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Correlating Molecular Phylogeny with Venom Apparatus Occurrence in
Panamic Auger Snails (Terebridae)

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Running title: Terebrid phylogeny and anatomy

Summary

Central to the analysis of the neuroactive compounds produced by predatory marine snails of the superfamily Conoidea (cone snails, terebrids, and turrids) is identifying those species with a venom apparatus. Previous analysis of South-West Pacific terebrid specimens has shown that some terebridae groups have secondarily lost their venom apparatus. In order to efficiently characterize terebrid toxins, it is essential to devise a key for identifying which species have a venom apparatus. The findings presented here integrate molecular phylogeny and the evolution of character traits to infer the absence or presence of the venom apparatus in the Terebridae. Using a combined dataset of South-West and Eastern Pacific terebrid samples, a phylogenetic hypothesis was constructed based on analyses of 16S, COI and 12S mitochondrial genes. Anatomical analysis was congruent with molecular characters, confirming that species included in the clade *Acus* do not have a venom apparatus, while those in the clade *Terebra* do. Interestingly, the findings from this study also imply two independent terebrid colonization from South-West Pacific to Panama (Eastern Pacific) occurred during the Miocene. Discovery of the association between terebrid molecular phylogeny and the occurrence of a venom apparatus provides a useful tool for effectively identifying the terebrid lineages that may be investigated for novel pharmacological active neurotoxins, enhancing conservation of this important resource, while providing supplementary information towards understanding terebrid evolutionary diversification.

Keywords: Terebridae, Conoidea, venom apparatus, molecular phylogeny, peptide toxins, Panama.

Introduction

The auger snails (family Terebridae) are a distinctive group of carnivorous, sand-dwelling gastropods included in the superfamily Conoidea, along with cone snails and turrids ^[1]. Species in this large gastropod superfamily (>10,000 species) generally use venom to capture their prey ^[2, 3]. Conoidean venoms are of considerable interest as they are a rich source of neuroactive peptides, widely used to investigate cellular communication in the nervous system ^[4-6]. Some Conoidean venom components have been used directly for a variety of biomedical applications ^[7, 8]. Several peptides from cone snail venoms have reached human clinical trials, and one (Prialt) has been approved as a drug for intractable pain ^[9, 10].

In contrast to cone snails, the Terebridae toxins are largely uncharacterized at the present time and no physiological target for any terebrid venom peptide has been defined. However, the very preliminary characterization carried out to date suggests that the venoms of the Terebridae have novel components, distinct from other conoidean venoms ^[11, 12]. Thus, terebrid venoms are potentially a rich, unexplored pharmacological resource.

A significant fraction of the ~ 300 - 400 species in the Terebridae do not have the characteristic anatomical structures that comprise the venom delivery apparatus of conoidean snails, namely a venom bulb, venom duct, and radula sac ^[13-16]. Analysis of shell morphology alone cannot generally determine whether or not a species in the Terebridae has a venom apparatus. Therefore, identifying *a priori* which species to collect for the analysis of venom components is problematic.

The first molecular phylogeny of the Terebridae based on a three-gene matrix of molecular markers 12S, 16S, and cytochrome oxidase I (COI), was recently published^[16].

The data suggests that the family Terebridae could be divided into at least 5 distinctive generic clades: *Acus*, *Terebra*, *Hastula*, *Myurella*, and a sister clade of the four others that includes *Terebra jungi* (recently revised to *Pellifronia jungi* ^[17]). Furthermore, based on species clusters, it was suggested that molecular data maybe a link to identifying which terebrid species have a venom apparatus and which do not. For these molecular criteria to reliably indicate which species of Terebridae are venomous, the criteria should be applicable to all Terebridae.

The original correlation between venom apparatus and molecular phylogeny was established using only IndoPacific species ^[16]. This paper examines the validity of correlating molecular phylogeny and venom apparatus by increasing the diversity of taxa sampled and the geographic coverage to include terebrid samples from the Eastern Pacific country of Panama. In terms of geographic distribution, the Panamic tropical molluscan marine fauna is arguably highly divergent from that of the IndoPacific. Thus, whether the molecular phylogeny/venom apparatus correlation established for IndoPacific Terebridae can be used to assess Eastern Pacific auger snails is a central issue addressed by this study. Presented here is the first molecular analysis of Panamic Terebridae, which is used to highlight both phylogenetic and taxonomic issues for this group.

Materials and Methods

Material

Panamic specimens used were dredged from the Las Perlas Archipelago in 2008, using The Smithsonian Tropical Research Institute research vessel RV-Urraca. The collected

material was specifically fixed for molecular and anatomical analysis. Living specimens were anesthetized in MgCl₂ isotonic with seawater for 1 or 2 hours. Samples were thoroughly dissected and a piece of tissue (usually foot) was cut and fixed in 95% ethanol. Table 1 lists all terebrid specimens used in this study, including the specific geographical coordinates of where they were collected (for map see, Figure 1). Taxonomic assignments were made based on shell morphology. Included with the 33 Panamic taxa are sequences from specimens collected in the Indo-Pacific and analyzed in Holford *et al.* 2009 ^[16]. Similar to the Indo-Pacific material, vouchers of the Panamic specimens will be deposited in the Muséum National d'Histoire Naturelle (MNHN) of Paris. Outgroups are identical to those used in Holford *et al.* 2009 ^[16] and identified in Table 1.

Sequencing

DNA was extracted from foot or other tissue using Qiagen QIAamp Dneasy Tissue kit. Fragments of mitochondrial genes 12S, 16S and COI were amplified using universal primers 12S1/12S3^[18], 16Sar/16Sbr^[19] and LCO1490/HCO2198^[20] respectively. PCR reactions were performed in 25 µl, containing 3 ng of DNA, 10X reaction buffer, 2.5 mM MgCl₂, 0.26 mM dNTP, 0.3 mM each primer, 5% DMSO, and 1.5 units of Qbiogene Q-Bio Taq or Advantage® 2 PCR Kit from Clontech. Amplification was performed as previously described ^[16]. PCR products were purified using USB ExoSAP-IT® or Quiagen PCR purification kit and sequenced. All genes were sequenced in both directions for increased accuracy of each sequence. Sequences were deposited in GenBank (Genbank accession numbers: FJ707376-FJ707472). COI sequences were also

deposited in BOLD (Barcode of Life Data Systems, project CONO - Conoidea barcodes and taxonomy).

Molecular and Phylogenetic analyses:

COI sequences were manually aligned and 12S and 16S were automatically aligned using ClustalW multiple alignment implemented in BioEdit version 7.0.5.3 ^[21]. The accuracy of automatic alignments was confirmed by visual inspection. Hyper-variable regions of 12S and 16S genes were excluded from further analyses due to ambiguities in the alignments. All the South-West Pacific Terebridae sequences obtained by Holford *et al.* 2009 ^[16] were added to this new dataset.

Phylogenetic analyses were based on reconstructions using two approaches: (i) Maximum Likelihood (ML) using PhyML 2.4.4^[22], where support of nodes were estimated using 100 bootstraps, and (ii) Bayesian Analyses (BA) consisting of six Markov chains, 10,000,000 generations each with a sampling frequency of one tree each thousand generations, run in four parallel analyses using Mr. Bayes ^[23]. The number of swaps that are tried each time the chain stops for swapping was 4, and the chain temperature was set at 0.05. Twenty-five percent of the first generations were discarded as burnin, which correspond to the time the chain took to reach the stationary distribution. For both ML and BA, the best-fitting model of evolution was applied, as determined by Modelgenerator V.85 following the Hierarchical Likelihood Ratio Test (with four discrete gamma categories). Each gene was first analysed separately and then the combined dataset was analysed. For the combined dataset one model of evolution for the

concatenation of the three genes has been used for the ML analysis. For the BA, a different model was applied for each gene as determined by Modelgenerator.

Character evolution

The phylogenetic positioning of the Panamic sequences allows us to discuss the evolution of several characters. Among them, the evolution of the presence/absence of the venom apparatus has already been analysed for the IndoPacific samples in Holford *et al.* 2009^[16]. All Panamic specimens were dissected to define their character state. To understand character-state evolution as well as biogeographic patterns, each taxon was coded for presence or absence of the venom gland and locality. The geographic distribution of the samples included was analyzed with two character states, IndoPacific or Panamic Gulf, and mapped on the tree using Mesquite V. 2.01^[24], with the option “tracing character history.” The parsimony ancestral reconstruction method was used.

Results

Distribution of the Panamic Terebridae

The 33 Panamic specimens analyzed were assigned to four different terebrid species: *A. strigatus*, *T. argyosia*, *T. ornata*, and *Terebra* cf. *formosa*. All taxonomic assignments made are based on shell morphology and later confirmed by molecular results. The *T. argyosia* specimens (collection sites 1, 2, 3, and 4) appear to be present both in the northern and southern ends of the archipelago (Figure 1A). *Acus strigatus* was found between Punta Coco, of Isla Del Rey and San Jose (sites 4 and 6). *T. ornata* was collected along the eastern coast of San Jose (site 5) and *Terebra* cf. *formosa* at site 7. Examples of the actual specimens analyzed are shown in Figure 1B.

Phylogenetic analyses

Partial sequences of COI, 12S, and 16S genes were obtained for the Panamic specimens collected. After alignment, DNA fragments of 658, 534 and 455 bp for COI, 12S and 16S genes, respectively, were obtained. No contradictions were observed when independently constructed gene trees for COI, 12S, and 16S genes were analyzed (results not shown). These sequences were combined with the Indo-Pacific terebrid sequences previously obtained ^[16] to reconstruct the molecular phylogeny illustrated in Figure 2. The best model of evolution for the COI, 12S and 16S and for the combined dataset is GTR+I+G (General Time Reversible model, with invariant sites and a gamma law parameter) for all of them, with $I = 0.51$ and $\alpha = 0.68$ for COI, $I = 0.6$ and $\alpha = 0.62$ for 12S, $I = 0.34$ and $\alpha = 0.32$ for 16S and $I = 0.41$ and $\alpha = 0.4$ for the combined dataset. Results obtained with Maximum Likelihood (ML) and Bayesian analyses (BA) are highly similar, however, the support values for ML were generally weaker.

Of the 5 distinct *Terebra* clades previously identified ^[16], Clade A (*P. jungi*), Clade B (*Acus*), Clade C (*Terebra*), Clade D (*Hastula*), and Clade E (*Myurella*), the Panamic sequences reported here fall into the *Acus* and *Terebra* clades. As a result, in order to reduce the size of the tree and to focus on the Panamic clades, only the *Acus* and *Terebra* are detailed in Figure 2. The other clades, represented by one specimen each, are identical to those in Holford *et al.* 2009 ^[16].

The phylogenetic analysis strongly indicates that the Panamic *Acus strigatus* specimens in our sampling are within the *Acus* clade (Posterior Probability (PP) = 1; Bootstraps (B) = 98). The *Acus* clade comprises a prevalence of Indo-Pacific species (*A. felinus*, *A. chloratus*, *A. maculatus*, *A. areolatus*, *A. crenulatus*, and *A. dimidatus*). The

monophyly of the Panamic specimens identified as belonging to the *Terebra* clade is well-supported (PP = 1; B = 96) within this group. As illustrated in the tree there are three distinct Panamic species present, *Terebra argyosia*, *Terebra ornata*, and *Terebra* cf. *formosa*.

Character evolution

All Panamic specimens collected were dissected and the presence or absence of a venom apparatus was noted (Table 1). The presence/absence of a venom apparatus is a character trait that can be correlated with the molecular phylogeny of these specimens. As indicated in Figure 2, the Panamic species that mapped to the *Acus* clade, *Acus strigatus*, did not have a venom apparatus (highlighted with a white box). However, *T. ornata*, *T. argyosia*, and *Terebra* cf. *formosa*, all have a venom apparatus and fall within the genus *Terebra*, which contains other terebrid species identified as having a venom apparatus^[13, 16, 25] (highlighted by a black box). The character evolution of the venom apparatus in the Terebridae was mapped previously for Indo-Pacific specimens^[16], indicating this group has lost the venom apparatus at least twice during its evolution.

Discussion

Predatory marine snails of the superfamily Conoidea produce several neurotoxins in their venom that are used to capture and subdue prey^[26-28]. In the family Terebridae, the characteristic venom apparatus of conoideans is not present in a significant fraction of all species of *Terebra*. For this work, four Panamic species, *Acus strigatus*, *Terebra argyosia*, *Terebra ornata*, and *Terebra* cf. *formosa*, were analyzed using a combination of

molecular phylogeny and character trait evolution based on the presence or absence of a venom apparatus (Figure 2). The molecular characters are completely congruent with anatomical data: all specimens without a venom apparatus are in the *Acus* clade, and all specimens with a venom apparatus are in the *Terebra* clade. Thus, DNA sequences can be used to infer if a terebrid species has a venom apparatus or not. This study confirms the correlation between phylogeny and the presence or absence of the venom apparatus previously established ^[16].

The phylogenetic results in Figure 2 also provide insight into the phylogeography and taxonomy of the Panamic Terebridae. The analysis of Panamic Conidae by Duda and colleagues established that three species, *Conus diadema*, *Conus nux* and *Conus dalli* traversed the East Pacific Barrier from the IndoPacific, the first species very recently (<1 mya) and the two others 9-10 mya ^[29]. It appears that there may be a parallel pattern in the Panamic Terebridae. The Panamic species *Acus strigatus* is the sister species of the IndoPacific species *Acus felinus* (PP = 0.99; BB = 54). No close relatives of *Acus strigatus* are known from the Atlantic, therefore *Acus strigatus* may well be the only species in the Eastern Pacific assignable to *Acus*. The lack of any related species in the Panamic region, combined with the greater diversity of IndoPacific forms, suggests that an ancestral form of *Acus strigatus* may have been a migrant from the IndoPacific, and that the loss of the venom apparatus occurred in the ancestral Indo-Pacific forms of *Acus*. This notion is supported by the fact that all Indo-Pacific *Acus* specimens do not have a venom duct as highlighted by the white box in Figure 2. For this geographic region in the tree, the shaded taxa are Panamic, all the other (and the corresponding nodes) are IndoPacific. Mapping of the venom duct onto the constructed terebrid molecular

phylogeny indicates the venom apparatus has been lost at least twice during evolution, confirming the result shown previously^[16]. Using the rate of evolution calculated for the 16S gene by Espiritu et al. 2001^[30], 0.33% per 10⁶ years, we estimate a time of divergence between *A. strigatus* and *A. felinus* comprised between 7.13 and 11.88 mya, a time similar to what has been proposed for two *Conus* species^[29]. This very interesting finding was unknown until the present analyses and requires further biogeographic inquires that will be conducted independently.

The three Panamic species *Terebra argyiosa*, *cf formosa* and *ornata* form a well supported monophyletic branch (PP = 1; B = 96) within the clade that includes the type species of the genus *Terebra*, *T. subulata*, therefore we provisionally treat all species in this clade as belonging to the genus *Terebra*. Subgeneric divisions may be feasible, but it seems best to defer the comprehensive taxonomic treatment of the genus *Terebra* until more molecular data has been collected.

The species-level taxonomy of *Terebra* species from the Panamic region is generally problematic. The results obtained so far provide a guide for suggesting which Panamic forms are likely to belong to *Terebra*, and thus have a venomous apparatus. However, considerable care should be taken before assigning definitive species designations for forms in this group. This problem is highlighted by the specimens of a variety of Eastern Pacific Terebridae shown in Figure 3. Note that the specimens assigned to *Terebra argyosia* and *Terebra ornata* from Mexico are quite different in shell pattern from the specimens from Panama. Two non-Panamic species are also included in the figure, an Indo-Pacific species, *Terebra subulata*, and an Atlantic species that we expect will also belong to the same *Terebra* clade, *Terebra taurina*.

In this instance the molecular characters used in the phylogenetic analyses confirmed the shell-based morphological characters used to identify different terebrid species. The specimens of *Terebra argyosia* comprise the largest group of Las Perlas specimens collected that have a venom apparatus. Molecular analysis implies that *T. argyosia*, *T. ornata* and *Terebra cf. formosa* are indeed three different species. However, the relatively small number of specimens included for *T. ornata* and *T. cf. formosa* does not allow an estimation of the intra and interspecific variability, and species delimitation hypotheses would be more accurately tested by adding replicates. The type locality for *T. formosa* is Panama^[31]. The shell of the *Terebra cf. formosa* specimen used in this study (Figure 1B) appears to have the three characteristic squarish brown spots on the body whorl, a short columella that is recurved and heavily plicated, and a smooth subsutural band as described in Bratcher & Cernohorsky^[31]. Therefore, as a test of the shell-based ID, the resulting relationships for *Terebra argyosia*, *Terebra cf. formosa* and *Terebra ornata* are in agreement with what is expected.

The Panamic *Terebra argyosia/ornata/formosa* complex used in this study have the traits necessary for probing the biochemical characterization of their venom, namely they are found in large quantity and can be easily collected. A combined phylogenetic and toxinological approach will accelerate the investigation of the Terebridae significantly. Genes that encode venom peptides belong to a special category termed “exogenes,” as their gene products act outside the organism^[5]. Such genes are expected to diverge from each other extremely rapidly. If the various Panamic forms in the *Terebra* clade are separate species, then their exogenes should have diverged and an entirely different spectrum of venom components would be found in each species. If, however,

these are morphological variants of the same species, the same gene sequences (with minor allelic variation) should be observed. Correlating molecular phylogeny with the presence of venom apparatus is a significant advance that will aid in the efficient discovery of new pharmacologically-active compounds from the Terebridae, and also inform the taxonomy and phylogeny of this group.

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Figure captions

Figure 1. Panamic terebrid collection site and specimens. A. The Las Perlas Archipelago, collection site of Terebridae analyzed. The study area where dredging was carried out was around the Las Perlas Islands that are located off the west coast of Panama (see Inset). The numbers shown refer to the stations for the Panamic Specimens listed in Table 1. B. Las Perlas specimens of *Acus* and *Terebra* analyzed in this study. Top left, *Acus strigatus*. Bottom left, *Terebra ornata*. Top right-most specimen, *Terebra cf. formosa*. All other specimens are *Terebra argyosia*.

Figure 2. Combined Phylogenetic analysis of Panamic and IndoPacific Terebridae. Shown is a consensus tree (BA) using COI, 16S, and 12S data sets. Posterior probabilities and bootstrap values are specified for each node. Shaded clades were collected in Panama. The bar on the right shows which taxa have venom glands (black bars) and which do not (white bars). Clade A refers to the sister group that includes *Pellifronia jungi*, Clades D and E refer to the *Hastula* and *Myurella* clades respectively; these clades were identified in Holford, et al. 2009 ^[16]. Representative shells are shown as follows: 1. *Acus felinus*. 2. *Acus strigatus*. 3. *Terebra argosyia*. 4. *Terebra subulata*. 5. *Cinguloterebra anilis*.

Figure 3. Eastern Pacific *Terebra* (with an IndoPacific and a Western Atlantic species for comparison). The figure shows the diversity of the venomous Eastern Pacific forms that we tentatively have assigned to Clade C. These are compared to the

left-most specimen, *Terebra subulata* from the IndoPacific and the right-most specimen, *Terebra taurina* from the Western Atlantic.

Table 1. List of terebrid samples used in this study. VA= venom apparatus

Genus	Species	COI	12S	16S	VA	Station number - Coordinates/Depth	MNHN number
Panamic Specimens							
<i>Acus</i>	<i>strigatus</i> (Sowerby, 1825)	x	x	x	No	3 - 08°11.8'N, 078°57.1'W/21.4 m	42093
<i>Acus</i>	<i>strigatus</i> (Sowerby, 1825)	x	x	x	No	4 - 08°11.8'N, 078°57.5'W/22.4 m	42105
<i>Acus</i>	<i>strigatus</i> (Sowerby, 1825)	x	x	x	No	5 - 08°14.7'N, 079°05.55'W/ 17.5 m	42136
<i>Acus</i>	<i>strigatus</i> (Sowerby, 1825)	x	x	x	No	5 - 08°14.7'N, 079°05.55'W/ 17.5 m	42137
<i>Acus</i>	<i>strigatus</i> (Sowerby, 1825)	x	x	x	No	9 - 08°30.1'N, 079°06.0'W/ 21 m	42159
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	1 - 08°37.18'N, 079°01.12'W/25 m	42068
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	1 - 08°37.18'N, 079°01.12'W/25 m	42069
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	2 - 08°15.61'N, 078°51.57'W/24.1 m	42071
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	2 - 08°15.61'N, 078°51.57'W/24.1 m	42072
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	2 - 08°15.61'N, 078°51.57'W/24.1 m	42073
<i>Terebra</i>	<i>ornata</i> (Gray, 1834)	x	x	x	Yes	1 - 08°37.18'N, 079°01.12'W/20 m	42074
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	3 - 08°11.8'N, 078°57.1'W/21.4 m	42084
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	3 - 08°11.8'N, 078°57.1'W/21.4 m	42085
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	3 - 08°11.8'N, 078°57.1'W/21.4 m	42086
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	3 - 08°11.8'N, 078°57.1'W/21.4 m	42087
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	3 - 08°11.8'N, 078°57.1'W/21.4 m	42089
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	3 - 08°11.8'N, 078°57.1'W/21.4 m	42090
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	3 - 08°11.8'N, 078°57.1'W/21.4 m	42091
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	3 - 08°11.8'N, 078°57.1'W/21.4 m	42092
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/24 m	42099
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/24 m	42100
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/24 m	42102
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/22.4 m	42103
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/22.4 m	42104
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/22.4 m	42118
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/22.4 m	42119
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/22.4 m	42120
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/22.4 m	42121
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/22.4 m	42122
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/22.4 m	42123
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/22.4 m	42124
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/22.4 m	42125
<i>Terebra</i>	<i>ornata</i> (Gray, 1834)	x	x	x	Yes	6 - 08°14.94'N, 079°05.7'W/14.3 m	42131
<i>Terebra</i>	<i>cf. formosa</i>	x	x	x	Yes	7 - 08°16.86'N, 079°02.67'W/39.2 m	42152
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	8 - 08°24.50'N, 079°04.66'W/18.4 m	42153
IndoPacific Specimens							
<i>Acus</i>	<i>maculatus</i> (Linnaeus, 1758)	x	x	x	No	9°37.4'N, 123°46.9'E, 3-20 m	30370
<i>Acus</i>	<i>dimidiatus</i> (Linnaeus, 1758)	x	x	x	No	15°32.5'S, 167°10.5'E, 5-10 m	30372
<i>Acus</i>	<i>dimidiatus</i> (Linnaeus, 1758)	x	x	x	No	15°36.9'S, 167°10.5'E, 6-33 m	30373
<i>Acus</i>	<i>crenulatus</i> (Linnaeus, 1758)	x	x	x	No	15°34.4'S, 167°13.1'E, 9 m	30377
<i>Acus</i>	<i>dimidiatus</i> (Linnaeus, 1758)	x	x	x	No	15°32.5'S, 167°10.5'E, 5-10 m	30379
<i>Acus</i>	<i>dimidiatus</i> (Linnaeus, 1758)	x	x	x	No	15°35.4'S, 166°59.7'E, 3-37 m	30381
<i>Acus</i>	<i>maculatus</i> (Linnaeus, 1758)	x	x	x	No	15°28.7'S, 167°15.2'E, 19 m	30389
<i>Acus</i>	<i>dimidiatus</i> (Linnaeus, 1758)	x	x	x	No	15°38.1'S, 167°05.9'E, intertidal	30428
<i>Acus</i>	<i>felinus</i> (Dillwyn, 1817)	x	x	x	No	9°37.4'N, 123°54.5'E, 6-8 m	30443
<i>Acus</i>	<i>felinus</i> (Dillwyn, 1817)	x	x	x	No	9°37.4'N, 123°54.5'E, 6-8 m	30445
<i>Acus</i>	<i>chloratus</i> (Lamarck, 1822)	x	x	x	No	15°22.6'S, 167°11.6'E, intertidal	30490
<i>Acus</i>	<i>crenulatus</i> (Linnaeus, 1758)	x	x	x	No	15°34.4'S, 167°13.1'E, 9 m	30494
<i>Acus</i>	<i>areolatus</i> (Link, 1807)	x	x	x	No	9°37.4'N, 123°46.9'E, 3-20 m	30587
<i>Cinguloterebra</i>	<i>cf. fujitai</i> (Kuroda & Habe, 1952)	x	x	x	Yes	9°27.4'N, 123°49.4'E, 273-356 m	15724
<i>Cinguloterebra</i>	<i>cf. fenestrata</i> (Hinds, 1844)	x	x	x	Yes	9°36.2'N, 123°43.8'E, 382-434 m	16735
<i>Cinguloterebra</i>	<i>cf. fenestrata</i> (Hinds, 1844)	x	x	x	Yes	9°29.4'N, 123°44.4'E, 271-318 m	30390
<i>Cinguloterebra</i>	<i>triseriata</i> (JE Gray, 1824)	x	x	x	Yes	9°35.3'N, 123°52.2'E, 84-87 m	30404
<i>Cinguloterebra</i>	<i>fenestrata</i> type I	x	x	x	Yes	9°39.2'N, 123°47.5'E, 255-268 m	30410
<i>Cinguloterebra</i>	<i>fenestrata</i> type II	x	x	x	Yes	9°39.2'N, 123°47.5'E, 255-268 m	30418
<i>Cinguloterebra</i>	<i>lima</i> (Deshayes, 1857)	x	x	x	Yes	15°32.5'S, 167°10.5'E, 5-10 m	30485
<i>Cinguloterebra</i>	<i>lima</i> (Deshayes, 1857)	x	x	x	Yes	8°39.5' S, 157°23.0' E, 214-243 m	30487
<i>Cinguloterebra</i>	<i>jenningsi</i> (RD Burch, 1965)	x	x	x	Yes	15°28.6'S, 167°15.1'E, 3-31 m	30544
<i>Cinguloterebra</i>	<i>anilis</i> (Röding, 1798)	x	x	x	Yes	15°35.2'S, 167°59.4'E, intertidal	30552
<i>Hastula</i>	<i>strigilata</i> (Linnaeus, 1758)	x	x	x	Yes	15°35.2'S, 167°59.4'E, intertidal	30420
<i>Myurella</i>	<i>affinis</i> (JE Gray 1834)	x	x	x	No	9°37.4'N, 123°54.5'E, 6-8 m	30430
<i>Terebra</i>	<i>guttata</i> (Röding, 1798)	x	x	x	Yes	15°33.1'S, 167°12.2'E, 3-40 m	30376
<i>Terebra</i>	<i>babylonia</i> (Lamarck, 1822)	x	x	x	Yes	15°31.1'S, 167°10.5'E, 7 m	30380
<i>Terebra</i>	<i>subulata</i> (Linnaeus, 1767)	x	x	x	Yes	15°36.6'S, 167°10.1'E, 8-20 m	30386
<i>Terebra</i>	<i>guttata</i> (Röding, 1798)	x	x	x	Yes	15°33.1'S, 167°12.2'E, 3-40 m	30387
<i>Terebra</i>	<i>laevigata</i> (JE Gray, 1834)	x	x	x	Yes	15°36.9'S, 167°10.5'E, 6-33 m	30394
<i>Terebra</i>	<i>tricolor</i> (GB Sowerby I, 1825)	x	x	x	Yes	15°33.1'S, 167°17.8'E, 15-25 m	30409
<i>Terebra</i>	<i>laevigata</i> (JE Gray, 1834)	x	x	x	Yes	9°36.8'N, 123°52.2'E, intertidal	30431
<i>Terebra</i>	<i>subulata</i> (Linnaeus, 1767)	x	x	x	Yes	9°37.4'N, 123°54.5'E, 6-8 m	30444
<i>Terebra</i>	<i>subulata</i> (Linnaeus, 1767)	x	x	x	Yes	9°32.8'N, 123°42.1'E, 3-35 m	30483
<i>Terebra</i>	<i>tricolor</i> (GB Sowerby I, 1825)	x	x	x	Yes	15°38.5'S, 167°15.1'E, 13 m	30493
<i>Terebra</i>	<i>laevigata</i> (JE Gray, 1834)	x	x	x	Yes	15°26.6'S, 167°15.2'E, intertidal	30597
<i>Terebra</i>	<i>laevigata</i> (JE Gray, 1834)	x	x	x	Yes	15°43.4'S, 167°15.0'E, 6 m	30603
<i>Terebra</i>	<i>laevigata</i> (JE Gray, 1834)	x	x	x	Yes	15°31'S, 167°09'E, intertidal	30613
<i>Terebra</i>	<i>laevigata</i> (JE Gray, 1834)	x	x	x	Yes	15°31'S, 167°09'E, intertidal	30632
<i>Pellifronia</i>	<i>jungi</i> (Lai, 2001)	x	x	x	Yes	9°37.5'N, 123°40.2'E, 606-631 m	30395
Outgroups							
<i>Cochlespira</i> sp. (Turridae)		x	x	x		21°10'S, 158°39'E, 650-723m	40568
<i>Conus nereis</i> (Conidae)		x	x	x	Yes	9°32.5'N, 123°41.8'E, 111-115m	17922
<i>Harpa</i> sp. (Harpidae)		x	x	x		9°32.5'N, 123°41.8'E, 111-115m	40569
<i>Iotyris cingulifera</i> (Turridae)		x	x	x		15°33.6'S, 167°16.6'E, 8-9 m	17685

Figure 1

A.



B.



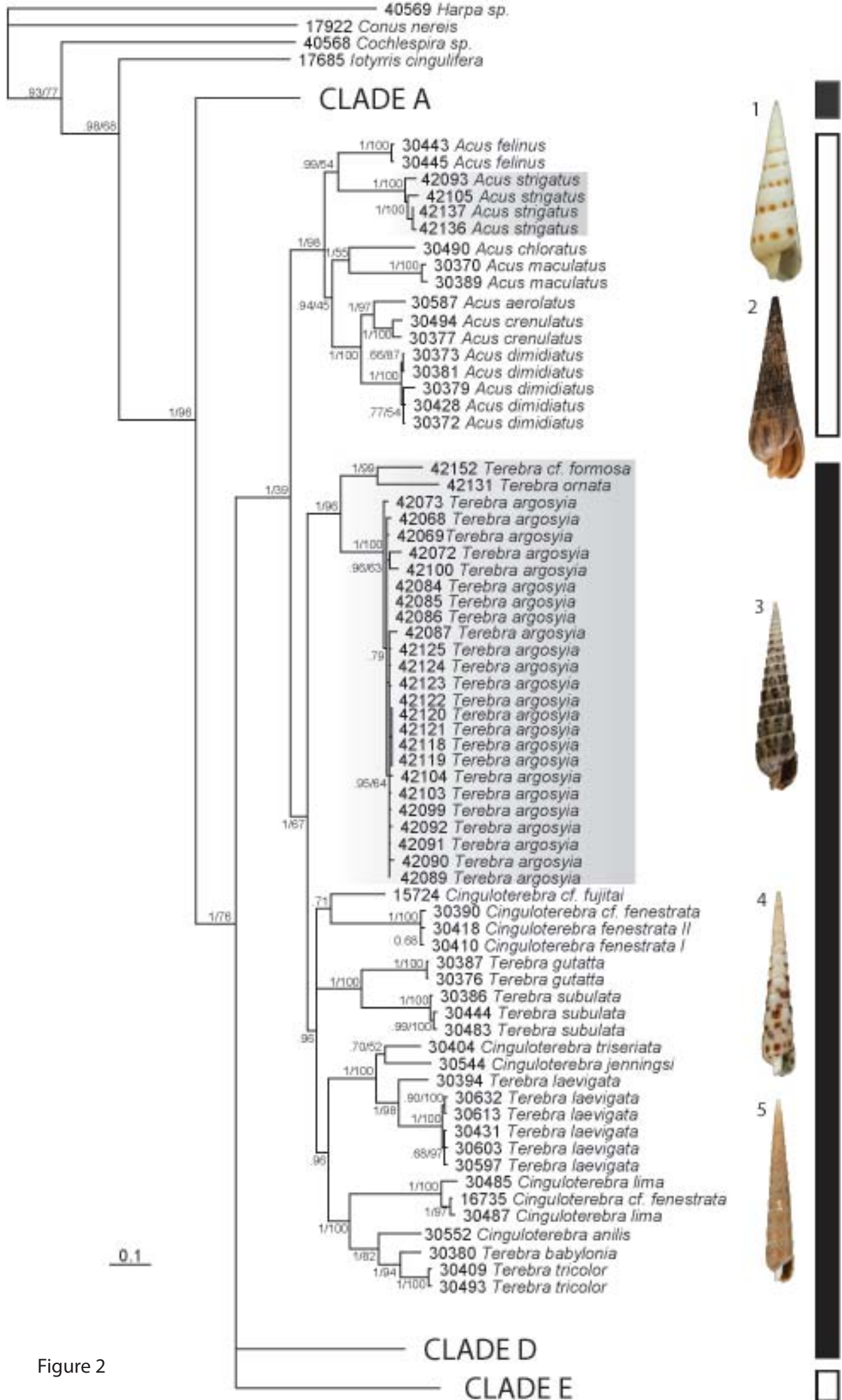


Figure 2

Figure 3

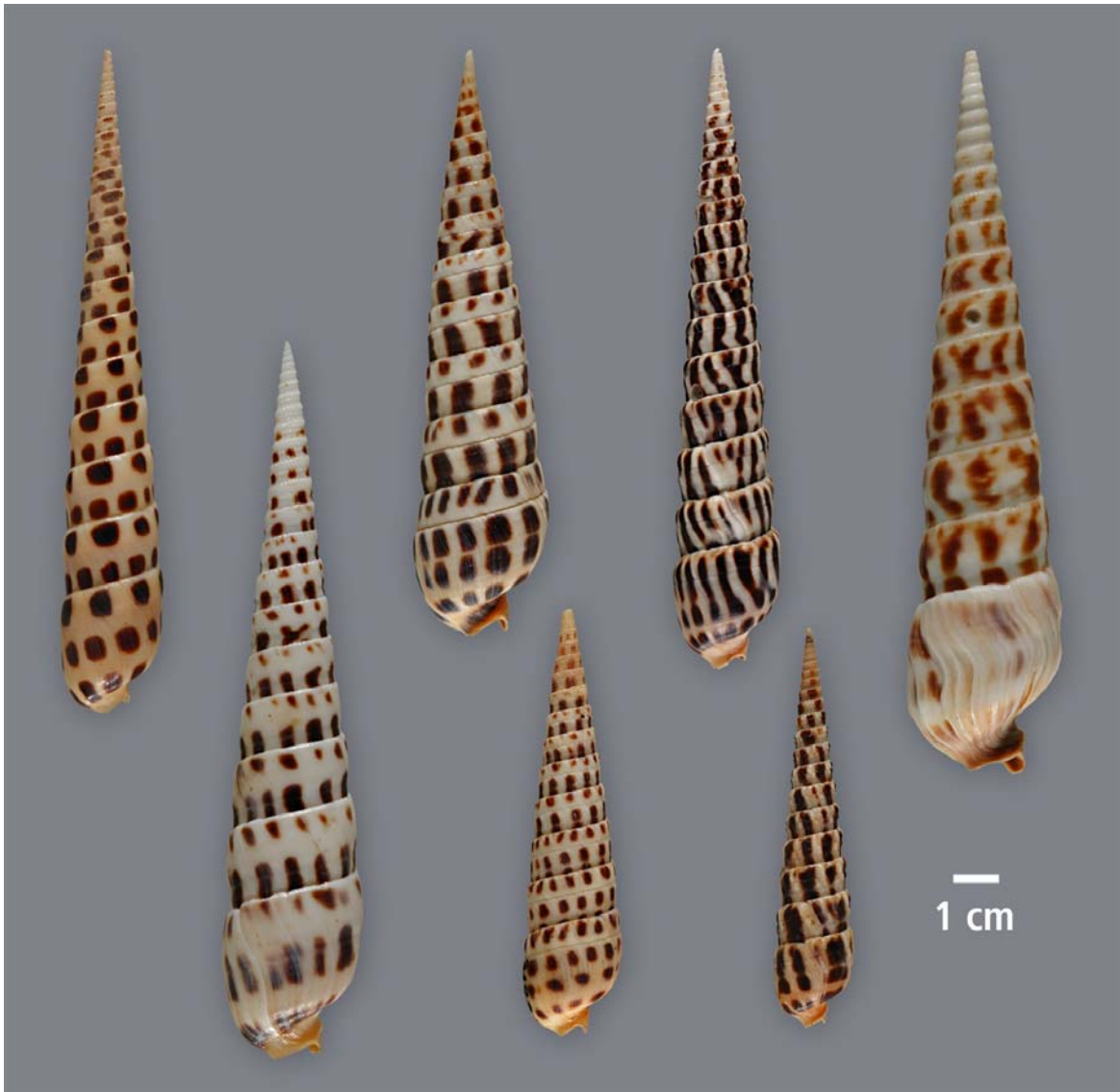


Table 1 List of terebrid samples used in this study. VA = venom apparatus

Genus	Species	COI	12S	16S	VA	Station number - Coordinates/Depth	MNHN number
Panamic Specimens							
<i>Acus</i>	<i>strigatus</i> (Sowerby, 1825)	x	x	x	No	3 - 08°11.8'N, 078°57.1'W/21.4 m	42093
<i>Acus</i>	<i>strigatus</i> (Sowerby, 1825)	x	x	x	No	4 - 08°11.8'N, 078°57.5'W/22.4 m	42105
<i>Acus</i>	<i>strigatus</i> (Sowerby, 1825)	x	x	x	No	5 - 08°14.7'N, 079°05.55'W/ 17.5 m	42136
<i>Acus</i>	<i>strigatus</i> (Sowerby, 1825)	x	x	x	No	5 - 08°14.7'N, 079°05.55'W/ 17.5 m	42137
<i>Acus</i>	<i>strigatus</i> (Sowerby, 1825)	x	x	x	No	9 - 08°30.1'N, 079°06.0'W/ 21 m	42159
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	1 - 08°37.18'N, 079°01.12'W/25 m	42068
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	1 - 08°37.18'N, 079°01.12'W/25 m	42069
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	2 - 08°15.61'N, 078°51.57'W/24.1 m	42071
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	2 - 08°15.61'N, 078°51.57'W/24.1 m	42072
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	2 - 08°15.61'N, 078°51.57'W/24.1 m	42073
<i>Terebra</i>	<i>ornata</i> (Gray, 1834)	x	x	x	Yes	1 - 08°37.18'N, 079°01.12'W/20 m	42074
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	3 - 08°11.8'N, 078°57.1'W/21.4 m	42084
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	3 - 08°11.8'N, 078°57.1'W/21.4 m	42085
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	3 - 08°11.8'N, 078°57.1'W/21.4 m	42086
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	3 - 08°11.8'N, 078°57.1'W/21.4 m	42087
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	3 - 08°11.8'N, 078°57.1'W/21.4 m	42089
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	3 - 08°11.8'N, 078°57.1'W/21.4 m	42090
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	3 - 08°11.8'N, 078°57.1'W/21.4 m	42091
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	3 - 08°11.8'N, 078°57.1'W/21.4 m	42092
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/24 m	42099
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/24 m	42100
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/24 m	42102
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/22.4 m	42103
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/22.4 m	42104
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/22.4 m	42118
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/22.4 m	42119
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/22.4 m	42120
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/22.4 m	42121
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/22.4 m	42122
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/22.4 m	42123
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/22.4 m	42124
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	4 - 08°11.8'N, 078°57.5'W/22.4 m	42125
<i>Terebra</i>	<i>ornata</i> (Gray, 1834)	x	x	x	Yes	6 - 08°14.94'N, 079°05.7'W/14.3 m	42131
<i>Terebra</i>	<i>cf. formosa</i>	x	x	x	Yes	7 - 08°16.86'N, 079°02.67'W/39.2 m	42152
<i>Terebra</i>	<i>argosyia</i> (Olsson, 1971)	x	x	x	Yes	8 - 08°24.50'N, 079°04.66'W/18.4 m	42153
IndoPacific Specimens							
<i>Acus</i>	<i>maculatus</i> (Linnaeus, 1758)	x	x	x	No	9°37.4'N, 123°46.9'E, 3-20 m	30370
<i>Acus</i>	<i>dimidiatus</i> (Linnaeus, 1758)	x	x	x	No	15°32.5'S, 167°10.5'E, 5-10 m	30372
<i>Acus</i>	<i>dimidiatus</i> (Linnaeus, 1758)	x	x	x	No	15°36.9'S, 167°10.5'E, 6-33 m	30373
<i>Acus</i>	<i>crenulatus</i> (Linnaeus, 1758)	x	x	x	No	15°34.4'S, 167°13.1'E, 9 m	30377
<i>Acus</i>	<i>dimidiatus</i> (Linnaeus, 1758)	x	x	x	No	15°32.5'S, 167°10.5'E, 5-10 m	30379
<i>Acus</i>	<i>dimidiatus</i> (Linnaeus, 1758)	x	x	x	No	15°35.4'S, 166°59.7'E, 3-37 m	30381
<i>Acus</i>	<i>maculatus</i> (Linnaeus, 1758)	x	x	x	No	15°28.7'S, 167°15.2'E, 19 m	30389
<i>Acus</i>	<i>dimidiatus</i> (Linnaeus, 1758)	x	x	x	No	15°38.1'S, 167°05.9'E, intertidal	30428
<i>Acus</i>	<i>felinus</i> (Dillwyn, 1817)	x	x	x	No	9°37.4'N, 123°54.5'E, 6-8 m	30443
<i>Acus</i>	<i>felinus</i> (Dillwyn, 1817)	x	x	x	No	9°37.4'N, 123°54.5'E, 6-8 m	30445
<i>Acus</i>	<i>chloratus</i> (Lamarck, 1822)	x	x	x	No	15°22.6'S, 167°11.6'E, intertidal	30490
<i>Acus</i>	<i>crenulatus</i> (Linnaeus, 1758)	x	x	x	No	15°34.4'S, 167°13.1'E, 9 m	30494
<i>Acus</i>	<i>areolatus</i> (Link, 1807)	x	x	x	No	9°37.4'N, 123°46.9'E, 3-20 m	30587
<i>Cinguloterebra</i>	<i>cf. fujitai</i> (Kuroda & Habe, 1952)	x	x	x	Yes	9°27.4'N, 123°49.4'E, 273-356 m	15724
<i>Cinguloterebra</i>	<i>cf. fenestrata</i> (Hinds, 1844)	x	x	x	Yes	9°36.2'N, 123°43.8'E, 382-434 m	16735
<i>Cinguloterebra</i>	<i>cf. fenestrata</i> (Hinds, 1844)	x	x	x	Yes	9°29.4'N, 123°44.4'E, 271-318 m	30390
<i>Cinguloterebra</i>	<i>triseriata</i> (JE Gray, 1824)	x	x	x	Yes	9°35.3'N, 123°52.2'E, 84-87 m	30404
<i>Cinguloterebra</i>	<i>fenestrata</i> type I	x	x	x	Yes	9°39.2'N, 123°47.5'E, 255-268 m	30410
<i>Cinguloterebra</i>	<i>fenestrata</i> type II	x	x	x	Yes	9°39.2'N, 123°47.5'E, 255-268 m	30418
<i>Cinguloterebra</i>	<i>lima</i> (Deshayes, 1857)	x	x	x	Yes	15°32.5'S, 167°10.5'E, 5-10 m	30485
<i>Cinguloterebra</i>	<i>lima</i> (Deshayes, 1857)	x	x	x	Yes	8°39.5' S, 157°23.0' E, 214-243 m	30487
<i>Cinguloterebra</i>	<i>jenningsi</i> (RD Burch, 1965)	x	x	x	Yes	15°28.6'S, 167°15.1'E, 3-31 m	30544
<i>Cinguloterebra</i>	<i>anilis</i> (Röding, 1798)	x	x	x	Yes	15°35.2'S, 167°59.4'E, intertidal	30552
<i>Hastula</i>	<i>strigilata</i> (Linnaeus, 1758)	x	x	x	Yes	15°35.2'S, 167°59.4'E, intertidal	30420
<i>Myurella</i>	<i>affinis</i> (JE Gray 1834)	x	x	x	No	9°37.4'N, 123°54.5'E, 6-8 m	30430
<i>Terebra</i>	<i>guttata</i> (Röding, 1798)	x	x	x	Yes	15°33.1'S, 167°12.2'E, 3-40 m	30376
<i>Terebra</i>	<i>babylonia</i> (Lamarck, 1822)	x	x	x	Yes	15°31.1'S, 167°10.5'E, 7 m	30380
<i>Terebra</i>	<i>subulata</i> (Linnaeus, 1767)	x	x	x	Yes	15°36.6'S, 167°10.1'E, 8-20 m	30386
<i>Terebra</i>	<i>guttata</i> (Röding, 1798)	x	x	x	Yes	15°33.1'S, 167°12.2'E, 3-40 m	30387
<i>Terebra</i>	<i>laevigata</i> (JE Gray, 1834)	x	x	x	Yes	15°36.9'S, 167°10.5'E, 6-33 m	30394
<i>Terebra</i>	<i>tricolor</i> (GB Sowerby I, 1825)	x	x	x	Yes	15°33.1'S, 167°17.8'E, 15-25 m	30409
<i>Terebra</i>	<i>laevigata</i> (JE Gray, 1834)	x	x	x	Yes	9°36.8'N, 123°52.2'E, intertidal	30431
<i>Terebra</i>	<i>subulata</i> (Linnaeus, 1767)	x	x	x	Yes	9°37.4'N, 123°54.5'E, 6-8 m	30444
<i>Terebra</i>	<i>subulata</i> (Linnaeus, 1767)	x	x	x	Yes	9°32.8'N, 123°42.1'E, 3-35 m	30483
<i>Terebra</i>	<i>tricolor</i> (GB Sowerby I, 1825)	x	x	x	Yes	15°38.5'S, 167°15.1'E, 13 m	30493
<i>Terebra</i>	<i>laevigata</i> (JE Gray, 1834)	x	x	x	Yes	15°26.6'S, 167°15.2'E, intertidal	30597
<i>Terebra</i>	<i>laevigata</i> (JE Gray, 1834)	x	x	x	Yes	15°43.4'S, 167°15.0'E, 6 m	30603
<i>Terebra</i>	<i>laevigata</i> (JE Gray, 1834)	x	x	x	Yes	15°31'S, 167°09'E, intertidal	30613
<i>Terebra</i>	<i>laevigata</i> (JE Gray, 1834)	x	x	x	Yes	15°31'S, 167°09'E, intertidal	30632
<i>Pellifronia</i>	<i>jungi</i> (Lai, 2001)	x	x	x	Yes	9°37.5'N, 123°40.2'E, 606-631 m	30395
Outgroups							
<i>Cochlespira</i> sp. (Turridae)		x	x	x		21°10'S, 158°39'E, 650-723m	40568
<i>Comus nereis</i> (Conidae)		x	x	x	Yes	9°32.5'N, 123°41.8'E, 111-115m	17922
<i>Harpa</i> sp. (Harpidae)		x	x	x		9°32.5'N, 123°41.8'E, 111-115m	40569
<i>Iotyrris cingulifera</i> (Turridae)		x	x	x		15°33.6'S, 167°16.6'E, 8-9 m	17685