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Phylogeny of the genus *Turris*: Correlating molecular data with radular anatomy and shell morphology

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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: *Turris babylonia*, (Linne, 1758), *Turris grandis,* (J. E. Gray, 1834), *Turris dollyae,* (Olivera, 1999), *Turris normandavidsoni* (Olivera, 1999) and *Turris spectabilis* (Reeve, 1843). With a change in species designation, *Turris assyria (*formerly *T. babylonia1010)* 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 *Annulaturris* Powell, 1966: *Turris annulata,* (Reeve, 1843), *Turris undosa*, (Lamarck, 1816), *Turris cristata,* (Vera-Peláez, Vega-Luz, and Lozano-Francisco 2000) *Turris cryptorrhaphe* (G. B. Sowerby, 1825) and *Turris nadaensis* (Azuma, 1973). Implications of the molecular phylogenetic results and its correlation with radular morphology are discussed.

1. 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 (1966); 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 Conidaem demanding a narrower definition of Turridae.

The first molecular phylogenetic investigation of Conoidea suggested an even more complex situation. Several subfamilies of

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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.

2. Materials and method

2.1. 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 and 30 m, and by gill nets at depths of 70–150 m. 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.

2.2. 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.

2.3. 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, 60 s); followed by 40 cycles of denaturation (95 °C, 20 s); annealing (55 °C, 20 s) and extension (72 °C, 30 s).

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.

2.4. Phylogenetic analysis

Individual 12SrRNA, 16SrRNA and COI equences 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

Table 1
Summary of Specimens Analyzed.

Species assignment based on shell morphology	Specimen ID	Radula	Locality	Genbank accession numbers		
				12S	16S	COI
A. Species generally assigned to Turris:						
Turris annulata	271		Aliquay	GU300000	GU345750	GU299967
Turris babylonia	1008	+	Danajon Bank,off Olango Is.	GU300001	GU345751	GU299968
Turris babylonia[a]	1010		Danajon Bank,off Olango Is.	GU300002	GU345752	GU299969
Turris babylonia	1012	+	Sogod	GU300003	GU345753	GU299970
Turris grandis	761		Philippines	GU300004	GU345754	GU299971
Turris cristata	1014	+	Danajon Bank,off Olango Is.	GU300005	GU345755	GU299972
Turris cristata	1015	+	Danajon Bank, off Olango Is.	GU300006	GU345756	GU299973
Turris cristata	1021	+	Danajon Bank, off Olango Is.	GU300007	GU345757	GU299974
Turris cryptorrhaphae	1016	+	Danajon Bank, off Olango Is.	GU300008	GU345758	GU299975
Turris dollyae	845		Sogod	GU300009	GU345759	GU299976
Turris dollyae	1013	+	Danajon Bank, off Olango Is.			
Turris nadaensis	599		Philippines	GU300010	GU345760	GU299977
Turris nadaensis	849		Sogod	GU300011	GU345761	GU299978
Turris nadaensis	850		Danajon Bank, off Olango Is.	GU300012	GU345762	GU299979
Turris nadaensis	1020	+	Danajon Bank, off Olango Is.	GU300013	GU345763	GU299980
Turris nadaensis	590		Sogod	GU300014	GU345764	GU299981
Turris nadaensis	589	+	Danajon Bank, off Olango Is.	GU300015	GU345765	GU299982
Turris normandavidsoni	Heralde		Philippines	GU300016	GU345766	GU299983
Turris normandavidsoni	1024	+	Danajon Bank, off Olango Is.			
Turris spectabilis	600		Philippines	GU300017	GU345767	GU299984
B. Species not assigned to Turris:						
Lophiotoma acuta	513		Panglao	GU300018	GU345768	GU299985
Lophiotoma cerithiformis	351		Oahu, Hawaii	GU300020	EU682298	GU299987
Lophiotoma cf jickelli	230		Philippines	GU300021	GU345770	GU299988
Lophiotoma olangoensis	315		Olango	GU300023	J868138	GU299990
Gemmula diomedea	515		Panglao	GU300027	GU345775	GU299994
Gemmula lisajoni	757		Sogod	GU300028	GU345776	GU299995
Gemmula monilifera	432		Batangas	GU300029	GU345777	GU299996
Gemmula speciosa	434		Batangas	GU300031	GU345778	GU299997
Turridrupa cf bijubata	700		Mactan	GU300032	GU345780	GU299999

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

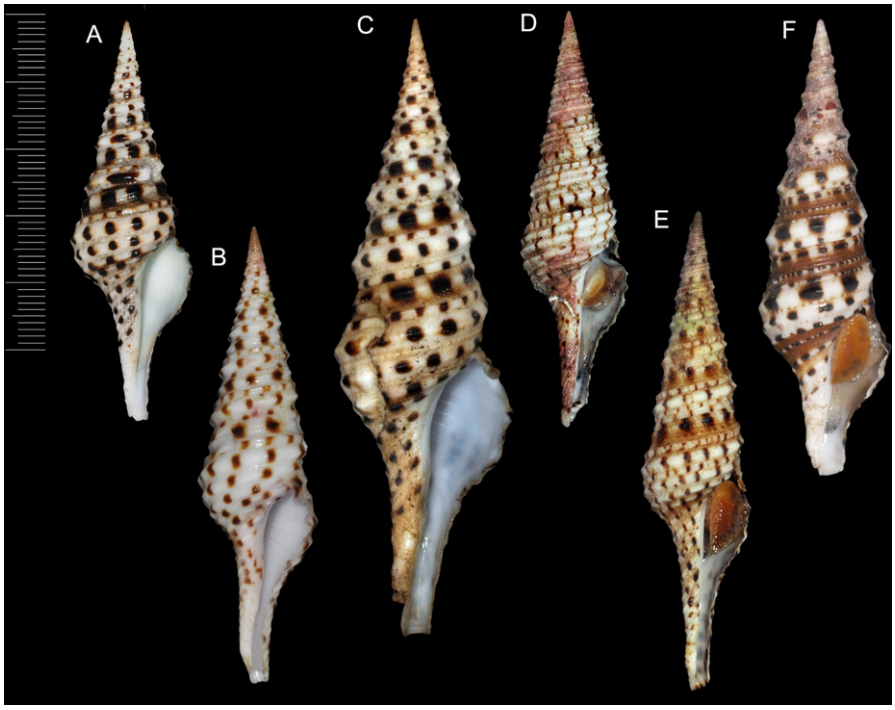

Fig. 1. Shells of some studied specimens of the genus *Turris*. A – *T. babylonia* #1008 (wide form); B – *T. babylonia* #1010 (narrow or the "niniveh" form, Olivera, 1999); C – *T. babylonia* #1012 (wide form); D – *T. dollyae* (#1013); E – *T. normandavidsoni* (#1024); F – *T. spectabilis* (#1031).

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 (see Figs. 1 and 2). To ensure that these were tests of topology alone, we constrained the topologies but not the branch length estimates.

3. Results

3.1. Radular morphology

The radulae of the specimens indicated in Table IA are illustrated in Figs. 3 and 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 *T. babylonia, 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 *T. cryptorrhaphe*, and a long, pointed awl-shaped cusp (Fig. 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

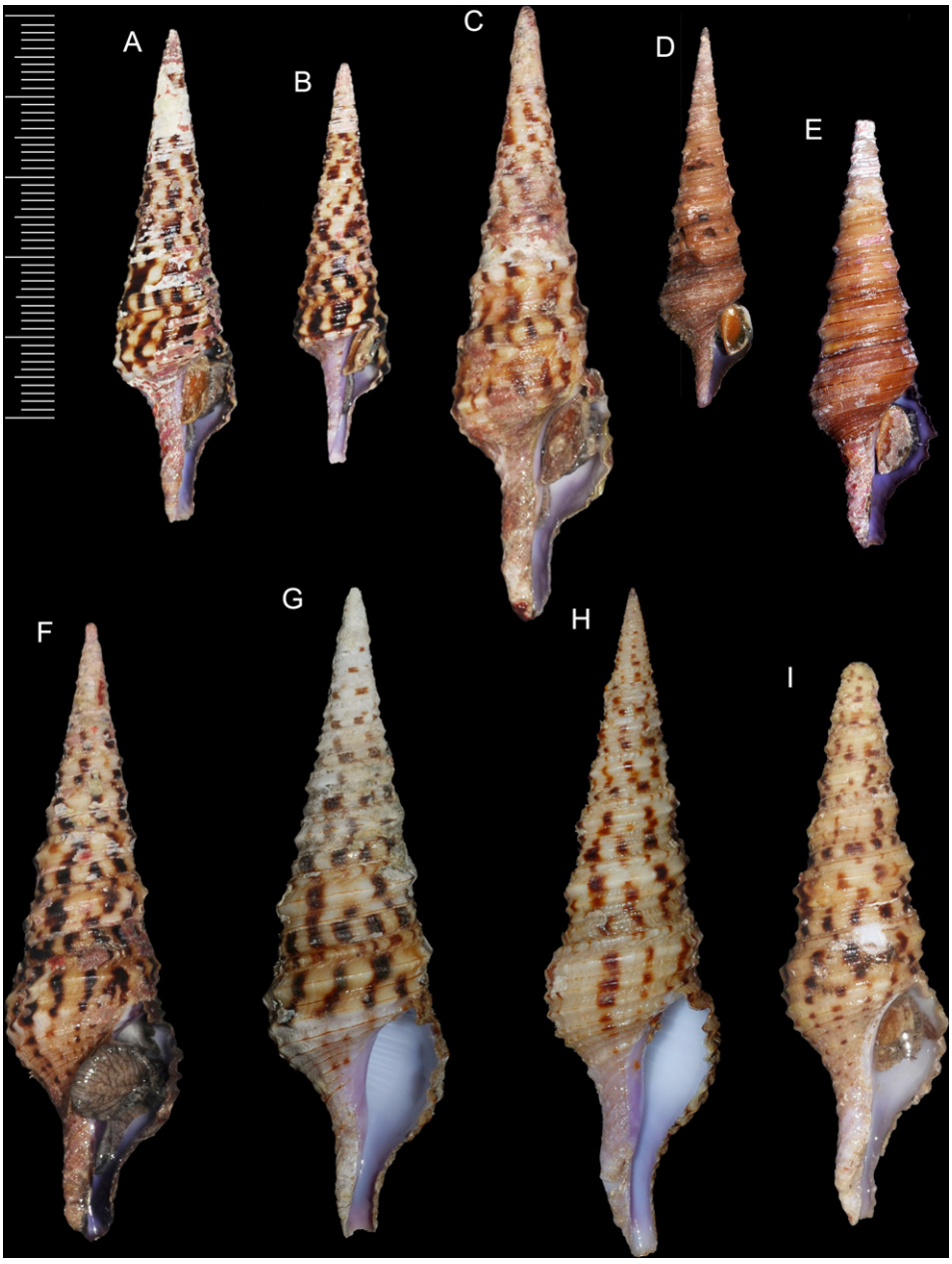

Fig. 2. Shells of some studied specimens of the genus *Turris*. A – *T. cristata* (#1014); B – *T. cristata* (#1015); C – *T. cristata* (#1021); D – *T. cryptorraphe* (#1016); E - *T.cryptorraphe* (#1017); F – *T. undosa* (#1020); G – *T. undosa* (#589); H – *T. nadaensis* (#590); I – *T. nadaensis*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

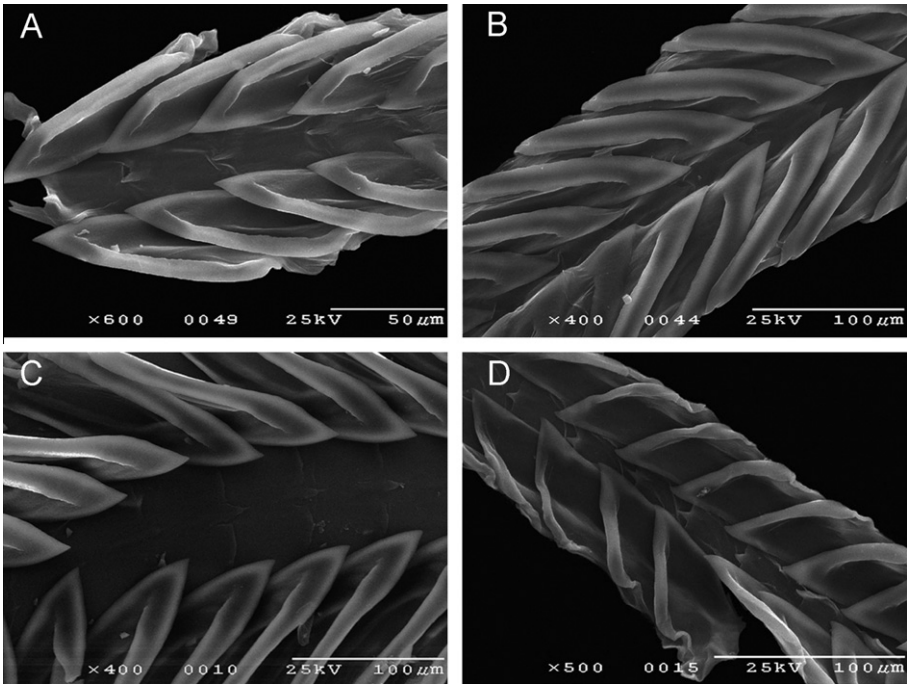

Fig. 3. Radular morphology of some *Turris* species. A – *T. babylonia* (#1012); B – *T. dollyae* (#1013); C – *T. normandavidsoni* (#1024); E – *T. spectabilis* (#1031).

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 *T. cryptorrhaphe*, *T. cristata, T. nadaensis* and *T. 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.

3.2. Molecular analysis

The trees inferred from the three individual genes, COI, 12S and 16S are poorly resolved (Supplementary Fig. 1). On the other hand, the tree inferred from the concatenated sequence of the three genes (Fig. 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 *T. annulata, T. cristata, T. cryptorrhaphe*, *T. nadaensis* and *T. undosa* to the exclusion of a clade comprising *Lophiotoma* and *Gemmula* species with the other *Turris* species *(T. babylonia, T. dollyae, T. grandis, T. normandavidsoni, T. spectabilis*, *Turris assyria*). The hypothesis that the *Turris* species are monophyletic is rejected (Shimodaira–Hasegawa test, ln likelihood difference = 62.3, $p \leqslant 0.0001$).

4. Discussion

4.1. 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 *T. babylonia*. These include in Clade II *T. cryptorrhaphe*, *T. nadaensis*, *T. “undosa”* (=*cristata*) and in Clade III *T. 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.

4.2. Radular mophology

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 *T. amicta* and *T. annulata* into the *Annulaturris*, Powell (1966) noted that in contrast to the marginals-only pattern observed for *T. babylonia* and *T. crispa*, *T. 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* speces is the more derived condition. However, this interpretation is based on a fairly sparse sampling of taxa within the subfamily Turrinae.

4.3. Reconciling molecular and radular evidence

Our findings are consistent with our optimal molecular tree (Fig. 5) supporting separation of the *Turris* species into two distinct clades within the Turrinae. The molecular tree supports a clade

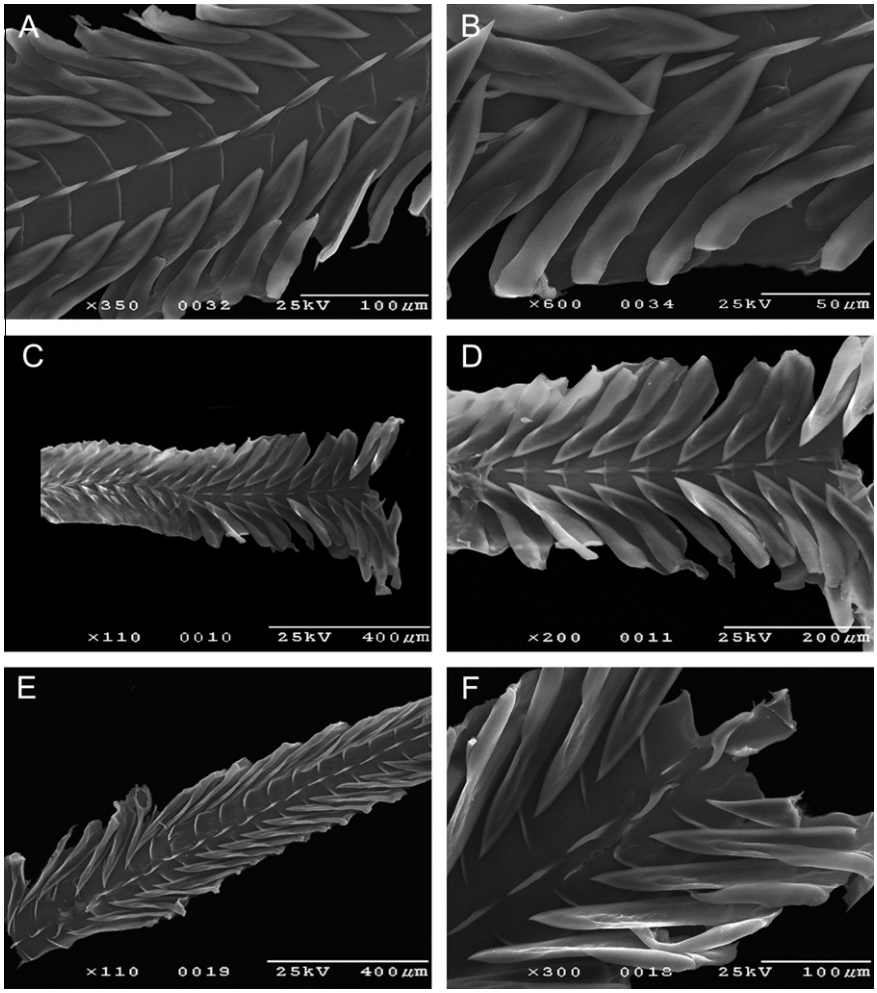

Fig. 4. Radular morphology of some *Turris* species. A, B – *T. cryptorrhaphe* (#1016); C, D – *T. cristata* (#1015); E, F – *T. nadaensis* (#1022).

including *T. annulata, T. cristata, T. cryptorrhaphe*, *T. nadaensis* and *T. undosa* (94% posterior probability, 63% ML bootsrap 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 seaparated from the other *Turris* species.

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

Based on shell morphology, three specimens conventionally assigned to *T. babylonia* fall into two divergent branches within the larger clade comprising *T. babylonia*, *T. dollyae*, *T. grandis*, *T. normandavidsoni*, *T. spectabilis*. Powell (1966) regarded *T. 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 ("niniveh form"*, Olivera, 1999). The type material for *T. 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 *T. 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 *T. babylonia* remains controversial (R. Kilburn, personal communication), the two morphospecies both widely assigned to *T. 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* (Smith, 1877) was not available for this analysis. Although supported by morphological data, the inference that *T. amicta* species falls in the clade (Fig. 5) that includes *T. cristata* and *T. annulata* is speculative. The relationships of subtropical species, such as *T. orthopleura* and *T. 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.

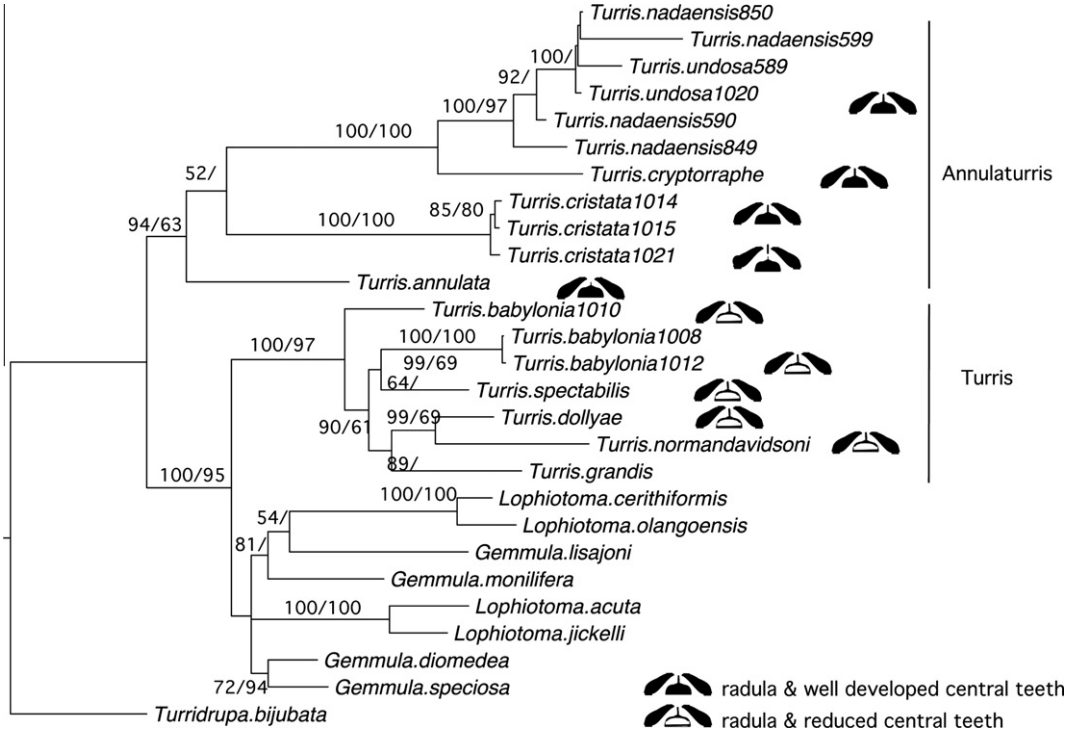

Fig. 5. Optimal tree inferred using gene-partitioned Bayesian methods from the concatenated alignments of 12SrRNA, 16S rRNAs and COI genes. The phylogeny describes the evolutionary relationships among *Turris* species and selected *Lophiotoma* and *Gemmula* species. *Turridrupa bijubata* is the out-group species. Some *Turris 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 – *Annulaturris*, provisionally given subgeneric status. Clade B – *Turris* s.s., provisionally given subgeneric status.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2011.01.019.

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