylogeny and classification of land snails and slugs (Gastropoda: Pulmonata: Stylommatophora). Malacologia, 30, 1-303.

Vagvolgyi J 1975. Body Size, aerial dispersal, and origin of the pacific land snail fauna. Soc. Syst. Biol. 24: 465–488.

Wade CM, Mordan PB, Clarke B, Wade CM, Mordan PB, & Clarke B 2001. A phylogeny of the land snails (Gastropoda:Pulmonata) A phylogeny of the land snails (Gastropoda:Pulmonata).

Wade CM, Mordan PB, & Naggs F 2006. Evolutionary relationships among the Pulmonate land snails and slugs (Pulmonata, Stylommatophora). Biol. J. Linn. Soc. 87: 593–610.

Winnepenninckx B, Steiner G, Backeljau T, & Wachter R De 1998. Details of Gastropod Phylogeny Inferred from 18S rRNA Sequences. Mol. Phylogenet. Evol. 9: 55–63.

Wu, J., Suppe, J., Lu, R., and Kanda, R. (2016), Philippine Sea and East Asian plate tectonics since 52 Ma constrained by new subducted slab reconstruction methods, *J. Geophys. Res. Solid Earth*, 121, 4670– 4741, doi:10.1002/2016JB012923.

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