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RESEARCH

# The Subfamily Turrinae in the Philippines: The Genus *Turris* (Röding, 1798)

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**Marine gastropods of the family Turridae, commonly known as turrids, comprise the largest living group of venomous snails. The taxonomy of this group, however, has been generally neglected. In this work, the genus *Turris* (Röding 1798) is discussed. Out of more than 200 different turrid genera, this genus comprises some of the largest and most distinctive living turrid species. The last comprehensive treatment of this particular genus (Powell 1964) identified seven species from the Philippines. In this paper, twelve distinct species of *Turris* found in the Philippine waters are recognized. Four new species are described: *Turris dollyae*, *T. normandavidsoni*, *T. pagasa* and *T. totiphyllis*. Insufficient material makes it premature to conclude whether three additional distinctive *Turris* forms are separate species, or unusual varieties of other species. The taxonomic status of the genus *Turris* and its relationship to other Turrinae is further discussed. Alternative hypotheses regarding the evolutionary origins of this group are also considered. In addition, two species of *Gemmula*, with particular affinities for species clades in *Turris* are noted: one is a new species and one is a renamed homony.**

Key words: Conacea, Turridae, toxoglossate, mollusc, clades, evolution

Toxoglossate molluscs (Conacea = Toxoglossa) comprise what is arguably the largest superfamily of venomous animals in terms of number of species (>3,000) (Powell 1966). Traditionally, toxoglossate molluscs are divided into three familiar groups: Conidae (cones), Terebridae (augers) and Turridae (turrids). Generally speaking, the cones and terebrids are easily recognized from their shells, and recent comprehensive taxonomic accounts of these groups have been published (Bratcher & Cernohorsky 1987, Röckel et al. 1995). The taxonomy of *Conus* has been analyzed not only by traditional malacological criteria. Recently, biochemical and molecular data that could be useful for deciding between different phylogenetic alternatives have been collected (for overviews, see Olivera et al. 1990 and Olivera et al. 1999). One of the first attempts to carry out molecular analysis of any toxoglossate molluscan group for purely taxonomic purposes (Dia-Monje 1994) was recently published in this journal (Monje et al. 1999).

The turrids are geologically the oldest of the three classical toxoglossate types, being well-represented in the Mesozoic. They are probably the most species-rich of all living gastropod lineages. Compared to cones and terebrids, turrids are remarkably diverse and much more heterogeneous.

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The only characteristic that all turrids share is the presence of a slit (or posterior sinus). Virtually nothing is known about most of the several thousand different turrids. More than 200 different turrid genera have been proposed and there is no consensus on how many different families comprise the turrids. It has recently been suggested, based on a cladistic analysis, that some of the traditionally turrid genera might, in fact, be more closely related to cone snails than to other turrids and that these are more properly placed within the family Conidae (Taylor et al. 1993).

The most familiar and best-known of all the turrids in the Philippines are those belonging to the genus *Turris* (Röding 1798) as narrowly defined by Powell (Powell 1964, Powell 1966). This genus includes some of the largest and most striking turrid species. The Indo-Pacific arc (from the Philippines to New Guinea) appears to be the center of distribution for this group. However, most species are found in moderately deep water. As a consequence, most *Turris* species have not been widely available for study. As Powell stated in his 1966 monograph, classification of the Turridae is greatly hampered because "a range of specimens is not often available, even by dredging."

Because of the impressive creativity of the Philippine shell gathering industry, new technologies for collecting deep-water molluscs of interest to collectors have been developed. In the last few decades, through the use of gill nets and hookah collecting in the central and southern Philippine Islands, Philippine shell-gathering fishermen have found turrid species that were previously rare or uncommon. Because of their availability, the author has initiated biochemical and molecular work on turrid venoms. In order to do proper work of any type with the turrids, a reasonable understanding of their basic taxonomy is essential. However, in many cases, even the most rudimentary separation into species is proving to be problematic. Given the more than 2,000 turrid species, the only practical way to address this problem is to examine one genus (or group of related genera) at a time. We shall initially concentrate our efforts on the subfamily Turrinae. A logical starting point is therefore the nominate genus of this group: *Turris*.

### Scope of this paper

In this paper, all known living forms conventionally assigned to the genus *Turris* (narrowly defined), which have been collected in the Philippines, are presented. The availability of a larger suite of specimens has made it possible to define four new species in this genus. A proposal for the evolutionary relationships between species clades in the genus and the possible origins of these clades is presented.

Like most taxonomic work, the proposals in this paper must be regarded as tentative. More material may reveal that forms proposed to be different species may in fact intergrade once a larger series is available and forms assigned to the same species may prove distinct upon closer examination of a larger sample set. However, this study comprises the minimal taxonomic characterization required before an effective molecular and biochemical characterization can be initiated on the venoms of *Turris* species. Taxonomic characterization is a necessary starting-point for other studies, however, results of the molecular studies and venom characterization should provide feedback that will be useful for rigorously evaluating the taxonomic framework proposed.

### Previous monographs on *Turris* from the Philippines

The standard references on Indo-Pacific Turrinae are Powell's three monographs (Powell 1964, 1966, 1967). Powell recognized seven distinct species of *Turris* from the Philippines out of the eight total in his monograph. The only other subsequent treatment of *Turris* from the Philippines is the *Shells of the Philippines* by Springsteen and Leobrera (1986) which discussed and illustrated seven species. In that work, the authors did not include *Turris annulata* (presumably because no specimens could be found in any Philippine collections) but illustrated *Turris nadaensis*, a species described after the monographs of Powell.

## Materials and Methods

### Specimen collection

*Turris* specimens examined were mostly from the author's collection. These were collected from

Table 1. Summary of distinct forms of the genus *Turris* found in the Philippines (as defined by Powell 1964 and Powell 1966)

| *Turris* | Specimen # in Plate I | Also Shown in Plate |
|---|---|---|
| *annulata*** | 9 | X |
| *babylonia* | 5 | IV, VI |
| *crispa* | 1a, b | II, V |
| *cryptorhaphe** | 12 | VIII, XI |
| *dollyae, n. sp.* | 2 | II, VI |
| *garmonsi* | 8 | VI |
| *nadaensis** | 10a, b, c | VIII |
| *normandavidsoni, n. sp.* | 3 | III, VI |
| *pagasa, n. sp.* | 4 | V, VI |
| *spectabilis* | 14 | VII |
| *toliphyllis, n. sp.* | 15 | VII |
| *undosa** | 12 | VIII, XI |
| Uncertain taxonomic status | | |
| "Iloilo" form (*T. babylonia*?) | 6 | IV, VI |
| "Sulu Sea" form (*T. babylonia*?) | 7 | IV |
| "angular" form (*T. nadaensis*?)* | 11 | |

Clade 1: no asterisk; Clade 2: *; Clade 3: **

various Philippine localities over the last 45 years. Specimens more recently obtained were collected primarily by using tangle nets in deep water (50-200 m) by trawling or by hookah in the localities indicated under each species.

### Species characterization

The primary diagnostic keys used were the monograph of Powell (1964) and the book of Springsteen and Leobrera (1986). Morphological observations were restricted to the shells of each species.

## Result and Discussion

### Overview of *Turris* Species in the Philippines

For the purpose of this monograph, the fifteen distinctive Philippines forms assigned to *Turris* (see Table 1 and Plate I) were divided into three groups. These appear to be coherent clades, which probably reflect general evolutionary relationships between the various species traditionally assigned to this genus.

**Clade I: The *babylonia* clade.** This includes the largest group of species. The monograph of Powell (1964) discussed four species from the Philippines in this group: *Turris crispa crispa*, *Turris babylonia*, *Turris spectabilis* and *Turris garmonsi*. These four species are also figured and discussed by Springsteen and Leobrera (1986). In the treatment of the Clade I below, we include eight species, and two forms whose assignment is uncertain.

**Clade II: The purple clade.** These include three species that were recognized by Springsteen and Leobrera (1986): *Turris cryptorhaphe*, *Turris undosa* and *Turris nadaensis* (the first two are also discussed by Powell) and a distinct form tentatively assigned to *T. nadaensis*. This group is characterized by the distinctive purple color of the aperture region often extending into the canal.

**Clade III: The *Annulaturris* clade.** This includes only one Philippine species assigned to *Turris annulata*, which appears to have little affinity with Clade I and Clade II species. Powell (1966) proposed the subgenus *Annulaturris* for *T. annulata*. We raise the possibility in this monograph that *Turris* (*Annulaturris*) *annulata* does not properly belong within the genus *Turris*. In this paper, we describe a new species of *Gemmula* which at least superficially seems to be similar in general shape to *T. annulata*. However, we believe that the new species is properly assigned to *Gemmula*, and not *Turris*. This therefore raises the question of whether *T. annulata* and the subgenus *Annulaturris* is properly in *Turris*, in *Gemmula* or is part of a distinctive transitional group intermediate between *Gemmula* and *Turris*.

### Clade I: The *babylonia* clade

The type of the genus is *Turris babylonia*. In the Philippines several forms appear to be part of a taxonomically confusing species complex closely related to both *T. crispa* and *T. babylonia*. Four new species that are part of this clade are described: *Turris dollyae*, *Turris normandavidsoni*, *Turris pagasa* and *Turris toliphyllis*. Some of the new species described here have been illustrated previously and identified as either *T. babylonia* or *T. crispa* by several authors. References in which these newly recognized forms have previously been illustrated will be cited where appropriate.

***Turris crispa crispa* (Lamarck, 1816)**
(Plate I, Specimens 1a and 1b; Plates II and VI)

This is the largest of all living species in both the

genus and the subfamily. This species can exceed 185 mm in length. *T. crispa* is primarily a deep-water species. Plate I shows the two variants of *T. crispa crispa* found in the Philippines. The large size and characteristic maculations on the typical form of this species are unmistakable (Plate I, Specimen 1A; Plates II and VI). *T. crispa* is trawled or collected by gill nets from a wide variety of different Philippine localities at depths of 80 to 150 meters. There is a white variety with almost no maculations (Plate I, Specimen 1b) which I assign to *T. crispa*; this is generally narrower than typical *T. crispa*. This form is much rarer in collected material from the Philippines.

In most previous treatments of *T. crispa*, a third form has been included within the species. From the much greater amount of material available, it seems clear that this form is distinct from *T. crispa*. Both typical *T. crispa* and this form apparently occur in several Philippine localities such as at Bogo, Cebu and around Panglao, Bohol. Since no intermediates between the two forms have been discovered, and this *T. crispa*-like form has not previously been described, a new name is proposed here, *T. dollyae*.

***Turris dollyae*, new species**
(Plate I, Specimen 2; Plates II and VI)

**Description.** The shell is large (80-123 mm), narrowly fusiform with a long siphonal canal. Adult specimens have 15-17 whorls, spire angle is 20-22°, ratio of aperture plus siphonal canal to total length is 0.48. Next to the upper suture are two fused spiral cords, the one adjacent to the suture generally smaller. Between the subsutural cords and the sinus cord is a deeply excavated area, with flat white threads. There are typically 5 or 6 spiral cords which are broad but come to a sharp apex, with secondary fine cords or threads in between. The canal is completely covered with additional spiral cords. The entire shell is marked with axial black maculations, much longer axially than along the spiral cord, with continuity between maculations across many cords in most but not all specimens. The large size, thin black axial markings and broadly excavated spiral area between the subsutural cords and the sinus cord are distinctive characteristics of the species.

**Discussion.** Most specimens labeled *T. crispa* collected from the Philippines are in fact *T. dollyae*, many collected from one locality (Tabaco Bay, Albay, Luzon Island) in fair numbers between 1960-1975. The holotype of *T. dollyae* from this locality is illustrated along with three paratypes in Plate II, and compared with a Philippine specimen of *T. crispa*.

The figure identified as *T. crispa crispa* from Luzon in the 1964 Powell monograph is in fact *T. dollyae* (Plate 181, Specimen 11). A specimen of *T. dollyae* is also figured in Springsteen and Leobrera (1986) and identified as *T. crispa* (Specimen 76, number 2, specimen on the right). Wilson (1994) illustrates a specimen of *T. dollyae* from Townsville, Queensland, Australia (Plate 38, Specimen 10B) (the other specimen labeled *T. crispa* from Queensland is the white form of *T. crispa crispa* without maculations). These literature records suggest that this species can be found throughout the Indo-Pacific arc, from Luzon to Queensland, Australia.

**Comparison.** *T. dollyae* is generally similar to *T. crispa* and *T. babylonia*, with mature *T. dollyae* larger than *T. babylonia*, and broader in outline, with a thicker canal than *T. crispa*. In many specimens of *T. crispa*, the maculations on the body whorl are restricted to the spiral ridges and are characteristically purplish-brown. The markings on *T. dollyae* are black and often run continuously in an irregular axial manner over several cords, particularly in the canal. When axial flammules do occur in *T. crispa*, the markings on the cord interstices are lighter in color than on the spiral cords. In *T. dollyae*, the markings are uniform black whether on the spiral cords or in between. The maculations of *Turris crispa* are aligned, with the longest dimension along the spiral cord, while these markings in *T. dollyae* are longer axially. In Philippine specimens, the spiral cords on *T. crispa* are generally narrower, making the intercord areas seem larger on the body whorl; in *T. dollyae* the cords are essentially contiguous to each other throughout the body whorl and siphonal canal. Another difference between the two species is that the gap between the subsutural area and the sinus cord is usually gently sloping in *T. crispa*, and sharply terraced in *T. dollyae*. In most specimens of *T. dollyae*, the peripheral cord is the most prominent spiral cord, while in Philippine specimens of *T. crispa*

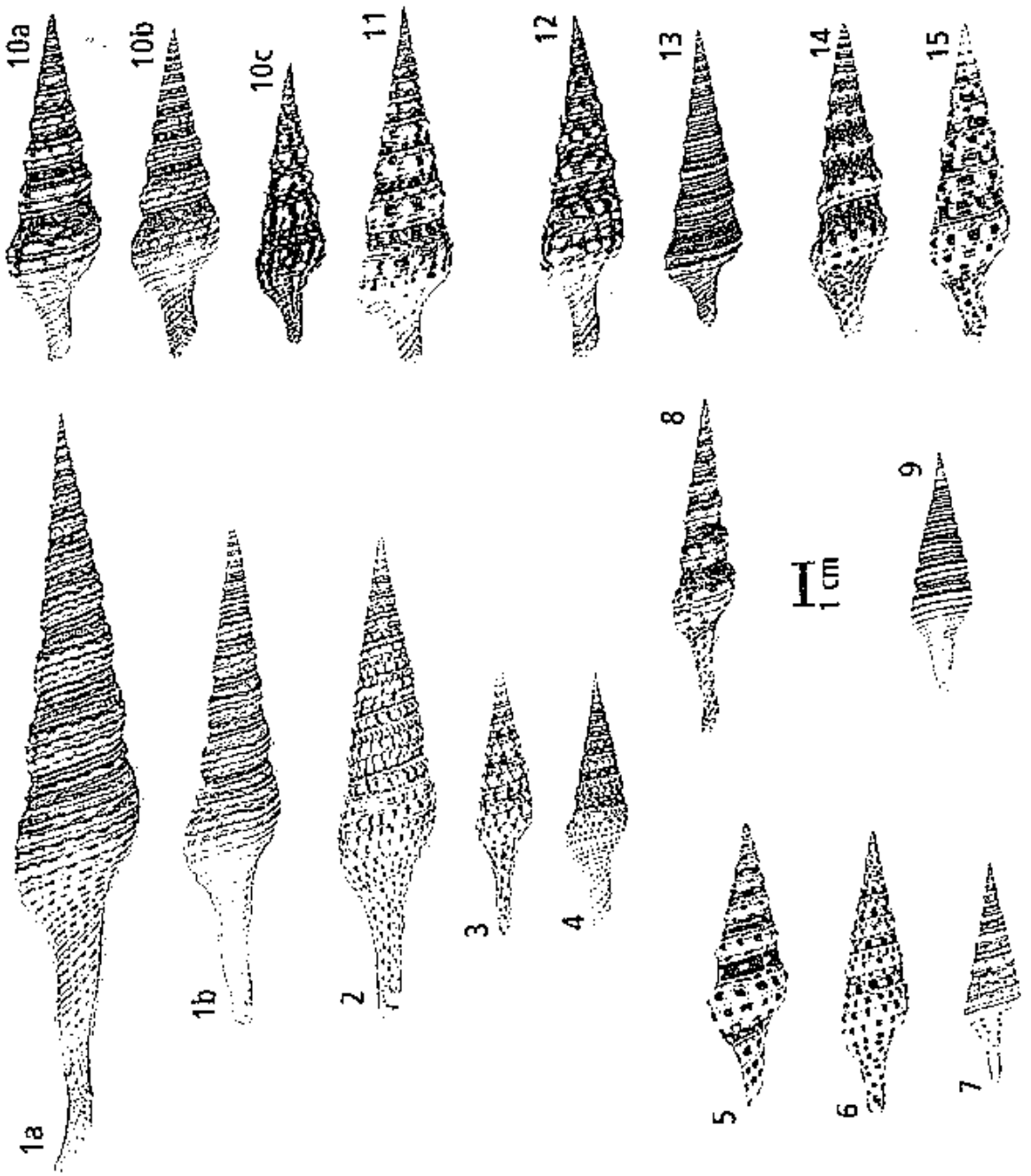



**Plate I.** Fifteen distinctive forms found in the Philippines of the genus *Turris*. 1. *Turris crispa crispa* (1A, regular form; 1B, unspoted form) 2. *Turris dollyae*. 3 *Turris normandavidsani*. 4. *Turris yokbeensis* 5 *Turris babylonia* (typical, "babylon" form). 6. "Ninivel" form (*Turris babylonia*?). 7. "Sulu Sea" form (*Turris babylonia*?) 8 *Turris garrisoni*. 9 *Turris nanolata*. 10 *Turris nadinensis* (10A, typical form; 10B, lighter broad variety; 10C, exceptionally dark form). 11. "Angular" form (*Turris nadinensis* variety?) 12 *Turris undosa* 13. *Turris cryptorhaphe*. 14 *Turris spectabilis*. 15 *Turris foliphyllis* The size bar is 1 cm

all primary cords on the body whorl have similar size.

**Nomenclature.** This new species is named for Dolores (Dolly) Hernandez to honor her outstanding contributions to Philippine science education. Before she obtained her graduate training, Dolly Hernandez was the author's teacher in his first chemistry and biology courses. I want to express my deep personal gratitude to Dolly Hernandez for steering me towards a scientific career combining chemistry and biology.

**Types.** The holotype will be deposited in the Philippine National Museum, paratypes will be deposited in the British Museum of Natural History, in the American Museum of Natural History and the U.S. National Museum. Other paratypes are in the Olivera collection. (see Appendix for measurements of individual types)

*Turris normandavidsoni*, new species
(Plate I, Specimen 3; Plate III)

**Description.** The shell is 58-85 mm in length, narrowly fusiform with a long siphonal canal, and covered with spiral cords decorated with regularly spaced blackish-brown maculations. There are two distinctly brownish zones on the body whorl, just anterior to the subsutural cord and between the body whorl and the siphonal canal. Spire angle of *T. normandavidsoni* is 20-22°, and the ratio of aperture plus siphonal canal to total length is 0.44. Next to the upper suture is a broad, complex subsutural cord with large black or dark brown maculations, followed by an excavated light brown area between the subsutural cord and the terraced sinus cord. On the larger spire whorls, two additional spiral cords are visible. There are 6-7 broad spiral cords on the body whorl and base, and an additional 6-7 spiral cords on the canal, with intermediate spiral cords in some specimens. The spiral cord next to the large peripheral cord is characteristically the smallest of the four primary cords on the body whorl.

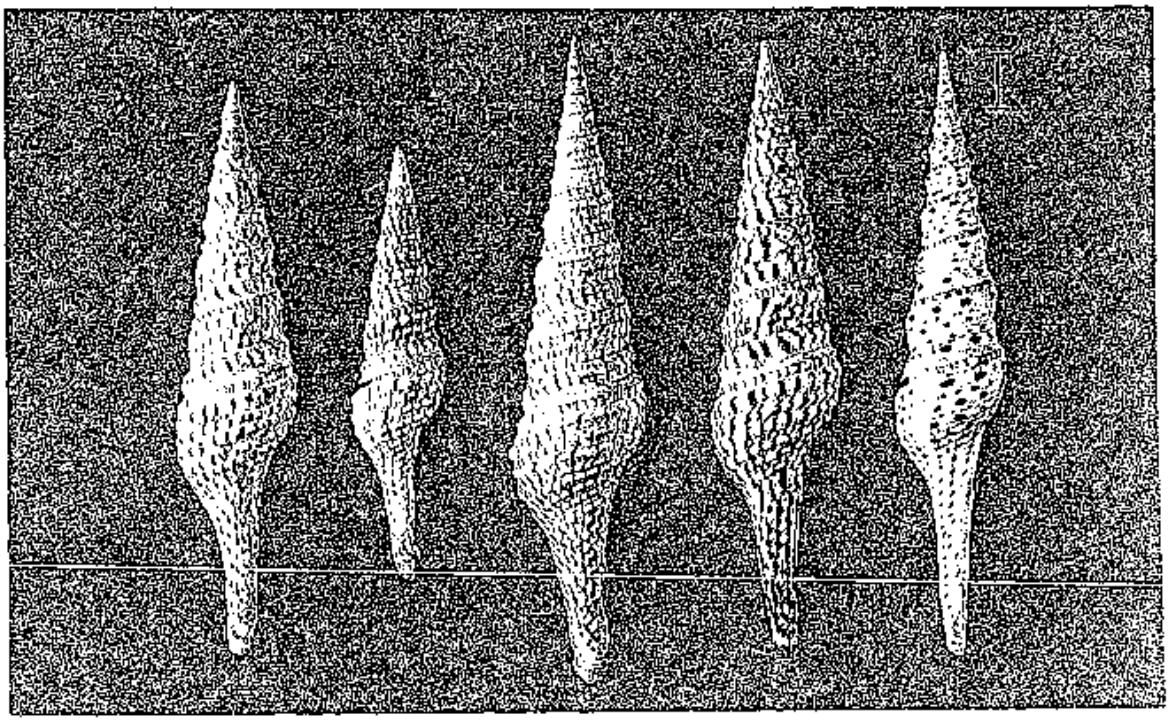
**Discussion.** *T. normandavidsoni* is a species superficially intermediate between *T. babylonia* and *T. crispa*. Very few specimens were known in Philippine collections until quite recently, and these were invariably confused with one of those two species. Powell figured what is probably a specimen of *T. normandavidsoni* in his 1964 monograph (Plate 181, Number 5; and assigned it to *T. babylonia* (although he recognized that it might be distinct). In Hinton's Seashells from New Guinea and the Central Indo-Pacific (Hinton 1972), a specimen of *T. normandavidsoni* is figured as *T. crispa* (Plate 30, Specimen 1). The availability of many more Philippine specimens, particularly from the Sogod, Cebu area, has made it easier to define this variable species, which has either been regarded by collectors as a small *T. crispa* form or an exceptionally thin *T. babylonia*. Shell pattern can be variable, from thin axial markings in the body whorl (see paratype 1) to rectangular spiral maculations (see paratype 5, Plate III).

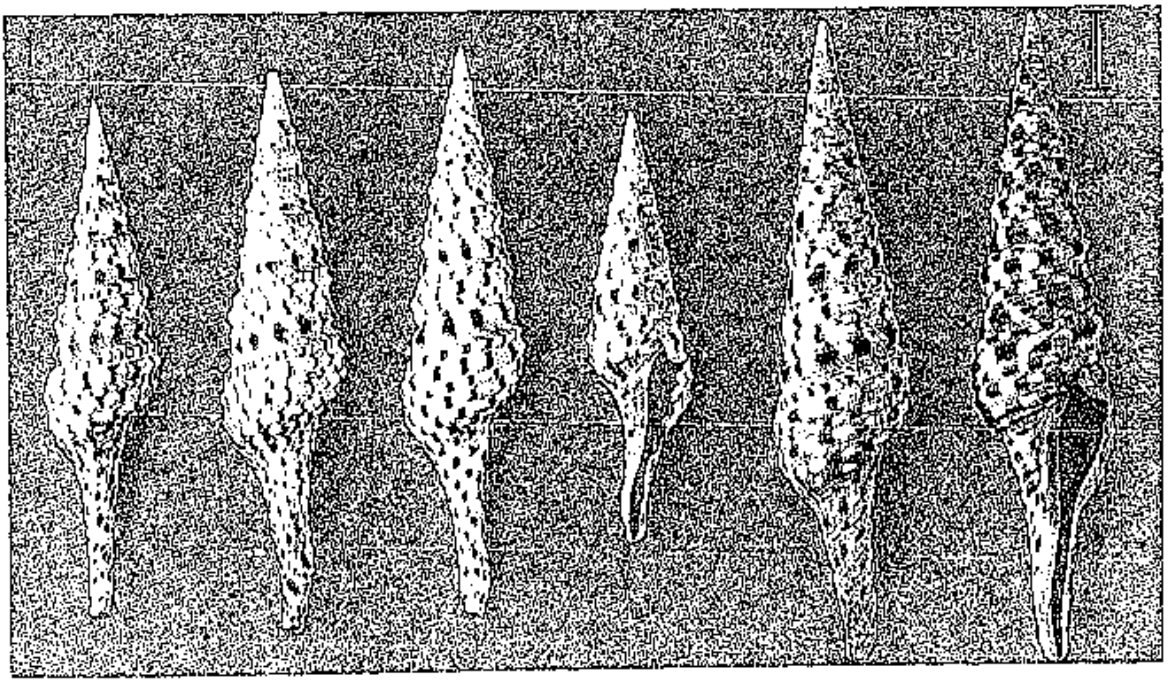
**Comparison.** *T. normandavidsoni* is very similar to, and has been confused with, *T. crispa*, *T. garronsii*, *T. dollyae* and the narrow "niniveh" form of *T. babylonia* (see below). *T. normandavidsoni* is generally smaller than either *T. crispa* or *T. dollyae*. The species is distinguished by the combination of the broad, strongly maculated subsutural cord complex and the sharply terraced sinus cord, making the zone between the subsutural cord and the sinus seem deeply excavated. In most Philippine specimens this region is colored uniformly olive brown or very light brown, often darker where the black maculations on the subsutural cord occur. In addition, most Philippine specimens have an olive brown color between cords at the base of the body whorl. However, some specimens from Olango Island, Cebu are lighter in color and smaller, while the few specimens from Luzon appear to be larger and darker, with the light brown zone greatly expanded in some specimens (Plate III, paratype 4).

The species is very variable in shell pattern (see Plate III). It is probably most closely related to *T. dollyae*, and like that species, in many Philippine specimens the maculations tend to have an axial rather than a spiral orientation. However, *T. normandavidsoni* is smaller in size with proportionally larger subsutural maculations.

The species range will extend at least to New Guinea and Fiji. Museum collections with specimens labeled *Turris crispa* from Fiji appear to be likely assignable to *T. normandavidsoni*.

**Nomenclature.** This species is named for Professor Norman Davidson, Caltech, Pasadena,





California, a wonderfully creative scientist and great mentor. It was the lucky break of my life to have become a graduate student in his laboratory.

**Types.** The holotype of *T. normandavidsoni* as well as most paratypes were collected from Sogod, Cebu by fishermen trawling in waters from 50 to 100 meters. Two paratypes were collected by hookah off Olango Island, Cebu, Philippines. The holotype and several paratypes are illustrated in Plate III. The holotype will be deposited in the Philippine National Museum, and paratypes will be deposited at the British Museum and the U.S. National Museum.

***Turris babylonia* (Linnaeus, 1758)**
(Plate 1, Specimen 5; Plate IV)

The type species of the genus, *T. babylonia*, was originally described by Linnaeus. This remains one of the more problematic species in terms of taxonomy. In the Philippines, at least three distinct forms have been assigned by most workers to *T. babylonia*. There is a thick, sturdy form with a heavy shell rather broad in outline. We will refer to this as the "babylon" form. Even within the typical form however, there is considerable variation, shown in Plate IV. The subsutural region and the base of the last whorl may be white, brownish-purplish or brownish-black. Plate IV illustrates an unusually melanistic Philippine specimen.

"Niniveh" form (*Turris babylonia*?) (Plate I, Specimen 6; Plate IV). A second form generally assigned to *T. babylonia*, which we refer to as the "niniveh" form, is proportionally narrower in outline and usually smaller than the typical *T. babylonia*. In addition, the shell is thinner and lighter. In the Philippines, specimens of the "niniveh" form have shells with a shiny surface, in contrast to the generally matte texture of the "babylon" form. The author has examined a large series of Philippine specimens and found that these two forms are always clearly separable.

Thus, based on Philippine specimens alone, the two forms would appear to be separable species. However, I have taken a conservative approach and have not designated the "niniveh" form as a separate species in this paper for two reasons. First, a casual examination of non-Philippine specimens reveals that the "niniveh" form tends to have a thicker and heavier shell in other localities, particularly the Moluccas. Thus, the possibility that intermediate forms will be found outside the Philippines between the "babylon" and "niniveh" forms needs to be thoroughly examined. I suspect that a wider geographic survey of the two forms will still prove them to be distinct, but this tentative judgement needs to be documented by a larger number of specimens from localities outside the Philippines. In addition, a number of names have been applied to the *babylonia* complex, and a careful examination of types is essential to determine which form each name refers to.

The comments of Powell in his monograph indicated that one potential name for the "niniveh" form might be *Turris raffrayi* (Tapparone-Canefri 1878). However, the summary statement in the original description of *Pleurotoma raffrayi* by Tapparone-Canefri is: "It has a strong resemblance to other Pleurotomas of the same group, specifically with *Pleurotoma spectabile* (= *Turris spectabilis*), but the canal is proportionally shorter, the shell larger and the spots have a different quality." The figure of the species which accompanied the original description shows a pattern of flammules on the body whorl (most similar to *T. nadaensis*, see below) rather than dots on the spiral cords. Together, the comparison to *T. spectabilis*, the comment that *P. raffrayi* has a shorter canal than *T. spectabilis* and the axial flammules shown in the original figure all make it unlikely that *P. raffrayi* is an appropriate name for this "niniveh" form.

In the Philippines the "babylon" and "niniveh" forms show characteristically different types of variants. In typical *T. babylonia*, there is a tendency for darker pigmentation in the subsutural and base regions. In some exceptional specimens, the entire shell is colored light brown or even black (see Plate IV). In the "niniveh" form, variants that have reduced maculations on the first few primary spirals of the body whorl, as well as color variants with lighter brown, instead of black maculations are found (Plate IV).

"Sulu Sea" form (*Turris babylonia*?) (Plate I, Specimen 7; Plate IV). There are a series of specimens from the Sulu Sea that are generally smaller with much thinner and more delicate shells

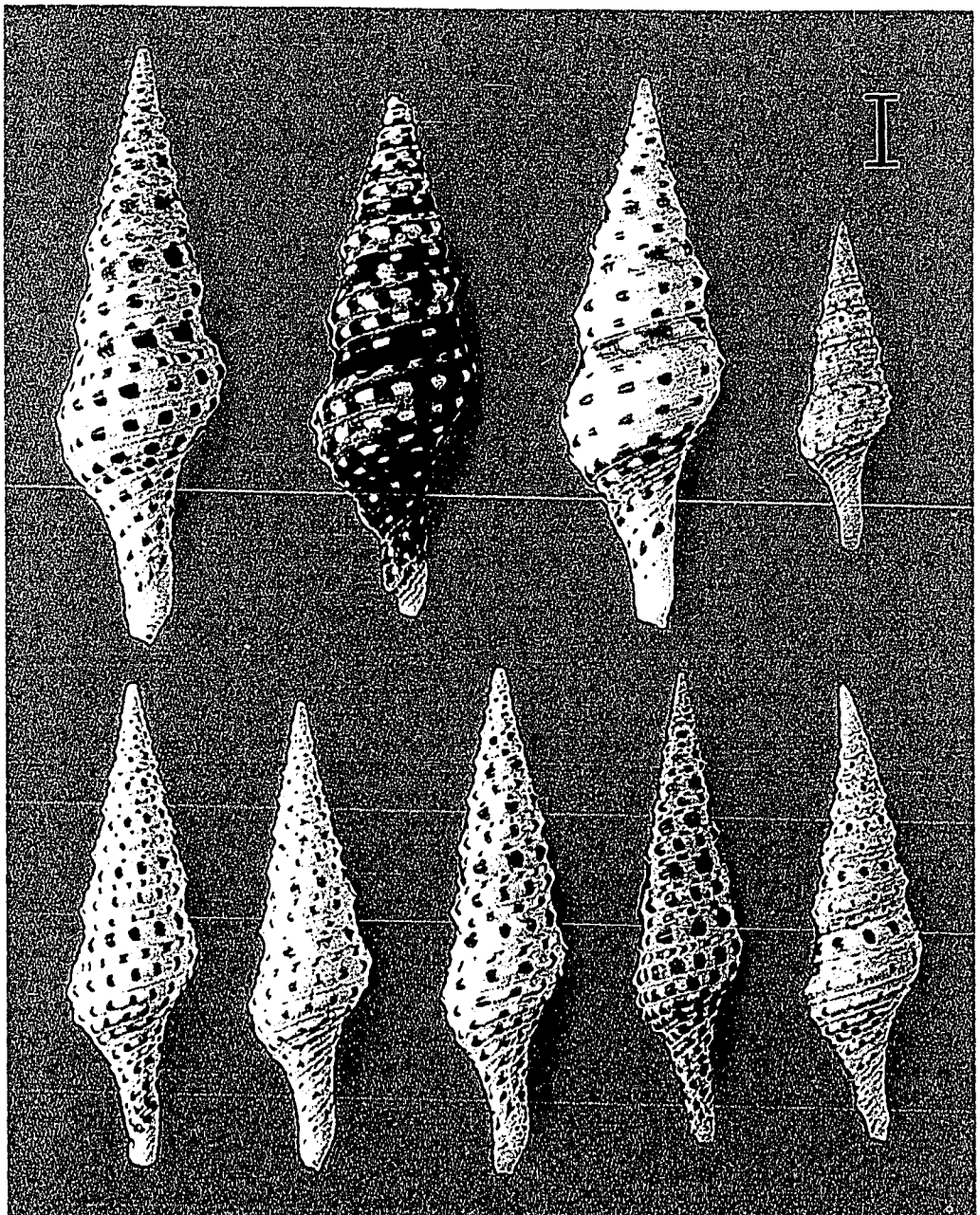


Plate IV. Three forms traditionally assigned to *Turris babylonia*. Top row, left three specimens are all the typical babylon form of *Turris babylonia*. The second specimen was collected by trawlers from off Cagayan de Oro, Northern Mindinao. The two other specimens are from unknown localities in the Philippines. Top row, rightmost, shows the "Sulu Sea form" (*T. babylonia* variety?). This form is noticeably thinner than typical *Turris babylonia*, or the ninuveh form. Bottom row, various specimens of the narrow "ninuveh form." Localities of specimens from top to bottom: Mindoro Island, Philippines; Dipolog, North Mindinao, Philippines; Olango, Cebu Island, Philippines; Cebu Island, Philippines; Sulu Sea, Philippines. Rightmost two specimens show extremes in coloration. The size bar is 1 cm.

(see Plate I, Specimen 7 and Plate IV). This is a variable form, most specimens lightly colored with ass distinct maculations (in some specimens coloration of maculations is the purplish-brown found in *Turris crispa*, instead of the black coloration of both forms assigned to *T. babylonia* above). Powell illustrated this form from Papua New Guinea, but some Philippine specimens are even lighter. The monograph on Australian gastropods by Wilson (Wilson et al. 1994) illustrates similar specimens from deep waters off West Australia, identified as *T. crispa* (see Plate 39, figs. 5A and B). If this is a distinct species, it is apparently present in West Australia while both "babylon" and "niniveh" forms have not been reported from there.

The "niniveh" form is easily confused with *T. normanodavisoni*. However, the region from the subsutural cord to the sinus cord is sharply terraced in *T. normanodavisoni*. In general, *T. normandavisoni* is narrower in outline than all three *babylonia* (?) forms described above.

*Turris pagasa*, new species
(Plate I, Specimen 4; Plate V)

**Description.** The shell is moderately large (61 to 98 mm), narrowly fusiform, with a turret-like spire and a moderately long siphonal canal. The protoconch is small with two smooth whorls. Adult shells have 13-16 teleoconch whorls. The spire angle is 25° and ratio of aperture to total length is 0.42-0.46. Spire whorls have a broad subsutural cord that comes to a sharp apex, maculated with dark brown blotches. The sinus cord is narrow, raised and square in outline with smaller dark brown maculations. A striking characteristic is the presence of numerous thin, raised, scaly axial lamellae between the subsutural and sinus cords extending to more anterior areas in some specimens. There is an unmaculated white gap between the sinus cord and larger peripheral cord. In the larger spire whorls, two smaller spiral cords are present below the larger peripheral cord, all with small squarish dark brown maculations. On the body whorl, 3 or 4 spiral cords are found at the periphery, followed by a gap where the future suture will form, with an additional 3 to 4 cords to the base and 3-4 primary cords on the canal with weaker secondary cords between them. All have fine squarish dark brown maculations more-or-less equal in size (in contrast, in the spire whorls the peripheral cord is noticeably stronger with larger maculations). The major cords on the body whorl have between 24-36 square maculations per spiral cord. The siphonal canal is noticeably curved, with a false umbilicus in larger specimens.

**Discussion.** This new form was unknown in Philippine material until recently. The shell is superficially similar to *T. crispa* and *T. babylonia* but it is probably most closely related to *T. crispa yeddoensis* from Japanese waters and *T. crispa intricata* from Hawaii. However, since it occurs in the same localities as *T. crispa crispa*, it cannot be considered a geographic subspecies of *T. crispa*, and is treated here as a distinct species.

*T. pagasa* has not previously been figured or recorded from the Philippines, and the few specimens known have been trawled or collected by gill nets in the central and southern Philippines.

**Comparison.** The shell of *T. pagasa* is much heavier than most Philippine *Turris*, reminiscent of dense white porcelain. The shell markings are finer and more square-shaped than in most *Turris* species. Since the sinus cord is about midway between the subsutural and peripheral cords, the noticeable white gap between the sinus and peripheral cords is characteristic of the species. In *Turris pagasa*, the black maculations on the sinus cord are set deeper than in most *Turris*, giving the sinus cord an irregular weakly gemmulate character.

*T. pagasa* differs from *T. crispa yeddoensis* in that the shell is thicker and has a more turreted outline, the maculations are generally less dense, particularly in the canal region where *T. pagasa* specimens tend to be pure white, and the canal is distinctly curved instead of straight as in *T. crispa yeddoensis*. The subsutural cords differ in structure and maculations. Many specimens of *T. crispa yeddoensis* tend to a grayish background cast; *T. pagasa* generally has a pure white background. Specimens of *T. pagasa* and two Japanese varieties, both assigned to *T. crispa yeddoensis* are compared in Plate V.

**Nomenclature.** The Filipino word "pagasa" means hope. This name seems appropriate for a species discovered in the closing days of the

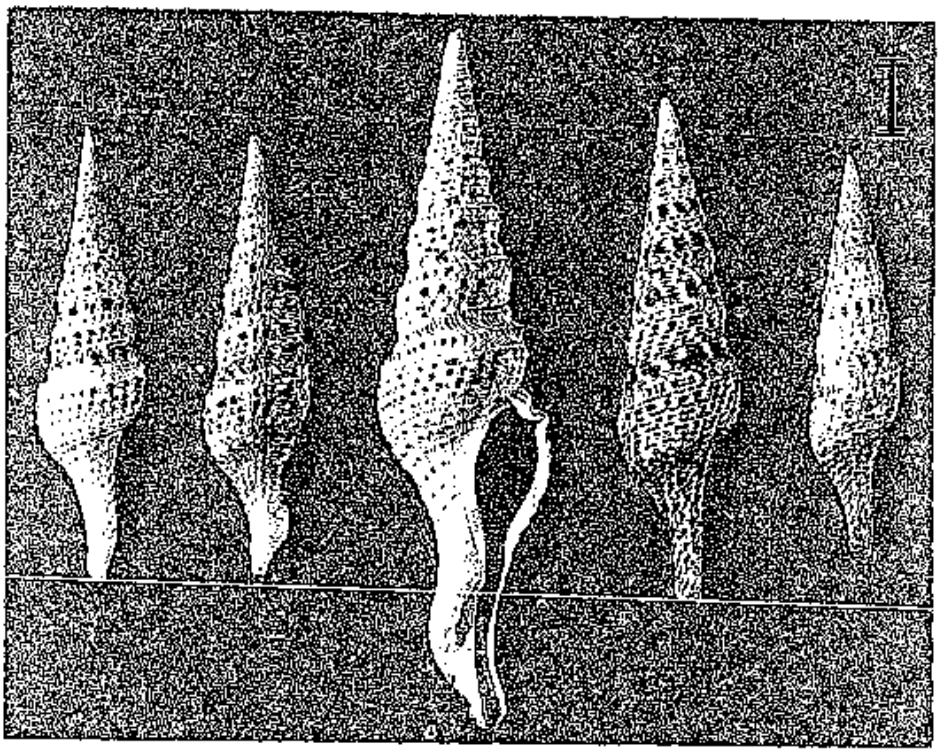


Plate V. *Turris pagasa*, new species, compared to Japanese specimens of *Turris crispa yeddoensis*. The three specimens on the left are *T. pagasa*. From left to right: holotype from Pamilacan Is., Bohol (gill nets 100 to 150 m), paratype #1, off Dipolog, Northern Mindanao, Philippines (collected by gill nets, 80 to 150 m), paratype #2 from Bogo, Cebu Island, Philippines (trawled, 50 to 100 m). The two specimens on the right are *Turris crispa yeddoensis*. The darker specimen is labeled "Tosa, Japan, 30 to 50 fathoms, March 1950, ex. M. Azuma collection." The rightmost specimen is labeled "Wada-cho, Wakayama Prefecture, Japan." The size bar is 1 cm.

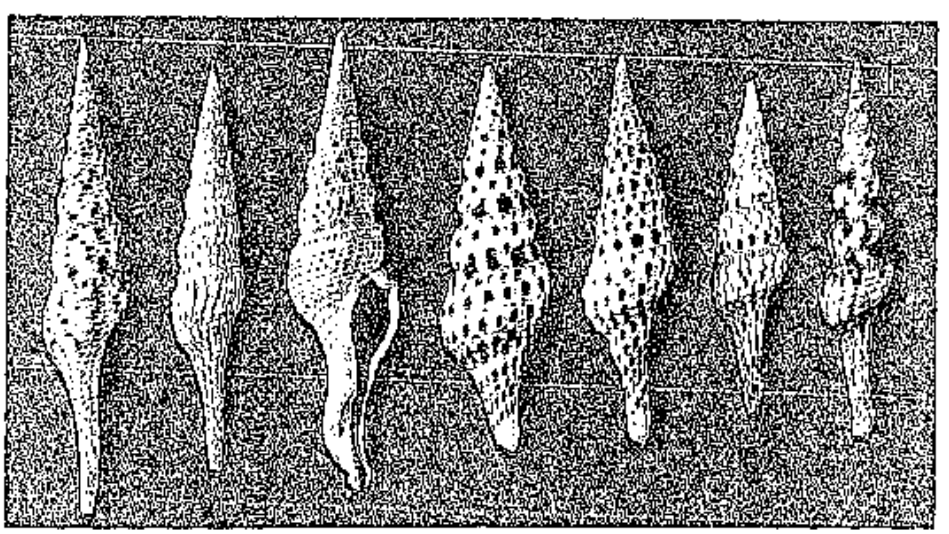


Plate VI. The *Turris babylonia*/*Turris crispa* complex. Specimens have been chosen that are approximately the same size, to emphasize differences in shell morphology between the seven species of Clade I with longer canals. (The comparative size of mature specimens was illustrated in Plate I.) From left to right: 1) *Turris crispa*, 2) *Turris dollyae*, 3) *Turris pagasa*, 4) *Turris babylonia*, 5) unusual form (*T. babylonia*?), 6) *Turris normandeaui*sp., 7) *Turris garoensis*. Thus, most specimens of *Turris crispa* are much larger than specimens of *Turris garoensis*, but a smaller-than-average specimen of the former and the largest specimen of the latter available are shown in this figure. The size bar is 1 cm.

millennium, representing the hope that in the new millennium, a new generation of Philippine scientists will devote themselves to the study and conservation of our unique and threatened fauna, both terrestrial and marine.

**Types.** The holotype will be deposited in the Philippine National Museum.

*Turris garnonsii* **(Reeve, 1843)**
(Plate I, Specimen 8 and Plate VI, rightmost specimen)

The "narrow form" of this species (Powell 1964) was previously known from just a few specimens in Philippine collections, but has now been available in fair quantities from both gill-net and hookah collecting. It is very distinctive and readily identified by its extremely narrow outline combined with a sharply constricted sutural region. In addition, the broad maculations of the subsutural region extend all the way from the suture to the sinus cord. Philippine specimens of *T. garnonsii* are not readily confused with any other *Turris* species. Both Powell (1964) and Springsteen and Leobrera (1986) illustrated typical Philippine specimens of this species. Specimens of *T. garnonsii* have been collected on Balicasag Island, Bohol by gill nets in 100-150 m and in the area around Olango Island between Cebu and Bohol by hookah at depths of about 50 m.

A few specimens of *T. garnonsii* with very short canals are present in old Philippine collections, but the collection locality has not been established. These are very similar to, but distinctly narrower than *T. totiphyllis* (see below).

**Species comparison**

The six species described above, and one of the distinct forms are illustrated in Plate VI. Typical specimens of each, selected to be comparable in size, are illustrated to make differences in shell proportion and pattern easier to compare. These are the species in Clade I with longer canals. The two remaining species have much shorter canals, more similar in proportion to *Xenoturris* (as noted, *T. garnonsii* also has a short-canal form). However, in all other aspects of their shell morphology, these clearly belong in the Clade I *Turris* group.

*Turris spectabilis* **(Reeve, 1843)**
(Plate I, Specimen 14; Plate VII)

*T. spectabilis* is a striking species, and is one of the two species in Clade I with a relatively short canal and long spire. The massive peripheral cord with its broad black and white maculations, and the brown coloration of each whorl posterior to the peripheral cord and in the base region are distinctive characteristics. Although there is considerable variation within the species in the coloration and distribution of brown and white areas, upon close scrutiny, the species can only be confused with *T. totiphyllis* (see below). The diagnostic differences are outlined in the discussion of that species. The original type in the Cuming collection was reported from Ticao Island but this could not be located in the British Museum (Powell 1964); other specimens in the Cuming collection figured by Reeve are labeled "Island of Cebu," which is still a locality where many Philippine specimens have been collected in recent years.

*Turris totiphyllis*, **new species**
(Plate I, Specimen 15; Plate VII)

**Description.** The shell is moderately large, 67 to 91 mm, with a high spire and relatively short siphonal canal. The spire angle is 24-26°, and ratio of aperture plus siphonal canal to total length is 0.38. Adult shell has 11-13 whorls. Each whorl has a subsutural cord region with unusually large black or blackish-brown maculations, followed by a continuous lighter brown zone, and a flat siphonal cord, with alternating blackish-brown or brown maculations, much reduced and almost white in some specimens. On the larger spiral whorls, in addition to the large, broad peripheral cord, two additional spiral cords, also maculated in black or brownish-black are visible. The body whorl has 4-5 spiral cords on a white background, and at the boundary with the siphonal canal is a uniformly colored black or brownish-black zone with 2-4 spiral cords. The siphonal canal is white or much lighter brown with three to four primary cords, and weaker cords interspersed.

**Discussion.** Shells of *T. totiphyllis* have been confused with *T. spectabilis*; both have a generally

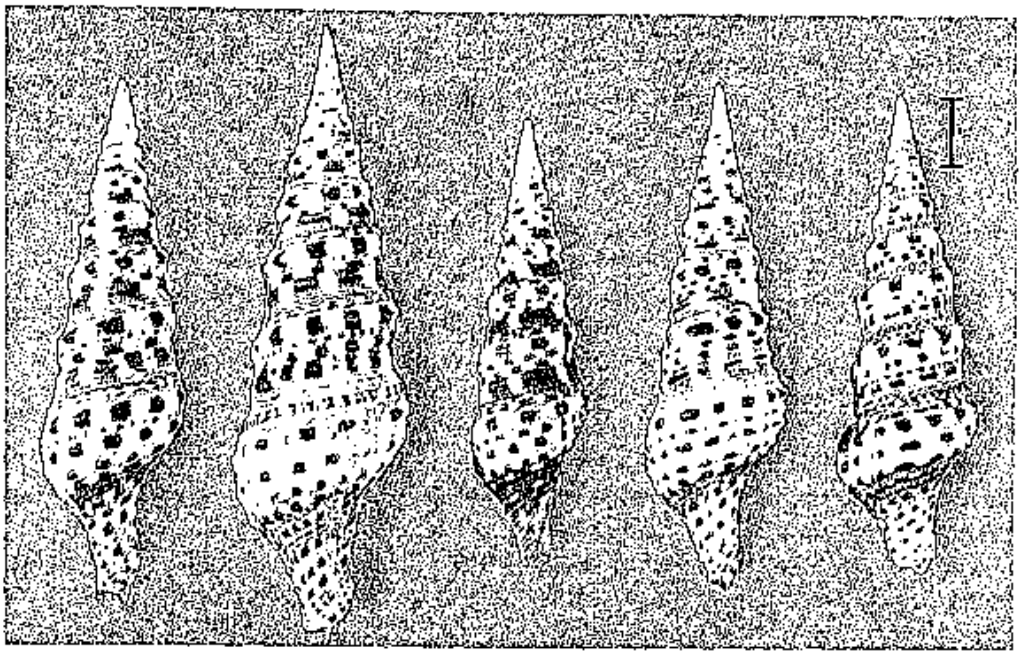


**Plate VII.** *Turris foliphyllis*, new species, compared to *Turris spectabilis*. All of the specimens shown are *Turris foliphyllis*, except the specimen on the extreme right. From left to right, holotype (collected between Olango Island, Cebu and northern Bohol, by hookah 20 to 60 m); paratype #1 (same locality); paratype #2 (Balicasag, Bohol Island, collected by gill nets 50 to 150 m). The two rightmost specimens are *Turris foliphyllis* and *Turris spectabilis*, both collected between Olango Island, Cebu and northern Bohol. This pair illustrates the differences in the slit region of these two species: note the two threads that border the slit in *Turris spectabilis*, and the single sinus rib in *Turris foliphyllis* (see text). The size bar is 1 cm.

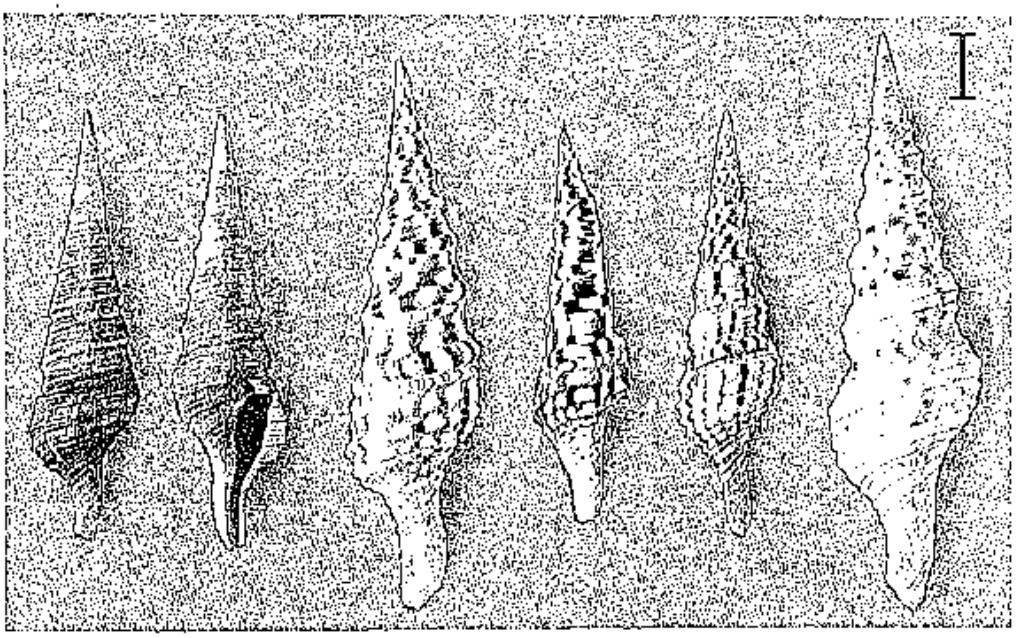


**Plate VIII.** Clade II *Turris* species. Left to right: *Turris cryptorhaphe* (Marinduque Island, Philippines), *Turris cryptorhaphe* (Olango Island, Cebu, collected by hookah 20 to 60 m), *Turris undosa* (Balicasag, Bohol Island, Philippines, gill nets 50 to 150 m), *Turris undosa* (Olango Island, Cebu, hookah between 20 to 60 m); *Turris nadaensis* (Olango Island, Cebu, hookah 20 to 60 m); *Turris nadaensis* (Sogod Bay, Cebu Island, trawled 50 to 100 m). The size bar is 1 cm.

elongated spire, short canal and share similar shell patterns. However, although easily separable from most Philippine specimens of *T. garnonsii* (the latter much more slender with a proportionately longer canal), *T. totiphyllis* is most similar to the *T. garnonsii* variety with a short canal.

**Comparison.** The shell pattern of *T. totiphyllis* generally resembles *T. babylonia* and *T. spectabilis* in that the primary cords have black maculations on a generally white (sometimes grayish) background. The body whorl has two brown-colored zones, one between the suture and the sinus cord, and the second at the base (i.e., the border between the body whorl and the canal. The color pattern of *T. spectabilis* is similarly organized (a pattern also found in certain morphological variants of *T. babylonia*). Most specimens of *T. babylonia* do not have these prominent dark brown areas characteristic of *T. spectabilis* and *T. totiphyllis* and have a proportionally longer and very straight canal, and a single smooth subsutural cord. *T. spectabilis* and *T. totiphyllis* are easily confused, but several differences are quite diagnostic. The sinus cord of *T. spectabilis* is typically not congruent with the posterior sinus, which is unusually wide for *Turris* species. In the body whorl of the mature *T. spectabilis*, a thin, raised black and white thread is aligned with the posterior edge of the sinus, with a second parallel thread slightly anterior, and not overlapping with the sinus. These threads define where the sinus is located, and are both posterior to the major peripheral cord. The presence of the two threads between the subsutural cord and the primary peripheral cord is highly characteristic of the mature body whorl of Philippine specimens of *Turris spectabilis*. In *T. totiphyllis*, the sinus cord is typically steeply terraced from the subsutural area. A second diagnostic difference is that in *T. spectabilis*, the subsutural cord may be reduced or minor, or moderately expanded (two cords can be fused); this is a variable characteristic. In *T. totiphyllis*, the subsutural cord area is massive and broadly maculated even in early spire whorls. The proportion of brown banding and white color on the whorls is also different; the brown zones are much more dominant in *T. spectabilis* than in *T. totiphyllis*, where in the subsutural area in particular, the brown zone is sometimes discontinuous (as in *T. garnonsii*). The new species can be distinguished from the short-canal variety of *T. garnonsii* in its much broader outline, and the presence of a continuous brown zone between the maculations in the subsutural area and the sinus cord.

**Nomenclature.** This new species is named for Toti and Phyllis Zaballero, for all the good times together.

**Types.** The holotype will be deposited in the Philippine National Museum, and paratypes have been deposited at the British Museum of Natural History and the U.S. National Museum. Other paratypes are in the Olivera collection. The holotype and most paratypes were collected in the central Philippines in the Cebu-Bohol area. One paratype is a specimen from an old collection, collected before 1970 from an unspecified Philippine locality. Recently collected specimens were found by hookah divers at night between 30-80 meters, and by gill nets in even deeper water.

### Clade II: The Purple-mouthed *Turris*

The Clade II species have certain common features, most characteristic is the purplish coloration of the aperture, often extending to the canal. In addition, the canal is relatively short. Finally, when present, the axial markings are qualitatively different from the spiral cord maculations of Clade I species, in that they are not primarily located on spiral cords but are continuous broad streaks. At least three Philippine species are included in this group, *T. cryptorrhaphe*, *T. undosa* and *T. nadaensis*. More deep water material may reveal that at least one form tentatively assigned here to *T. nadaensis* may be a distinct species. This clade may be widespread in Indian Ocean localities as well, since the rare *T. tanyspira* (Kilburn, 1975) from Mozambique is almost certainly a member of this species clade.

***Turris cryptorrhaphe* (Sowerby, 1825)**
(Plate I, Specimen 13; Plate VII)

*T. cryptorrhaphe* is a very distinctive species; the uniform blackish-brown color, lack of maculations and purplish aperture distinguish this form from any other *Turris* species. One characteristic of many *T. cryptorrhaphe* specimens is the presence of a darker

thread at the apex of several primary cords. *T. cryptorrhaphe* was previously rare, but it is now collected in fair numbers in the Cebu-Bohol area in ~30-60 m by hookah. Most specimens from this locality have multiple growth scars.

Superficially, *T. cryptorrhaphe* seems very distinctive from *T. undosa* and *T. nadaensis*, since the two latter species both have dark brown maculations. However, the three species may be more closely related than the shell patterns would suggest. The characteristic presence of a dark brown thread at the apex of spiral cords in specimens of *T. cryptorrhaphe* is also found in the spiral cords of the body whorl of many specimens of *T. nadaensis* and more rarely in *T. undosa*. This feature has not been observed in other *Turris* species.

***Turris undosa* (Lamarck, 1816)**
(Plate I, Specimen 12; Plate VIII)

*T. undosa* is a distinctive species closely similar to *T. nadaensis*. The two species have been confused by many authors. However, *T. undosa* can be distinguished by its prominent, massive subsutural cord. As a result, this species does not appear at all constricted in the sutural region giving the spire a straight outline in contrast to the more rounded whorls of *T. nadaensis*. Powell (1964) figured *T. undosa* in Plate 181, Specimen 20 of his 1964 monograph, but in Plate 25, figs. 9 and 10, the species illustrated as *T. undosa* are in fact *T. nadaensis*. Springsteen and Leobrera (1986) illustrate the two species correctly. *T. undosa* is relatively constant in its shell morphology and pattern, in contrast to *T. nadaensis*, which is much more variable.

***Turris nadaensis* (Azuma, 1973)**
(Plate I, Specimen 10; Plate VIII)

*T. nadaensis*, though relatively recently recognized, appears to be relatively widespread in the central and southern Philippines. However, it is variable. The majority of specimens collected to date are from the Cebu-Bohol area and there is considerable variation in how light or dark the maculations are (see Plate I, specimens 10a,b,c and Plate VIII).

*T. nadaensis* can be confused with *T. undosa* because both have a purple aperture and brownish-black maculations. In general, the dark markings on *T. nadaensis* are narrower and less prominent than those on *T. undosa*, extending from the peripheral cord to the suture. As is discussed under *T. undosa* above, one diagnostic difference is that the massive, raised subsutural cord region of *T. undosa* is absent in *T. nadaensis*, giving the latter much more rounded whorls. Specimens of *T. undosa* are uniformly maculated in all whorls, but in *T. nadaensis*, there is a tendency for the last whorl in mature specimens to be much lighter with more sparse maculations (see Plate I, Specimen 10B and Plate VIII, rightmost specimen). There is also considerable variation from locality to locality in how dark specimens are. The range of variations is shown in Plate I, specimens 10a, b, c and in Plate VI. The violet color of the canal and the aperture also varies considerably from one specimen to another. In immature specimens, a sharply delineated region is either light purplish or dark violet from the base all through the siphonal canal. In mature specimens, this purplish region can be much reduced and in some specimens is only obvious when seen from the aperture. In contrast, in *T. undosa*, the canal region is always purple, even in mature specimens. Mature specimens of *T. nadaensis* often have a false umbilicus. As noted above, many specimens have a dark thread at the apex of some of the spiral cords, particularly towards the base (Plate VIII, specimen at right) but this is not a consistent characteristic.

One exceptional specimen, collected in Balut Island, is quite distinct from typical Philippine *T. nadaensis* specimens in its broader outline and thicker canal (Plate I, Specimen 10b). The maculations on the last whorl are absent, though earlier whorls seem to have a similar pattern to typical *T. nadaensis*. The spiral cords are obsolete in the specimens illustrated, but dark brown threads are present. The Balut Island specimen is the closest Philippine example to an unusual specimen of *T. nadaensis* illustrated by Wilson (1994) from Queensland, Australia (Plate 39, Specimen 15) which was identified as *T. undosa*. The illustration of Tapparone-Canefri (Tapparone-Canefri 1878) of *T. raffrayi*, which was collected in New Guinea, seems

closer to the Australian specimen of *T. nadaensis* than to any other *Turris* species known to the author. If this assignment were indeed the correct one, and could be definitively confirmed, then the name *T. raffrayi* would have priority over *T. nadaensis*.

"Angular" form (*Turris nadaensis* variety?) (Plate I, Specimen 11). There is another distinctive variety collected in the Philippines known from a single specimen which is tentatively assigned to *T. nadaensis*. More specimens may show that this is a different species (see Plate I, Specimen 11). This form has a greater similarity to *T. undosa* in shell pattern than other forms of *T. nadaensis*, but does not have the massive subsutural cord. The whorls are much more angular than *T. nadaensis* and the peripheral cord is proportionally larger and sharper in outline than in specimens of *T. undosa* and *T. nadaensis*. A similar specimen was figured by Hinton (1972) from Papua New Guinea as *T. undosa* (Plate 30, Specimen 6), suggesting that this form may have a widespread distribution in the Indo-Pacific, and is not a localized variant of *T. nadaensis*. However, more specimens are needed for the taxonomic status of this form to be clarified.

**Clade III: the *Annulaturris* clade**

***Turris annulata* (Reeve, 1843)**
(Plate I, Specimen 9; Plate X)

So far this species is rare with very few Philippine specimens known. No specimens were illustrated by Springsteen and Leobrera (1986) in their comprehensive illustration of Philippine turrids. Philippine specimens are similar to the specimen figured as *T. annulata* by Powell (1964) from Tosa, Japan. The only other recent figure of any specimen assigned to this species is found in the catalog of the Ninomiya collection (Horikoshi, 1989) where a specimen from Phuket Island, Thailand is illustrated as *T. annulata* (Plate 32, Figure 1). The latter conforms to what Powell (1964) refers to as the "typical form," and it clearly differs in a number of respects from Philippine and Japanese specimens. Powell (1964) suggested that the two forms might be separable at the subspecific level.

*T. annulata* appears from shell morphology to be highly divergent from the two clades described above. One notable feature of the two specimens examined is that although one has relatively smooth cords throughout, in the specimen figured the sinus cord is weakly gemmulate. Furthermore, Powell indicated that the sinus cord was not the peripheral cord, but this is much more ambiguous in Philippine specimens. Indeed, in the specimen figured, the sinus cord appears to be peripheral, a feature which makes assignment to the genus *Turris* even more uncertain. The apparent gemmulate nature of the sinus cord was figured by Tyron (1884), but not present in the specimens examined by Powell (1964); this may be a variable feature of the species.

**The Genus *Turris*: Monophyletic or Polyphyletic?**

In the genus *Turris*, as defined by Powell (1964, 1967), the fifteen distinct forms found in Philippine waters appear to fall naturally into three clades. In this section, we address whether the three clades form a natural taxonomic group at the generic level. A consideration of the shell morphology is suggestive that this might not be the case. The only known Philippine species in Clade III, the broader form of *Turris annulata*, seems greatly diverged from the species in the other two clades. In proposing the subgenus *Annulaturris*, Powell noted that the radular morphology of *Turris amicta*, the other species assigned to the subgenus, was different from that of other species in the genus; most *Turris* species do not have the broad central tooth reported to be present in *T. amicta*. This was apparently the major rationale for separating the *T. annulata*/*T. amicta* clade into a subgenus. The radula of *T. annulata* has not yet been described.

In this author's best judgment, *T. annulata* is probably only distantly related to other Philippine species included in the genus *Turris*. The tendency towards a weakly gemmulate sinus cord, and the fact that the sinus and peripheral cord are essentially equivalent in size in Philippine specimens (instead of being distinctly smaller and displaced at a position clearly posterior to the periphery of each whorl) are characteristics consistent with this suggestion. In the following sections, we present possible links between some specific *Gemmula*/*Lophiotoma* species and the

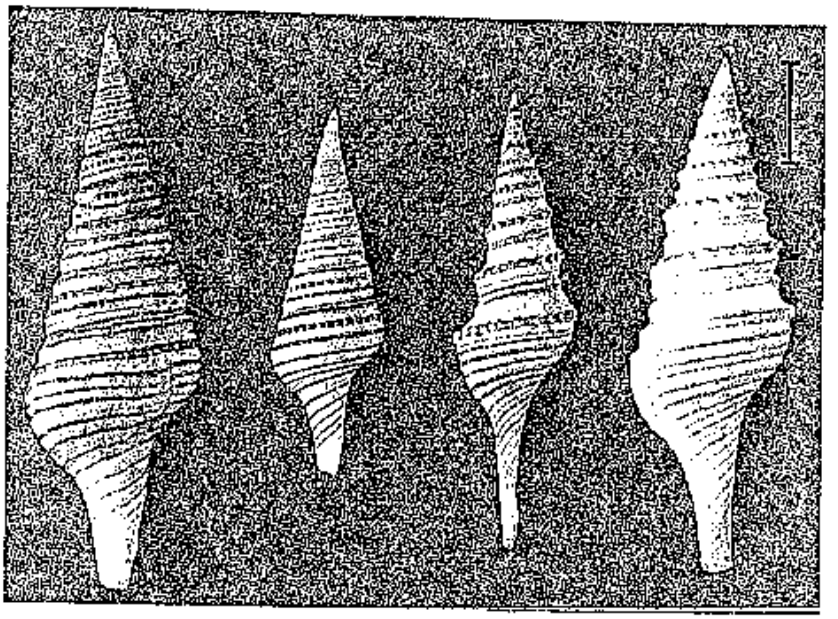


Plate IX. *Gemmula lululimi*, new species. The two specimens on the left are *Gemmula lululimi*, which are compared to *Gemmula speciosa*, the two specimens on the right. Far left, holotype, Balut Island, southern Philippines (gill nets, 50 to 150 m); second from left, paratype 1, Pamilacan Is., off Panglao, Bohol, Philippines (gill nets, 50 to 150 m). Note the generally similar organization of the spiral ribs, and the striking difference in the shell outline of the two species. The size bar is 1 cm.

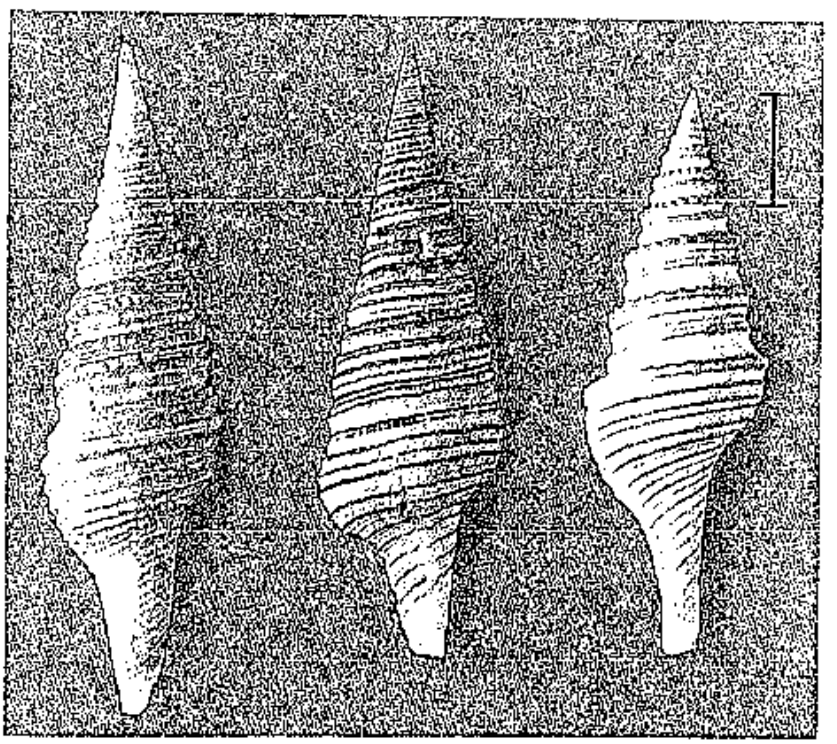


Plate X. A comparison of *Turris annulata* (far left), *Gemmula lululimi* (middle) and *Gemmula speciosa* (right). Note the similar shell outline of *Turris annulata* and *Gemmula lululimi* - in both cases, the sinus cord is noticeably gemmulate (while other spiral cords are not), a feature particularly obvious in the earlier whorls of the spire. The size bar is 1 cm.

three *Turris* species clades. Clearly the taxonomy of other Turrinae will need to be more carefully examined by a variety of criteria before an informed decision with regard to the correct taxonomic assignment of *T. annulata* and other clades in *Turris* can be made.

From shell morphology, the Clades I and II *Turris* species appear more closely related to each other than to *T. annulata*. It is possible that all species in the two clades evolved from a common ancestor sometime before the Pliocene (no fossils related to Clades I and II species appear earlier than the Pliocene - from Powell's 1964 comments, the Miocene fossils assigned to *Turris* from Australia are likely related to *T. annulata*). In contrast, other Turrinae (such as *Gemmula*) have a robust fossil record much further back in the Tertiary. The biogeography is also consistent with a relatively recent origin for Clade I and II species. These groups are strictly Indo-Pacific, with the greatest density of species present in the Indo-Pacific arc from the Philippines to New Guinea. In contrast, there are *Gemmula* species in the Atlantic and Eastern Pacific, where *Turris* is absent.

What are the closest relatives of Clade I and Clade II *Turris* species? There are two hypotheses that can be considered *a priori*. The two clades (I and II) may have diverged from all other Turrinae, an implication of including them in the same genus. However, it is possible that even after excluding the Clade III species from *Turris*, the group may still prove not to be monophyletic.

We compare species from other groups in Turrinae with Clade I and Clade II *Turris* species. These comparisons lead to a useful (and experimentally testable) question: are Clade I and Clade II *Turris* species more closely related to each other than to any other Turrinae? If the answer were affirmative, then *Turris* (with *Annulaturris* removed) would be a monophyletic group, and assignment of both species clades to the genus *Turris* would accurately reflect the evolutionary history of the group. On the other hand, based on shell morphology alone, we present one specific alternative possibility: that Clade I species may be more closely related to certain *Lophiotoma* spp., and Clade II species to one branch of the genus *Gemmula* than they are to each other. If this were borne out by further analysis, it would suggest that the present classification of the Turrinae does not accurately reflect true phylogenetic relationships. It is useful to frame these alternatives since in principle, future molecular, anatomical and biochemical work could provide data relevant to these issues, if such work were focused on the appropriate species in the Turrinae.

### Specific evolutionary hypotheses

The purpose of this section is to consider the broader phylogeny of species in the genus *Turris*. As indicated in the Discussion above, the three clades, comprising all species in the genus *Turris* (as defined by Powell) may or may not comprise a monophyletic group. Here, alternative hypotheses, each with its own set of experimental predications, are developed. These hypotheses are based on shell morphology alone, since soft tissues were not generally available for analysis. The specific alternatives based on shell characters are intended to provide an incentive for carrying out further studies on the key species discussed.

We start with two general themes: the first, that the three clades presently assigned to *Turris* arose out of some *Gemmula*/*Lophiotoma*/*Polystira*-like ancestor(s), seems a reasonable assumption on the basis of the fossil record, biogeography and shell morphology. A second assumption is that a morphological transformation, which we will call the G-T transformation (for *Gemmula*-*Turris*), played a role in the morphological conversion of shells of *Turris* species from their ancestral form. We present some compelling evidence that such a morphological transformation can occur, perhaps relatively rapidly.

The basis for postulating the G-T transformation is the discovery of an unusual species, which is problematic to assign at the generic level because of its unique characteristics. This taxon, recently collected in deep waters in the central and southern Philippines is closely allied to *Gemmula speciosa*, a well-known Indo-Pacific species, in every respect except one. Because of the position of the slit and the sinus cord, this form would not seem to be typical of species in the genus *Gemmula*, but could just as easily be assigned to the genus *Turris*. Nevertheless,

the gemmulate nature of the sinus cord and all other aspects of shell morphology make this a *Gemmula*. The morphological change that it has undergone when compared to *G. speciosa* is the prototypic example of a G-T transformation.

### *Gemmula lulutimi*, new species
(Plates IX and X)

**Description.** The shell is 37-58 mm with 15-17 whorls. Spire angle is 25-27°. The spire is high cone-shaped with a relatively sharp siphonal canal and the ratio of aperture and canal to total length is 0.39. Each spire whorl has three major spiral cords visible. The sinus cord is placed above the major peripheral cord and is gemmulate but continuously colored with a golden-brown as are all spiral cords. The strong cord above the sinus cord borders a region which is perpendicular to the axis of the spire and which has a different texture from the rest of the shell, looking oily and colored light brown in some of the whorls. In addition to the three primary spiral cords visible on the spire whorls, four additional primary cords are present on the body whorl and five additional cords on the thicker section of the canal. The very tip of the canal is cordless and colored white. The species is entirely unique in the genus in that the sinus cord is neither peripheral nor prominently raised.

**Discussion.** This species has the same golden spiral cords and whitish background as *G. speciosa*. The number of spiral cords, the continuous coloration of the cords and the presence of gemmules on the sinus cord are all characteristics the two species have in common (see Plate IX). However, they have a dramatically different shell morphology. While the sinus cord is highly prominent on the periphery in *T. speciosa*, it has been transformed into a cord that is much less prominent and located posterior to the periphery in *G. lulutimi*. This makes the shell morphology strikingly different. In effect, the shell of *G. lulutimi* has changed from that of a typical *Gemmula* to one that is much more similar to *T. annulata* (see Plate X).

The shell morphology of *G. lulutimi* is most unusual, and as pointed out above, the position of the sinus cord could have justified assignment to *Turris*. However, the striking similarity to *G. speciosa* is the overriding consideration in concluding that the species is a *Gemmula*. Not only are the nature of the spiral cords similar, but the texture of the white background has an unusual satin-like quality in both species, all suggesting a close relationship. The arrangement of the spiral cords varies between the two specimens of *G. lulutimi* within the range observed for *G. speciosa*. Thus both *G. lulutimi* and *T. annulata* are unusual. Given the generic 'rules' specified in Powell's monographs, they are rule-breakers that do not properly fit in either *Gemmula* or *Turris*. In effect, *T. annulata* and *G. lulutimi* both have shell characters somewhat intermediate between *Gemmula* and *Turris*.

**Types.** The holotype was collected by gill nets from Balut Island (100-150 m). The only other known specimen of *G. lulutimi* is a smaller specimen collected by gill nets from Pamilacan Island, Bohol, Philippines. The holotype and paratype are figured in Plate IX and compared to *G. speciosa*.

**Nomenclature.** This species is named for my wife, Lourdes (Lulu) Tan Olivera.

## A hypothesis for the origin of Clade I and Clade III *Turris* species

The G-T transformation described above for *G. speciosa* and *G. lulutimi* strongly suggests that both species were derived from a common ancestor and that the latter had undergone the G-T transformation while *Gemmula speciosa* did not. It seems reasonable to assume that the standard *Gemmula*-like state of *G. speciosa* was ancestral, given the much more ancient fossil record of *Gemmula*-like forms). We suggest that a similar transformation may have given rise to Clade I *Turris* species.

Two potential species to illustrate this hypothesis are shown in Plate XI. We suggest that *T. indica* and *T. pagasa* may have come from a common lineage and *T. pagasa* (or an ancestral species) had undergone a G-T transformation, while for *T. indica* such a morphological transformation did not occur. Thus, this is very similar to the *G. speciosa*/*G. lulutimi* pair (although not quite as close). It is interesting to note that in both species, there is some variation in the relative strength of the sinus cord versus the next posterior cord (which is the

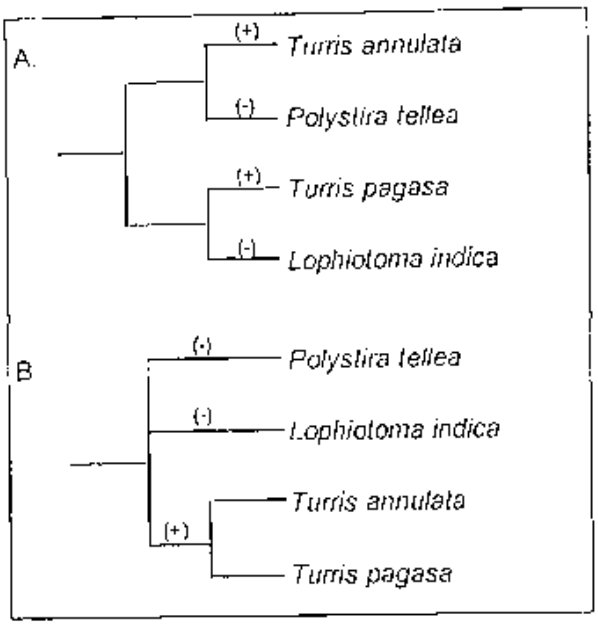



Figure 1. Two hypothetical alternative trees for Clade I and Clade II *Turris* species and other Turrinae. The tree at the bottom shows a scheme consistent with *Turris* being a monophyletic group, and Clade I species (such as *Turris pagasa*) sharing a common ancestor with *Turris annulata* and all other *Turris* species. On top is one specific alternative hypothesis for a polyphyletic origin of species presently assigned to the genus *Turris*. Clade I *Turris* species such as *Turris pagasa* are postulated to be more closely related to other Turrinae such as *Lophiotoma indica* than to *Turris annulata*. (In this specific hypothesis, *Turris annulata* is *Polystira*-like. Other trees consistent with a polyphyletic origin for species in *Turris* are feasible.) The (+) and (-) indicate whether the species is hypothesized to have undergone a G-T transformation (see text since the last common ancestral species.

peripheral cord in *T. pagasa*). In the two specimens of *L. indica* shown in Plate XI, the peripheral cord is definitely the major cord in the smaller specimen, but the next cord anterior to the sinus is relatively stronger in the larger specimen, a characteristic leaning towards *Turris*. We note that the structure of the cords is generally similar in the two species. Thus, a reasonable hypothesis for the origin of Clade I *Turris* species is that an ancestral form, from which *L. indica* may also be derived, had undergone a G-T transformation to give rise to an ancestral Clade I *Turris* species, possibly similar to *T. pagasa*. This scenario is really derived from the discovery of the *G. speciosa*/*G. lulutimi* pair, which indicated that such a morphological transformation might occur with little change in other aspects of shell morphology.

If this hypothesis were true, and if *T. annulata* were indeed inappropriately grouped with the majority of *T.* species, then anatomical and molecular studies should show that there is a greater similarity between *L. indica* and Clade I *Turris* species such as *T. pagasa*, than between *T. annulata* and Clade I *Turris* species. This is a strong experimental prediction which is testable as shown in Specimen 1. In contrast, the present phylogeny requires that this experimental prediction be wrong.

If the prediction above is borne out, then the true affinities of *T. annulata* would need to be explored. In the opinion of the author, the shell structure seems more like some species of the American genus *Polystira* (in particular forms like *P. tellea*), and *T. annulata* may be derived from an ancestor like the fossil *Polylira* (see Figure 1).

## Phylogeny of Clade I and Clade II *Turris* species: two alternatives

A similar set of alternatives can also be laid out for Clade I and Clade II *Turris* species. These could all be a monophyletic group, with a common ancestor that diverged from other Turrinae. However, one plausible alternative is presented here.

This is based on the implicit assumption that the purple colored canal and aperture region is an important, conserved genetic character (which may or may not be true). Thus, if we examine other Turrinae for this characteristic, there is a form which was named *Gemmula concinna* (Dunker, 1856) which shows the unusual purplish color so characteristic of Clade II *Turris* species. Thus, an evolutionary scenario in which an ancestor that evolved the purplish coloration in the aperture/canal region underwent a G-T transformation (to yield Clade II *Turris* species such as *T. cryptorrhaphe*), while another descendant lineage did not undergo the morphological transformation, giving rise to the non-Turris *G. concinna*. If this were the case, Clade I and Clade II *Turris* species may have arisen independently, both by G-T transformations of *Gemmula*/*Lophiotoma*-like ancestors, but from different lineages. It will be of interest to assess these alternative explanations using a combination of anatomical examination of soft tissues of the relevant

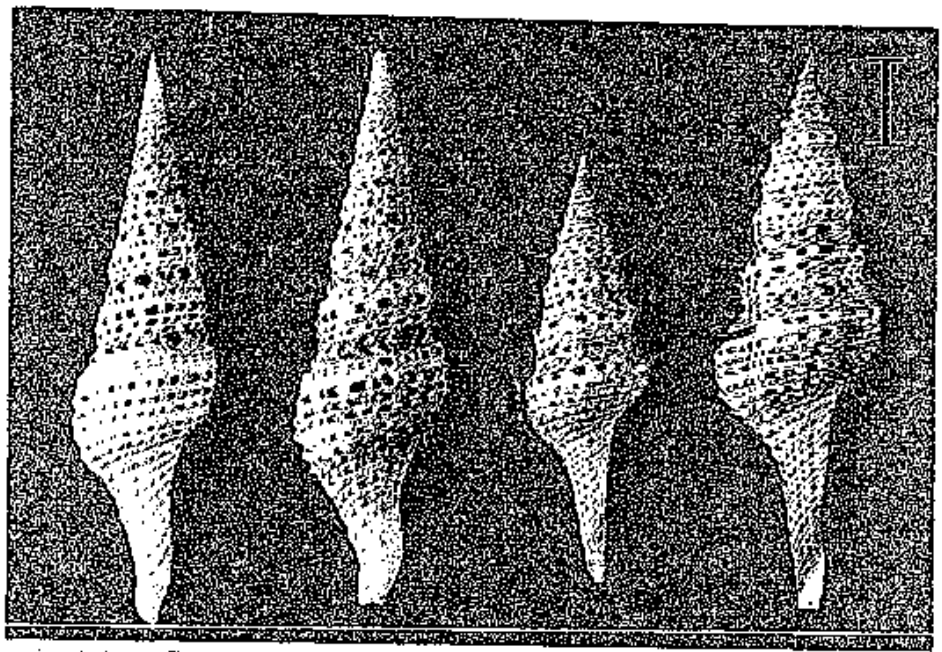


Plate XI. A comparison between *Turris pagasa* (left two specimens) and *Lophiotoma indica* (right two specimens). Note the generally similar maculations on the ribs of both shells, but the very different shape. As is discussed in the text, a G-T transformation would convert *Lophiotoma indica* into a form that looked similar to *Turris pagasa*. (It should be noted that the particular specimens of *Lophiotoma indica* shown in the figure are somewhat atypical, and some workers have assigned this form to *Lophiotoma acuta* instead of *Lophiotoma indica*.) The size bar is 1 cm.

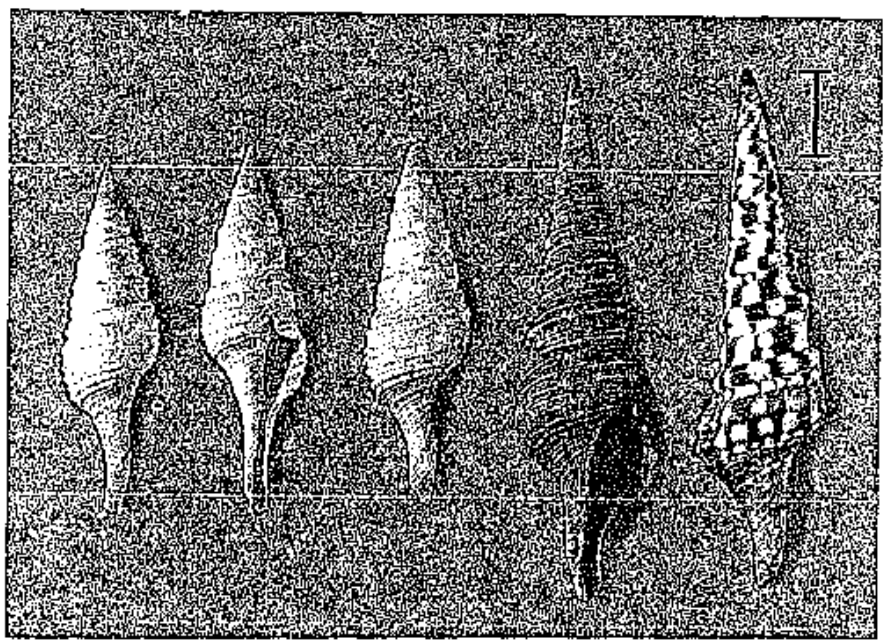


Plate XII. *Gemmula lisajoni*, renamed homony. The three specimens on the left are *Gemmula lisajoni*, followed by *Turris cryptorhaphe* (second from right) and *Turris undosa* (far right). The characteristic purplish color of the canal and aperture is compared between these three forms. The three specimens of *Gemmula lisajoni*, numbered left to right specimens 1, 2 and 3, are all from Mactan Island, Cebu Philippines, collected by gill nets (50 to 150 m). The size bar is 1 cm.

species, as well as by collecting the appropriate molecular data. We believe that this type of phylogenetic prediction is useful since the differentiating molecular experiments can be carried out given modern molecular methodology, and definitive judgements made between alternative hypotheses of the types proposed above.

The *Gemmula* with the purple canal shown in Plate XII (where it is compared to Clade II *Turris* species) has long been known by the name *G. concinna*. It has also been recognized that this name is preoccupied, which both Powell (1964) and Springsteen and Leobrera (1986) commented on. As Powell stated, "Nothing exactly matching Dunker's *concinna* is known to the writer so this preoccupied species is left unnamed until it is rediscovered from a definite locality. A specimen from the Andaman Islands in the United States National Museum, attributed to *concinna* lacks the overall brown and violet-stained anterior end and is in fact inseparable from the South African *gilchristi*." A definite locality for the species was rediscovered when specimens were found using gill nets off Mactan Island in the Philippines, and one such specimen was in fact figured by Springsteen and Leobrera (1986) (who noted that their assignment of *G. concinna* to this form was not valid).

Since this very distinctive species is apparently without a valid name, it is illustrated and named here.

*Gemmula lisajoni*, new name
(Plate XII)

**Discussion.** This species is unmistakable, since it is the only known turrid with a typical gemmulate sinus cord on a golden-brown shell, but with a pinkish-violet-stained anterior end, including the entire canal. The canal is slightly curved, and the contrast between the golden-brown shell and the pinkish-purple canal is most striking and instantly identifiable as was clear from the comments of Powell (1964). Although he apparently never saw a specimen of this species, he was able to match Dunker's description with a figure on a tablet.

**Types.** One of the specimens shown in Plate XII has been deposited in the Philippine National Museum. All three specimens were collected off Mactan Island, by gill nets between 50 to 150 m.

**Nomenclature.** This species is named for my children, Felicia Marie (Lisa), and Juan Ariston (Jon). The name *lisajoni*, with its contrasting colors, is a momento of their contrasting personalities as children, which added spice to the joys of parenthood.

An obvious question is whether the color of the anterior canal of *Gemmula lisajoni* is homologous or analogous to the violet-colored canal of Clade II *Turris* species. Clearly, the two groups seem otherwise considerably diverged from each other, but if indeed this is a homology, a molecular analysis may reveal an unexpected link between these forms. If it is an analogy, *Gemmula lisajoni* should be just as divergent from any *Turris* as other *Gemmula* species. Additional anatomical and molecular data should permit a clearcut choice between these two alternatives.

## Prospects

Table 2 lists the measurements and locality data for specimens of new and renamed *Turris* and *Gemula* species in the Olivera collection, which provided the basis for the descriptions and comparisons presented in this article. We expect that when a larger suite of specimens of some of the new species described here are available from localities outside the Philippines, an even greater range of variation for each species will be recognized. Thus, the few specimens of *T. dollyae* the author has seen from New Guinea and Australia are distinctive from Philippine shells, but are still clearly assignable to this species [one is illustrated in the recent book on Australian shells by Wilson (Wilson et al. 1994), and identified as *T. crispa*].

The availability of many more Philippine *Turris* specimens has been indispensable for clarifying the distinct forms of this genus. One source of taxonomic confusion is that the differences in shell morphology between species is often subtle. In addition, some species are quite variable (i.e., *T. babylonia*, *T. normandavidsoni*, *T. nadaensis*). Thus, in the past, when only an occasional specimen became available, it was very difficult to assign. For several centuries, miscellaneous forms were identified

Table 2. Locality and dimensions of the new Turrinae species

| Species | Measurement (mm) | | Locality |
|---|---|---|---|
| | Height | Width | |
| *Turris dollyae* | | | |
| Holotype | 119.0 | 25.6 | Tabaco Bay, Albay, Luzon |
| Paratype # 1 | 79.5 | 16.9 | Segod,Cebu |
| Paratype # 2 | 104.9 | 22.7 | Bogo, Cebu |
| Paratype # 3 | 111.5 | 24.2 | Panglao, Bohol |
| Paratype # 4 | 122.9 | 24.5 | Panglao, Bohol |
| Paratype # 5 | 103.0 | 22.0 | Panglao, Bohol |
| Paratype # 6 | 58.7 | 20.3 | Panglao, Bohol |
| Paratype # 7 | 114.3 | 24.9 | Tabaco Bay, Albay, Luzon |
| Paratype # 8 | 85.0 | 17.7 | Northern Cebu |
| Paratype # 9 | 86.3 | 18.9 | Northern Cebu |
| Paratype # 10 | 90.2 | 19.5 | Northern Cebu |
| Paratype # 11 | 80.4 | 17.5 | Northern Cebu |
| Paratype # 12 | 116.1 | 25.0 | "Philippines" (old collection) |
| Paratype # 13 | 101.7 | 21.3 | Bogo, Cebu |
| Paratype # 14 | 84.4 | 18.0 | Bogo, Cebu |
| Paratype # 15 | 87.5 | 18.2 | Bogo, Cebu |
| Paratype # 16 | 90.9 | 18.2 | Mactan Is., Cebu |
| *Turris normandavidsoni* | | | |
| Holotype | 65.2 | 15.2 | Segod, Cebu |
| Paratype # 1 | 72.1 | 17.1 | Segod, Cebu |
| Paratype # 2 | 73.4 | 16.3 | Segod, Cebu |
| Paratype # 3 | 55.6 | 14.6 | Olango Is., Cebu |
| Paratype # 4 | 82.5 | 18.6 | Barangas Bay, Luzon |
| Paratype # 5 | 84.2 | 19.8 | Not specified (old collection) |
| Paratype # 6 | 70.3 | 15.8 | Segod, Cebu |
| Paratype # 7 | 78.6 | 15.7 | Segod, Cebu |
| Paratype # 8 | 67.5 | 15.5 | Segod, Cebu |
| Paratype # 9 | 66.8 | 15.2 | Segod, Cebu |
| Paratype # 10 | 62.0 | 14.8 | Olango Is., Cebu |
| Paratype # 11 | 58.6 | 15.7 | Olango Is., Cebu |
| Paratype # 12 | 64.2 | 15.6 | Olango Is., Cebu |
| Paratype # 13 | 64.4 | 14.1 | Segod, Cebu |
| Paratype # 14 | 62.6 | 14.5 | Segod, Cebu |
| Paratype # 15 | 79.0 | 17.0 | Segod, Cebu |
| *Turris pagasa* | | | |
| Holotype | 63.5 | 15.2 | Pamilacan Is., Bohol |
| Paratype # 1 | 61.3 | 17.3 | Dapalag, Northern Mindanao |
| Paratype # 2 | 98.4 | 24.3 | Bogo, Cebu |
| *Turris fotuphyllis* | | | |
| Holotype | 75.7 | 21.2 | Olango Is., Cebu |
| Paratype # 1 | 90.2 | 24.5 | Olango Is., Cebu |
| Paratype # 2 | 67.2 | 18.9 | Balicasag, Bohol |
| Paratype # 3 | 75.7 | 21.1 | Balicasag, Bohol |
| Paratype # 4 | 66.0 | 22.8 | Balicasag, Bohol |
| Paratype # 5 | 66.8 | 20.5 | Balicasag, Bohol |
| Paratype # 6 | 70.3 | 19.8 | Olango Is., Cebu |
| Paratype # 7 | 79.0 | 22.6 | "Philippines" (old collection) |
| *Gemmula lufulimi* | | | |
| Holotype | 58.1 | 17.9 | Batan Is. |
| Paratype # 1 | 36.7 | 11.5 | Pamilican Is., Bohol |
| *Gemmula lisajoni* | | | |
| Specimen # 1 | 41.5 | 11.2 | Mactan Is., Cebu |
| Specimen # 2 | 43.7 | 12.7 | Mactan Is., Cebu |
| Specimen # 3 | 43.3 | 13.6 | Mactan Is., Cebu |

as either *T. babylonia* or *T. crispa* (= *Turris grandis*, Gray, 1834). Although this article is very much a "work in progress," it is intended to provide an updated taxonomic framework for future studies on this genus. The Powell monographs (Powell 1964, 1966, 1967), though over 30 years old, still serve as a definitive resource in that these remain the only comprehensive treatment of the Turrinae. The update we have provided has necessarily focused only on Philippine forms, and only the genus *Turris* (s.s.).

One general impression gained from this survey is that the genus is enjoying a species radiation in the Philippines and the Indo-Pacific arc which is relatively recent, resulting in forms that are far larger than is the norm for tropical Turridae. The underlying biological adaptations that are the basis for this relatively recent (in geological terms) radiation of *Turris* species remains completely unknown, and this remains the major scientific question to be addressed in the future.

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