

Published in final edited form as:

*Mol Phylogenet Evol.* 2011 May ; 59(2): 263–270. doi:10.1016/j.ympev.2011.01.019.

## Phylogeny of the Genus *Turris*: Correlating Molecular Data with Radular Anatomy and Shell Morphology

Alexander Fedosov<sup>1,2,\*</sup>, Maren Watkins<sup>1,\*</sup>, Francisco M. Heralde III<sup>3</sup>, Patrice Showers Corneli<sup>1</sup>, Gisela P. Concepcion<sup>2</sup>, and Baldomero M. Olivera<sup>1</sup>

<sup>1</sup>Department of Biology, University of Utah, Salt Lake City, UT, USA

<sup>2</sup>Marine Science Institute, University of the Philippines, Diliman, Quezon City, Philippines

<sup>3</sup>Department of Biochemistry and Molecular Biology, College of Medicine, University of the Philippines, Manila, Philippines

### Abstract

There are over 10,000 species of venomous marine molluscs, the vast majority of these, which are generally referred to as “turrids”, are traditionally assigned to a single family, Turridae (Powell 1966). Here, we provide an initial molecular analysis of the type genus of the family, *Turris* Röding, 1798, thought to be among the most well characterized groups in the family. We show that the type genus is not monophyletic.

We analyzed specimens conventionally assigned to 9 different *Turris* species using molecular markers, combined with the shell morphology and radular anatomy whenever feasible. The results suggest that species assigned to the genus *Turris*, provisionally assigned to two different subgenera are not monophyletic. Five previously described species belong to the subgenus *Turris* (*s.s.*) Röding 1798: *T. babylonia*, (Linne, 1758), *T. grandis*, (J. E. Gray, 1834), *T. dollyae*, (Olivera, 1999), *T. normandavidsoni* (Olivera, 1999) and *T. spectabilis* (Reeve, 1843). With a change in species designation, *T. assyria* (formerly *T. babylonia*1010) is added to a well-defined clade, which is in turn more closely related to *Lophiotoma* and *Gemmula* species than to the other five *Turris* species.

We show that these five species conventionally assigned to *Turris* do not belong in the same subgenus, and form a clade provisionally designated as *Annulaturreis* Powell, 1966: *T. annulata*, (Reeve, 1843), *T. undosa*, (Lamarck, 1816), *T. cristata*, (Vera-Peláez, Vega-Luz, and Lozano-Francisco 2000) *T. cryptorrhaphe* (G. B. Sowerby, 1825) and *T. nadaensis* (Azuma, 1973). Implications of the molecular phylogenetic results and its correlation with radular morphology are discussed.

---

© 2011 Elsevier Inc. All rights reserved.

Correspondence to: Patrice Showers Corneli.

\*These authors contributed equally to this work.

**Publisher's Disclaimer:** This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

## Keywords

*Turris*; *Gemmula*; *Lophiotoma*; radulae; molecular phylogeny; shell morphology; morphospecies

---

## Introduction

Traditionally comprising three major families: the Conidae (“cone snails”), the Terebridae (“auger snails”), and the Turridae *s.l.* (Powell, 1966; McLean, 1971; Ponder, 1973; Ponder and Waren, 1988), the superfamily Conoidea is an extremely biodiverse group of venomous marine snails. Venoms of conoideans are a complex mixture, with more than a hundred individual peptide components, comprising a largely untapped pharmacological resource (Olivera et al., 1990; Olivera, 1999).

Members of the Turridae include the first conoideans that appear abundantly at the Eocene/Oligocene boundary about 34 million years ago (Tucker, 2004). The extant species traditionally assigned to Turridae encompass a huge morphological diversity. Recent fieldwork in the tropical Pacific (Bouchet et al., 2002) has led to an estimate of over 10,000 recent species of “turrids”.

The last comprehensive treatment of the genus *Turris* was that of Powell (1964); eight species were defined, with one, *Turris crispa*, divided into 4 subspecies. Subsequently, Powell (1966) recognized that two of these species, *Turris annulata* and *Turris amicta*, diverged significantly from the six, and for these he designated a subgenus, *Annulaturris*. This treatise on turrids summarized the nine subfamilies and more than 500 genera proposed to belong to the family Turridae. A later in-depth study of foregut anatomy and radular morphology in a number of conoideans (Taylor, et al. 1993) led to a proposal for the complete revision of traditional taxonomy of Conoidea. Taylor and co-workers demonstrated that some of the subfamilies previously included in the Turridae were more closely allied to *Conus* and they assigned these taxa to the family Conidae demanding a narrower definition of Turridae.

The first molecular phylogenetic investigation of Conoidea suggested an even more complex situation. Several subfamilies of Turridae (e.g. Crassispirinae and Cochlespirinae), were found to be polyphyletic or paraphyletic groups (Puillandre et al., 2008) suggesting that continuous reassessment of Conoidean taxonomy will be required as newer data are acquired. Recently, it was proposed (Tucker and Tenorio, 2009) that the species conventionally in Turridae be placed in two separate superfamilies, some to a newly proposed superfamily, Turroidea, (with the terebrids), with other lineages remaining in the superfamily Conoidea (with the cone snails).

Genus *Turris* Roding, 1798, the type genus of the family Turridae consists of approximately 20 recent and 20 extinct species. (Tucker, 2004). The genus *Turris* defines the subfamily Turrinae (type species, *Turris babylonia*), the only subfamily of Turridae for which monophyly has not been rejected. Previously published studies on the molecular phylogeny of Turrinae include the analysis of species in *Unedogemmula/Lophiotoma* (Heralde et al., 2007), and *Xenuroturris* (Kantor et al., 2008). Although a number of new species have been

described in the genus *Turris* in the last decade (Olivera et al., 1999; Vera-Peláez, Vega-Luz, and Lozano-Francisco, 2000; Bozzetti, 2006) neither an in-depth evaluation of the genus nor an examination of phylogeny using any criteria except shell morphology has been carried out. Here our goal is to provide a framework for understanding intrageneric relationships within *Turris* by as we correlate shell and radular morphology with molecular data.

## Materials and method

### Specimens

Material for present study was collected at different localities within Philippines with most specimens from either the Danajon Bank near Olango Island, or from Sogod, Cebu Island, both in Cebu province in the central Visayas. The specimens analyzed are summarized in Table 1. We include *Turridrupa*, *Lophiotoma* and *Gemmula* species to determine how each of the *Turris* species fit into the subfamily Turrinae: we do not assume monophyly of the genus *Turris*. Most specimens were collected by hookah at depths between 10–30 meters, and by gill nets at depths of 70–150 meters. The specimens were kept alive, and dissected within 1–2 days. Shells were photographed, and foot samples preserved in 95% alcohol for molecular analysis. Samples of the buccal mass with surrounding tissues were preserved in 70% alcohol for preparation of the radula.

### Radular morphology

Buccal complexes were dissected to isolate the radular sac, then soft tissues were dissolved in solution of potassium hypochlorite (5%) and cleaned radulae were prepared for further SEM examination.

### DNA extraction, amplification and sequencing

Genomic DNA was prepared from 10 mg footpad tissue using the Gentra PUREGENE DNA Isolation Kit (Gentra Systems, Minneapolis, MN) according to the manufacturer's standard protocol.

Ten ng of genomic DNA was used as a template for polymerase chain reaction (PCR) with oligonucleotide primers corresponding to 12S-I (5' TCG CAG CAG YCG CGG TTA) and 12S-III (5' AGA GYG RCG GGC GAT GTG T) mitochondrial rRNA segments (Simon et al., 1991) and 16SH (5' CCG GTC TGA ACT CAG ATC ACT G) and 16LC (5' GTT TAC CAA AAA CAT GGC TTC) mitochondrial rRNA segments (Palumbi, 1996), and oligonucleotides corresponding to COI dgLsimiCO-1490 (5' GGT CAA CAA ATC ATA AAG AYA TGY G 3') and COI dgHCO-2198 gene segments (5' TAA ACT TCA GGG TGA CCA AAR AAY CA 3'). The PCR cycling profile was as follows: Initial denaturation (95°C, 60s); followed by 40 cycles of denaturation (95°C, 20s); annealing (55°C, 20s) and extension (72°C, 30s).

The resulting PCR products were purified by gel electrophoresis, recovered from agarose using High Pure PCR Product Purification Kit (Roche Diagnostics, Indianapolis, IN). A number of recent studies (e.g. Buhay, 2009) show that active mitochondrial genes, encoding

cytochrome c oxidase subunit 1 often incorporate into the nuclear genome where they become inactive and start to accumulate multiple substitutions. Thus typical PCR product may contain a mixture of molecules of different sequences clearly decreasing the quality of the sequences. The preferred method of obtaining reliable sequence is to clone PCR products and sequence multiple clones in order to determine the mitochondrial consensus sequence. Consequently, the eluted DNA fragments were annealed to pNEB206A vector using the USER Friendly Cloning kit (New England BioLabs, Inc., Beverly, MA) following manufacturer's suggested protocol and the resulting products transformed into DH5a competent cells. The nucleic acid sequences of these 12S, 16S and COI-encoding clones were determined according to the standard protocol for automated sequencing.

The voucher specimens used in this analysis will be deposited at the Philippine Biodiversity Resources Center, Marine Science Institute, University of the Philippines, Quezon City, Philippines.

### Phylogenetic Analysis

Individual 12SrRNA, 16SrRNA and COI sequences were aligned with Clustal and then refined by eye using the graphical interface of MacClade4.08 (Maddison and Maddison 2005) to correct obviously homologous regions that Clustal failed to recognize. These include cases which required a simple shift in the position of a gap to avoid a stop codon not present in other sequences or to complete a codon whose members flanked the Clustal inferred gap. We refined the rRNAs alignments with Rcoffee (Notredame et al. 2000) to account for secondary structure. Because Rcoffee runs are restricted to 50 taxa and 1000 base pairs, the Clustal alignments were divided into smaller subsets, aligned with Rcoffee and then concatenated for further analysis. Alignments within Rcoffee are guided by secondary structure characteristics (Notredame et al. 2000). The color-coded CORE indices were used to identify the best among alternative alignments that include the Clustal and Rcoffee alignments and hand refined versions of each.

Sequences were concatenated with MacClade4 (Maddison and Maddison 2005) and then optimized using MrBayes (Huelsenbeck and Ronquist, 2001) with GTR+I+G maximum likelihood model parameters estimated separately for each gene. Each analysis comprised two simultaneous runs with four chains each. Two million generations reduced the average standard deviation of the split frequencies below 0.01. Plots of the number of generations against the maximum likelihood scores indicated equilibrium. Further diagnostics included the potential scale reduction factor (PSRF) that measures the fit of branch length and all parameters. Trees and parameters from the first 25% of the generations were discarded (the burn in) after completion of the MCMC (Markov Chain Monte Carlo) search.

For the maximum likelihood analyses of the individual genes, we estimated parameters for GTR+I+G models of sequence evolution and optimized the tree and using Phylml (Guindon and Gascuel, 2003). Our analysis of 1000 bootstrap replicates provided measures of support on the clades of the maximum likelihood trees. For the concatenated sequences of several genes we used RAxML (Stamatakis, et al. 2008) to optimise the maximum likelihood tree using the GTR+I+G model with parameters estimated separately for each gene and to analyse the bootstrap replicates

Finally we tested various alternative topologies (e.g. monophyly of the *Turris* species) using Shimodaira-Hasegawa tests with GTR+I+G optimised parameters in PAUP4b10 (Swofford, 2002) to determine whether any differed significantly from the optimal tree. Rather than simply moving the two intact *Turris* clades together, we optimized with maximum likelihood the relationships among all the *Turris* species simultaneously within the monophyly constraint. To ensure that these were tests of topology alone, we constrained the topologies but not the branch length estimates.

## Results

### Radular morphology

The radulae of the specimens indicated in Table IA are illustrated in Figures 3–4. The most striking feature is the presence, absence, or state of reduction of a distinctive central tooth. As previously reported by Powell, in many species of *Turris*, there is either no central tooth or only a rudimentary tooth. The most reduced central teeth are characteristic of *Turris babylonica*, *Turris normandavidsoni*, and *Turris spectabilis* (see Fig 3). In these specimens, the base of the central tooth is indistinct and the cusp is rudimentary. In *Turris dollyae*, the base of the central teeth is triangular or bow-shaped, with a triangular, short and blunt cusp. Finally, a strong central tooth was found in *Turris cryptorrhaphe*, *Turris cristata*, *Turris nadaensis* and *Turris undosa*. In these species, the central tooth has a distinct, wide base, especially in *Turris cryptorrhaphe*, and a long, pointed awl-shaped cusp (Figure 4).

Another important radular character is the structure of the marginal teeth. In general, the wishbone teeth, characteristic of the Turrinae, have strongly thickened margins, which form a major axial element and the accessory limb of each tooth (Kantor and Taylor, 2000). In most species of the genus *Turris* that have been examined for this study, both axial elements are well pronounced, spread through the entire length of the tooth and become confluent at its tip. In specimens of *Turris cryptorrhaphe*, *Turris cristata*, *Turris nadaensis* and *Turris undosa* examined, the accessory limb is weakly developed and the major axial elements do not coalesce at the tip of the tooth, so the margins of the tooth at the tip are not thickened and instead form a kind of blade.

### Molecular analysis

The trees inferred from the three individual genes, COI, 12S and 16S are poorly resolved (Supplementary Figure 1). On the other hand, the tree inferred from the concatenated sequence of the three genes (Figure 5) is comparatively well resolved. Contrary to traditional taxonomy, the tree suggests that the genus *Turris* is not monophyletic. This tree comprises a clade, hereafter referred to as *Annulaturris*, that includes *Turris annulata*, *Turris cristata*, *Turris cryptorrhaphe*, *Turris nadaensis* and *Turris undosa* to the exclusion of a clade comprising *Lophiotoma* and *Gemmula* species with the other *Turris* species (*T. babylonica*, *T. dollyae*, *T. grandis*, *T. normandavidsoni*, *T. spectabilis*, *T. assyria*). The hypothesis that the *Turris* species are monophyletic is rejected (Shimodaira-Hasegawa test, ln likelihood difference=62.3, p 0.0001).

## Discussion

### ***Turris* phylogeny: recent literature**

Following the discoveries of nine new species in the Philippines by Olivera (1999) and Vera-Pelaes et al. (2000), Olivera (1999) considered several species of the genus *Turris* to diverge from the major clade (“Clade I”) that includes *Turris babylonica*. These include in Clade II *Turris cryptorrhaphe*, *Turris nadaensis*, *Turris “undosa” (= cristata)* and in Clade III *Turris annulata*. The various hypotheses discussed earlier, suggesting the division of *Turris* species into widely divergent clades (e.g. Powell, 1966), are refined by the evidence from radular anatomy and molecular phylogeny that we present here. Two recent books for shell collectors illustrate many species of *Turris* (Poppe, 2008; Robin, 2008) and facilitate comparison of molecular and radular traits with shell traits.

### **Radular morphology**

In his 1964 analysis of the genus, Powell indicated that species in *Turris* were characterized by having only marginal teeth, and that these were wishbone shaped. The radular anatomy was one characteristic feature of species in this genus. In later separating *Turris amicta* and *Turris annulata* into the *Annulaturris*, Powell (1966) noted that in contrast to the marginals-only pattern observed for *Turris babylonica* and *Turris crispa*, *Turris amicta* had a large well-formed central tooth, with a long slender central cusp on a broadly rectangular base that is recurved at the edges, and that the pair of marginals were “of considerably modified wishbone type”.

We have demonstrated that the presence of a central tooth with a distinct central cusp is a character of several of the *Turris* species analyzed (*T. cristata*, *T. cryptorrhaphe*, and *T. nadaensis* and *T. undosa*). Thus, the radular morphology presented in this study provides support for the division of the genus *Turris* into infrageneric groups. Relatively few species of the Turrinae have been analyzed with respect to their radular anatomy. However, the available data suggests that the characteristic radular morphology observed for the species in *Annulaturris*, with a large central tooth, is a more primitive condition, and that a marked reduction or loss of the central tooth that is observed in other *Turris* species is the more derived condition. However, this interpretation is based on a fairly sparse sampling of taxa within the subfamily Turrinae.

### **Reconciling molecular and radular evidence**

Our findings are consistent with our optimal molecular tree (Figure 5) supporting separation of the *Turris* species into two distinct clades within the Turrinae. The molecular tree supports a clade including *Turris annulata*, *T. cristata*, *T. cryptorrhaphe*, *T. nadaensis* and *T. undosa* (94% posterior probability, 63% ML bootstrap support) as a distinct clade within the *Turris*. A provisional taxonomic solution is to use a name for this clade previously provided by Powell, *Annulaturris* (Powell, 1966). Together with topology tests (Kishino-Hasegawa and Shimodaira-Hasegawa) that reject monophyly of the *Turris* species, it is clear that the proposed *Annulaturris* species should be considered to be well separated from the other *Turris* species.



The tree is a striking example of how misleading shell morphology can be; *Turris cristata*, with similar color pattern to the forms assigned to the *Turris nadaensis* complex is often mistaken for *Turris nadaensis*, while *Turris cryptorrhaphe* appears unmistakably different. Nevertheless, based on all three genes, it is clear that *Turris cryptorrhaphe* is more closely related to the various forms in the *nadaensis/undosa* clade than to *Turris cristata*.

Based on shell morphology, three specimens conventionally assigned to *Turris babylonia* fall into two divergent branches within the larger clade comprising *T. babylonia*, *T. dollyae*, *T. grandis*, *T. normandavidsoni*, *T. spectabilis*. Powell (1964) regarded *Turris babylonia* 1008 and 1012 as the “typical form”. The specimen 1010 belongs to a separate species, which has been regarded as a distinct form of *T. babylonia* (“*niveh form*”, Olivera, 1999). The type material for *Turris babylonia*, stored in the Linnaean society in London, consists of two syntypes. One is conspecific with our specimens 1008 and 1012 while the other is rather similar to our *Turris assyria* (or *babylonia*, specimen 1010). The fact that the type appears to be a mixture of two species is taxonomically problematic with resolution remaining for future studies. And yet while the true identity of the type specimen for *Turris babylonia* remains controversial (R. Kilburn, personal communication), the two morphospecies both widely assigned to *Turris babylonia* clearly belong in the same clade (*Turris s.s.* and not *Annulaturris*).

Nevertheless, further molecular, anatomical and shell morphological analyses are indicated. For example, the type species of *Annulaturris*, *T. amicta* (E.A. Smith, 1877) was not available for this analysis. Although supported by morphological data, the inference that *T. amicta* species falls in the clade (Figure 5) that includes *Turris cristata* and *Turris annulata* is speculative. The relationships of subtropical species, such as *Turris orthopleura* and *Turris ruthae*, also needs to be assessed. As discussed by Kilburn (1983), these species have shell morphological and radular characters that suggest that they are not in *Turris s.s.*

Compared to the relatively unreliable shell morphology, the combination of differences in radular morphology and multiple molecular markers provides a firmer definition for the type species of the family Turridae, and the clade to which the type species belong, defined here as *Turris*, excluding the *Annulaturris ssp.* We predict that these new insights into the phylogeny of *Turris* and its close relatives will be reflected in the analysis of the gene products expressed in their venoms, an analysis that we have begun. A phylogenetic framework has been an extremely useful guide to the discovery of unique pharmacological agents from *Conus* venoms. Similarly, an understanding of evolutionary history, summarized by our phylogeny of the *Turridae*, will extend future venom research.

## Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

## Acknowledgments

We are grateful to Yuri Kantor for his advice during the course of this work. We thank anonymous reviewers and editors for suggestions that greatly improved the manuscript. This study was supported by PharmaSeas, a program funded by the Department of Science and Technology, Republic of the Philippines (to GPC), by Grant GM48677 from the National Institutes of General Medical Sciences, U.S. Public Health Service (to BMO), by an International

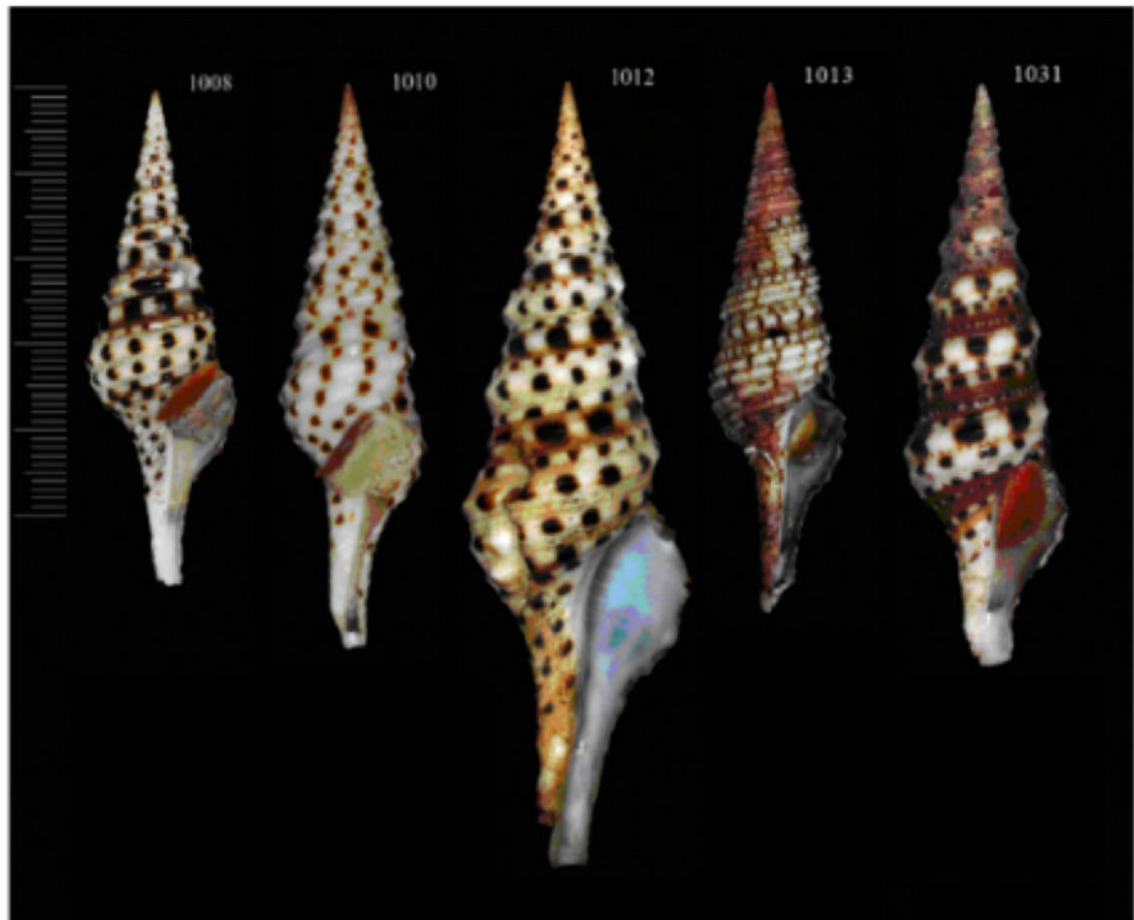
Cooperative Biodiversity Grant from the Fogarty Center, National Institutes of Health and by a grant from the Russian Fund for basic research RFBR-09-04-00911.

## References

- Bouchet P, Lozouet P, Maestrati P, Heros V. Assessing the magnitude of species richness in tropical marine environments: high numbers of molluscs at a New Caledonia site. *Biological Journal of the Linnean Society*. 2002; 75:421–436.
- Bozzetti L. *Turris ankaramanyensis* (Gastropoda: Hypsogastropoda: Turridae) nuova specie dal Madagascar meridionale. *Malacologia Mostra Mondiale*. 2006; 52:8–9.
- Buhay JE. “COI-like” Sequences are Becoming Problematic in Molecular Systematic and DNA Barcoding Studies. *Journal of Crustacean Biology*. 2009; 29:96–110.
- Heralde FM 3rd, Concepcion GP, Watkins M, Ownby J-P, Bandyopadhyay P, Olivera BM, Santos AD. Molecular phylogeny of some Indo-Pacific genera in the subfamily Turrinae H. Adams and A. Adams, 1853 (1838) (Gastropoda: Neogastropoda). *The Nautilus*. 2007; 121:131–138.
- Huelsenbeck JP, Ronquist F. MRBAYES: Bayesian inference of phylogeny. *Bioinformatics*. 2001; 17:754–755. [PubMed: 11524383]
- Kantor YI, Puillandre N, Olivera BM, Bouchet P. Morphological proxies for taxonomic decision in turrids (mollusca, neogastropoda): a test of the value of the shape of shell and radula characters using molecular data. *Zool J Linn Soc*. 2008; 25:1156–1170. [PubMed: 19267627]
- Kantor YI, Taylor JD. Formation of marginal radular teeth in Conoidea (Neogastropoda) and the evolution of the hypodermic envenomation mechanism. *Journal of Zoology*. 2000; 252(2):251–262.
- Kilburn RN. Turridae (Mollusca: Gastropoda) of southern Africa and Mozambique. Part 1. Subfamily Turrinae. *Ann Natal Mus*. 1983; 25:549–585.
- Kohn AJ. Food specialization in *Conus* in Hawaii and California. *Ecology*. 1966; 47:1041–1043.
- Maddison, D.; Maddison, W. *MacClade 4.08*. Sinauer Assoc; Sunderland, MA: 2005.
- McLean JH. A revised classification of the family Turridae with the proposal of new subfamilies, genera and subgenera from the eastern Pacific. *The Veliger*. 1971; 14:114–130.
- Olivera BM. The subfamily Turrinae in the Philippines: the genus *Turris* (Röding, 1798). *Philippine J Sci*. 1999; 128:295–318.
- Olivera BM, Rivier J, Clark C, Ramilo CA, Corpuz GP, Abogadie FC, Mena EE, Woodward SR, Hillyard DR, Cruz LJ. Diversity of *Conus* neuropeptides. *Science*. 1990; 249:257–263. [PubMed: 2165278]
- Olivera BM, Seronay RA, Fedosov AE. *Turris babylonia*; re-evaluation of a species complex and description of *Turris assyria*, new species. *Philippine Science Letters*. 2010
- Olivera BM, Teichert RW. Diversity of the neurotoxic *Conus* peptides: a model for concerted pharmacological discovery. *Molecular Interventions*. 2007; 7:251–260. [PubMed: 17932414]
- Olivera BM, Walker C, Cartier GE, Hooper D, Santos AD, Schoenfeld R, Shetty R, Watkins M, Bandyopadhyay P, Hillyard DR. Speciation of cone snails and interspecific hyperdivergence of their venom peptides. Potential evolutionary significance of introns. *Ann NY Acad Sci*. 1999; 870:223–237. [PubMed: 10415486]
- Palumbi, SR. Nucleic acids II: the polymerase chain reaction. In: Hillis, DM.; Moritz, C.; Mable, BK., editors. *Molecular Systematics*. Sinauer & Associates Inc; Sunderland, Massachusetts: 1996. p. 205–247.
- Ponder WF. The origin and evolution of Neogastropoda. *Malacologia*. 1973; 12:295–338. [PubMed: 4788271]
- Ponder WF, Waren A. Classification of Caenogastropoda and Heterostropha – A list of family-group names and higher taxa. *Malacological review Suppl*. 1988:288–317.
- Poppe, GT. *ConchBooks*. 2008. Philippine Marine Mollusks.
- Powell AWB. The molluscan families Speightiidae and Turridae. *Bulletin of the Auckland Institute and Museum*. 1966; 5:1–184. + 123 plates.

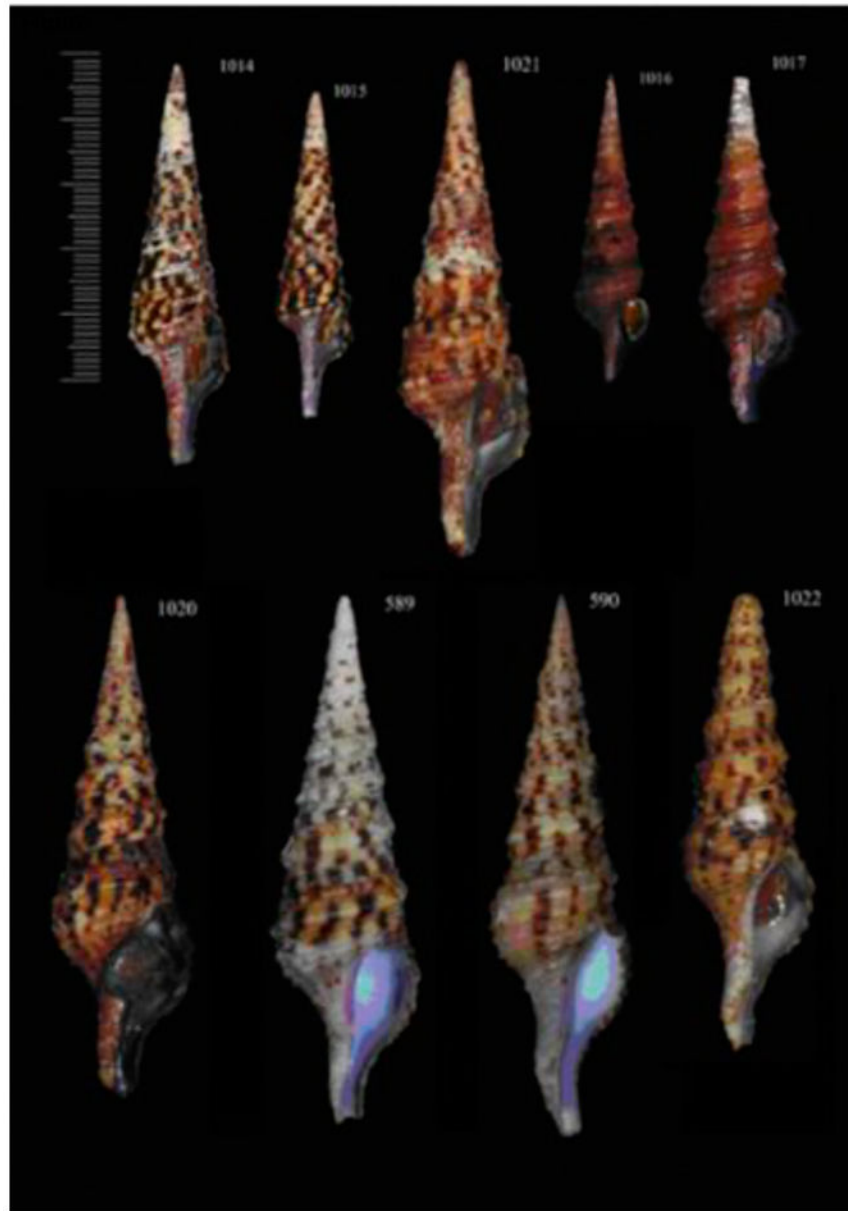


- Puillandre N, Samadi S, Boisselier MC, Sysoev AV, Kantor YI, Cruaud C, Couloux A, Bouchet P. Starting to unravel the toxoglossan knot: molecular phylogeny of the “turrids” (Neogastropoda: Conoidea). *Molecular Phylogenetic Evolution*. 2008; 47:1122–1134.
- Robin, A. *Xenophora and Conchbooks*. Hackenheim, Germany: 2008. *Encyclopedia of Marine Gastropods*.
- Stamatakis, Hoover P, Rougemont J. A Rapid Bootstrap Algorithm for the RAxML Web-Servers. *Systematic Biology*. 2008; 75(5):758–771. [PubMed: 18853362]
- Simon, C.; Franke, A.; Martin, A. The Polymerase Chain Reaction: DNA Extraction and Amplification. In: Hewitt; Johnson, AWB.; Young, JPW., editors. *Molecular Techniques in Taxonomy*, G. New York: Springer-Verlag; 1991. p. 329-355.
- Swofford, DL. *Phylogenetic Analysis Using Parsimony (\*and Other Methods)*. Version 4. Sinauer Associates; Sunderland, Massachusetts: 2002. PAUP\*.
- Taylor, JD.; Kantor, Y.; Sysoev, AV. *Bulletin. Natural History Museum; London: 1993. Foregut anatomy, feeding mechanisms, relationships and classification of the Conoidea (=Toxoglossa) (Gastropoda); p. 125-170.*
- Tucker JK. Catalog of recent and fossil turrids (Mollusca: Gastropoda). *Zootaxa*. 2004; 682:1–1295.
- Tucker, JK.; Tenorio, MJ. *Conchbooks*. 2009. Systematic classification of Recent and fossil conoidean gastropods.
- Vera-Peláez JL, Vega-Luz R, Lozano-Francisco MC. Five new species of the genus *Turris* Röding, 1798 (Gastropoda; Turridae; Turrinae) of the Philippines and one new species of the Southern Indo-Pacific. *Makakos: Monografía*. 2000; 2:1–29.

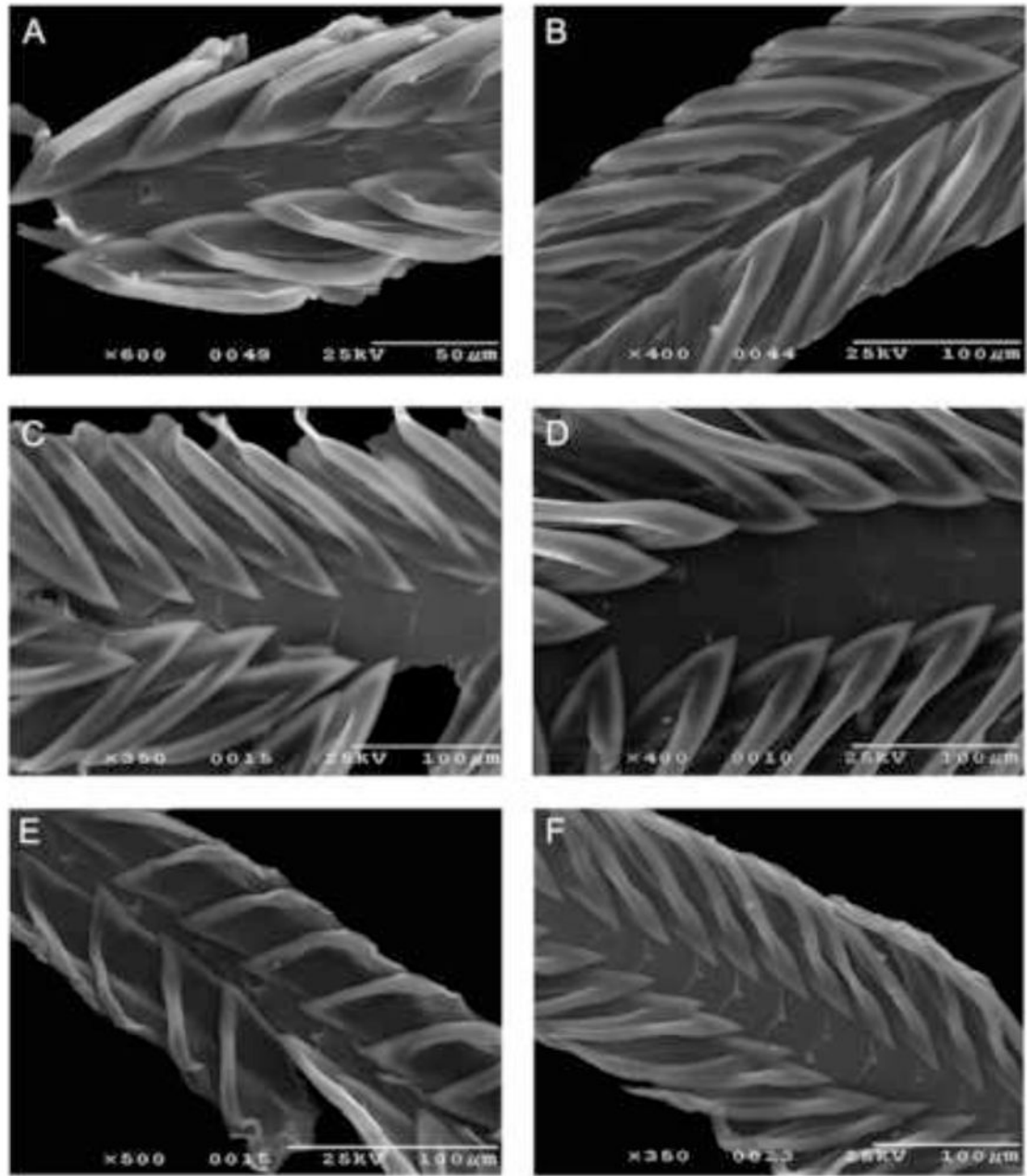


**Figure 1.**

Shells of some studied specimens of the genus *Turris*. A–C - *T. babylonia* #1008, *T. babylonia* (#1010, *assyria* or the “*niniveh*” form, Olivera, 1999), *T. babylonia* #1012 correspondingly D – *T. dollyae* (#1013); E – *T. garnonsii* (#1019); F – *T. normandavidsoni* (#1024); G – *T. spectabilis* (#1031); H – *T. totiphyllis* (#1028)

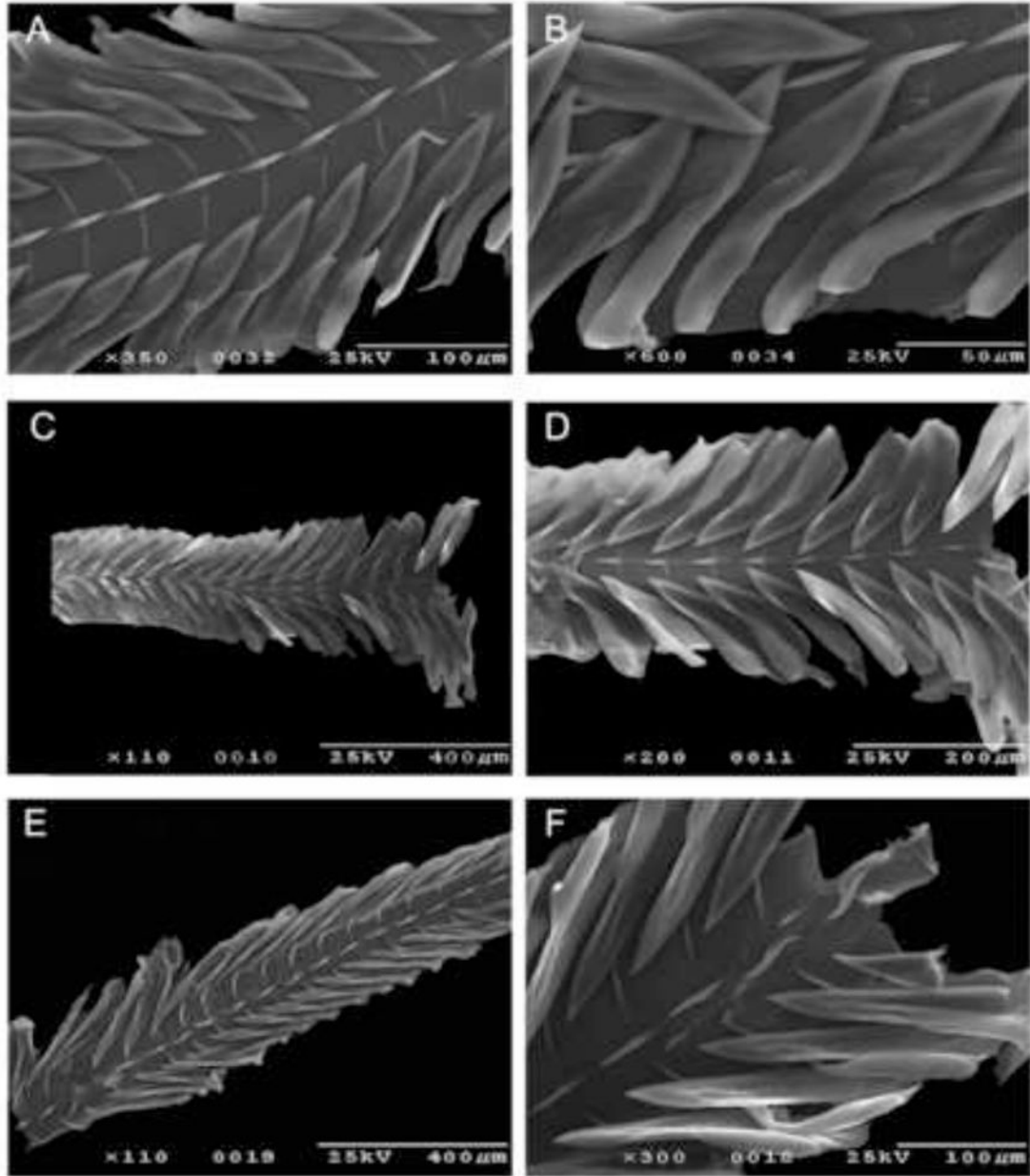


**Figure 2.** Shells of some studied specimens of the genus *Turris*. A – *T. cristata* (#1014); B – *T. cristata* (#1015); C – *T. cristata* (#1021); D – *T. cryptorraphe* (#1016); E – *T. cryptorraphe* (#1017); F – *T. undosa* (#1020); G – *T. undosa* (#589); H – *T. nadaensis* (#590); I – *T. nadaensis* (#1022); J – *T. nadaensis* (#1023)

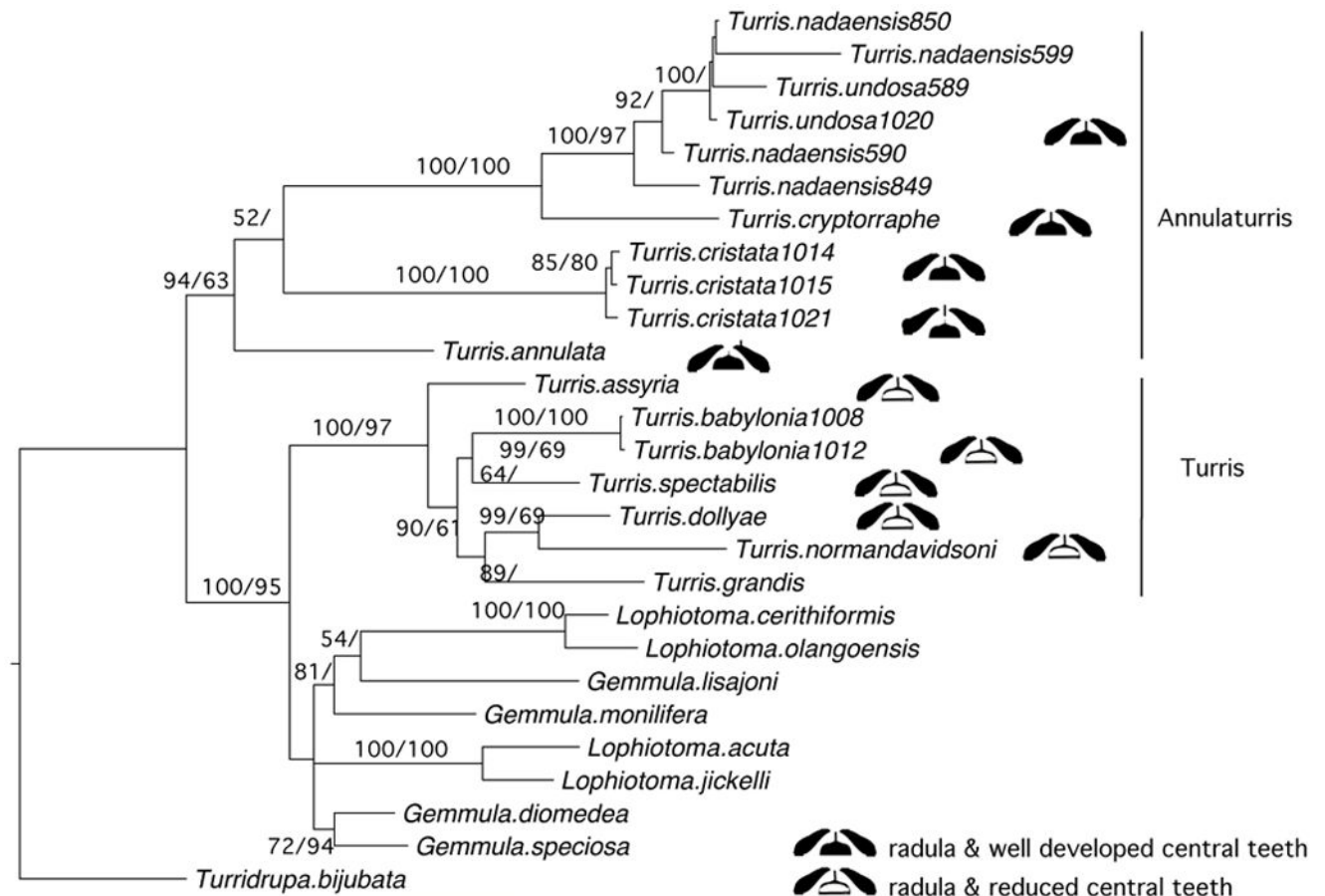


**Figure 3.**

Radular morphology of some *Turris* species. A – *T. babylonia* (#1012); B – *T. dollyae* (#1013); C – *Turris garnonsi* (#1019); D – *T. normandavidsoni* (#1024); E – *T. spectabilis* (#1031); F – *T. totiphylis* (#1028)



**Figure 4.**  
Radular morphology of some *Turris* species. A, B – *T. cryptorrhaphe* (#1016); C, D – *T. cristata* (#1015); E, F – *T. nadaensis* (#1022)



**Figure 5.**

Optimal tree inferred using gene-partitioned Bayesian methods from the concatenated alignments of 12SrRNA, 16S rRNAs and COI genes. The phylogeny describes the evolutionary relationships among *Turriss* species and selected *Lophiotoma* and *Gemmula* species. *Turridrupa bijubata* is the out-group species. Some *Turriss* taxa are labeled to indicate radulae and central tooth type relative to the optimal molecular tree. Branches are labeled with posterior probabilities greater than 50% from the Bayesian analysis of the three genes. Maximum likelihood bootstrap values over 50% appear to the right of the posterior probabilities. Clade A – *Annulaturriss*, provisionally given subgeneric status. Clade B – *Turriss s.s.*, provisionally given subgeneric status.



Table 1

Summary of Specimens Analyzed

Species assignment based on shell morphology	Specimen ID	Radula	Locality	Genbank		Accession		Numbers	
				12S		16S		COI	
<b>A. Species generally assigned to <i>Turris</i>:</b>									
<i>Turris annulata</i>	271		Aliquay	GU300000		GU345750		GU299967	
<i>Turris babylonia</i>	1008	+	Danajon Bank, off Olango Is.	GU300001		GU345751		GU299968	
<i>Turris babylonia</i> *	1010		Danajon Bank, off Olango Is.	GU300002		GU345752		GU299969	
<i>Turris babylonia</i>	1012	+	Sogod	GU300003		GU345753		GU299970	
<i>Turris grandis</i>	761		Philippines	GU300004		GU345754		GU299971	
<i>Turris cristata</i>	1014	+	Danajon Bank, off Olango Is.	GU300005		GU345755		GU299972	
<i>Turris cristata</i>	1015	+	Danajon Bank, off Olango Is.	GU300006		GU345756		GU299973	
<i>Turris cristata</i>	1021	+	Danajon Bank, off Olango Is.	GU300007		GU345757		GU299974	
<i>Turris cryptorhaphae</i>	1016	+	Danajon Bank, off Olango Is.	GU300008		GU345758		GU299975	
<i>Turris dollyae</i>	845		Sogod	GU300009		GU345759		GU299976	
<i>Turris dollyae</i>	1013	+	Danajon Bank, off Olango Is.						
<i>Turris nadaensis</i>	599		Philippines	GU300010		GU345760		GU299977	
<i>Turris nadaensis</i>	849		Sogod	GU300011		GU345761		GU299978	
<i>Turris nadaensis</i>	850		Danajon Bank, off Olango Is.	GU300012		GU345762		GU299979	
<i>Turris nadaensis</i>	1020	+	Danajon Bank, off Olango Is.	GU300013		GU345763		GU299980	
<i>Turris nadaensis</i>	590		Sogod	GU300014		GU345764		GU299981	
<i>Turris nadaensis</i>	589	+	Danajon Bank, off Olango Is.	GU300015		GU345765		GU299982	
<i>Turris normandavidsoni</i>	Heralde		Philippines	GU300016		GU345766		GU299983	
<i>Turris normandavidsoni</i>	1024	+	Danajon Bank, off Olango Is.						
<i>Turris spectabilis</i>	600		Philippines	GU300017		GU345767		GU299984	
<b>B. Species not assigned to <i>Turris</i>:</b>									
<i>Lophiotoma acuta</i>	513		Panglao	GU300018		GU345768		GU299985	
<i>Lophiotoma cerithiformis</i>	351		Oahu, Hawaii	GU300020		EU682298		GU299987	
<i>Lophiotoma cf jickelli</i>	230		Philippines	GU300021		GU345770		GU299988	

Species assignment based on shell morphology	Specimen ID	Radula	Locality	Genbank	Accession	Numbers
<i>Lophitotoma olangoensis</i>	315		Olango	12S GU300023	16S J868138	COI GU299990
<i>Gemmula diomedea</i>	515		Panglao	GU300027	GU345775	GU299994
<i>Gemmula lisajoni</i>	757		Sogod	GU300028	GU345776	GU299995
<i>Gemmula montifera</i>	432		Batangas	GU300029	GU345777	GU299996
<i>Gemmula speciosa</i>	434		Batangas	GU300031	GU345778	GU299997
<i>Turridrupa cf. bijubata</i>	700		Mactan	GU300032	GU345780	GU299999

\* This form has been designated *Turris assyria*, new species in an another paper (Olivera, Seronay, Fedosov, 2010) — see text.