Larger Forms in *Lophiotoma*: Four New Species Described in the Philippines and Three from Elsewhere in the Indo-Pacific

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ABSTRACT

A group of venomous turriform gastropods in the subfamily Turrinae, genus *Lophiotoma*, has been investigated. Previously, forms in this group were identified as either *Lophiotoma unedo* or *Lophiotoma indica*. Our analysis has led to the description of four new species from the Philippines (*L. bisaya*, *L. friedrichbonhoefferi*, *L. panglaoensis*, and *L. tayabasensis*) and one each from Australia (*L. capricornica*), South Africa/Mozambique (*L. dickkilburni*), and Madagascar (*L. madagascarensis*). A new subspecies, *L. indica queenslandica*, is also described. In addition, 11 distinctive forms related to these taxa that may or may not deserve separate taxonomic status are defined; these need further evaluation. It is hypothesized that the forms of *Lophiotoma* discussed in this report are closely related to a particular subset of *Gemmula*, the *G. kieneri*/*G. interpolata* group.

Keywords: toxoglossate mollusc, venomous snail, Turridae, *Lophiotoma*, shell morphology, *Conacea*

INTRODUCTION

This paper is part of a series that has the long-term goal of defining and evaluating distinctive forms of Indo-Pacific Turrinae. The first paper dealt with Philippine forms of *Turris* (Olivera, 1999). In this and the second paper of this series (Olivera, 2002), we have initiated a definition of the larger *Lophiotoma*. The focus of the present paper are *Lophiotoma* related to (and generally identified as) *Lophiotoma indica* and *Lophiotoma unedo*. We introduce the group through a broad review of the relevant taxonomy.

The last comprehensive treatment of Indo-Pacific Turrinae carried out by Powell (1964 & 1966) used several shell-based morphological criteria to define genera or subgenera. These included the position of the sinus, the presence or absence of gemmules, protoconch characters, and the length of the siphonal canal. Both Kilburn (1983) and Bouchet (1990) have suggested that protoconch morphology, while useful for species differentiation, should only be one of the many morphological parameters considered in proposing new genera. Thus, the subgenus *Lophioturris* proposed by Powell for forms with blunt paucispiral protoconchs (including *L. indica*) will not be recognized here, in consonance with the suggestions of Kilburn and Bouchet.

In the second paper of this series, it was suggested that the length of the siphonal canal was a morphological character that could change more rapidly than previously thought. Some forms with long canals (presently assigned to *Lophiotoma*) seemed more

closely related to species with short siphonal canals (traditionally assigned to *Xenuroturris*) than to other species conventionally included in *Lophiotoma* (the example considered was "*Xenuroturris*" *cingulifera* and *Lophiotoma albina*, which except for the siphonal canal appear to be closely related). Thus, we suggest that turrid genera or subgenera based on the length of the siphonal canal alone, without other distinguishing criteria, should also be avoided. Finally, the presence or absence of gemmules may not be as straightforward a character as Powell indicated; he argued that in the context of the fossil record, the presence or absence of gemmules on the sinus cord was a key indicator of the evolutionary history of the group. Some of the species that we discuss in this manuscript were assigned by Powell to the genus *Gemmula* (in the subgenus *Unedogemmula*). Kilburn suggested a closer relationship between *Unedogemmula* and the *Lophiotoma* (s.s.) than Powell's monograph indicated, and felt that "phenetic resemblances between *Lophiotoma* and *Unedogemmula* are certainly greater than between *Gemmula* and *Unedogemmula*" (Kilburn, 1983). His suggestion that "*Unedogemmula*" spp. should be included in *Lophiotoma* rather than *Gemmula* has been adopted by Taylor et al. (1993) and Higo et al. (1999), and will be adopted here.

In this series, as a response to the problem of generic assignments, we provisionally use only three major genera in the Turrinae for forms that are broadly distributed over the Indo-Pacific: *Turris*, *Gemmula* and *Lophiotoma*. Some other groups in the Turrinae, such as *Fusiturris*, are small with a narrow geographic distribution; the other large genus in the Turrinae, *Polystira*, is a Western Atlantic/Eastern Pacific group. Thus, *Lophiotoma* is provisionally treated as conceptually broader than in Powell's treatise, encompassing not only all species he assigned to *Lophiotoma* (s.s.), but all of the species assigned to *Lophioturris*, *Xenuroturris*, and *Unedogemmula* as well. This is only a provisional, if convenient, solution: we recognize that the species we include in *Lophiotoma* will ultimately be grouped into different infraspecific taxa. However, because the present divisions probably do not accurately represent the true evolutionary relationships between the subgroups, using *Lophiotoma* broadly defined seems the best interim solution.

Consequently, all of the forms discussed in this paper are treated as *Lophiotoma* (s.l.); in the literature, the two most commonly used specific names, often referred to as *Lophioturris indica* and *Gemmula* (*Unedogemmula*) *unedo*, are now included in *Lophiotoma*. The species related to *Lophiotoma indica* and *Lophiotoma unedo* comprise a confusing series of larger forms that bring to mind Hedley's remark that the turrids "are considered by those who meddle with them to be more perplexing than any other molluscan family" (Hedley, 1922). We have several reasons for examining these species groups at this time. The immediate reason is somewhat pedestrian: our laboratories are engaged in an analysis of the venoms of toxoglossate molluscs, with an initial focus on *Conus*. As we initiated work on venoms of the larger Turrinae, we began to recognize the problematic taxonomy of even supposedly well-known forms. The imminent characterization of venoms provided an urgent need for defining distinct forms, and if possible, assigning appropriate names.

Every large *Lophiotoma* is labeled as either *L. indica* or *L. unedo* in most collections. Any larger shells that are relatively narrow and/or reticulated with darker markings are generally identified as *Lophiotoma indica*, and those larger forms that are broader and lighter in color as *Lophiotoma unedo*. These names have been applied to a confusing set of diverse forms. In this work, all distinct morphological forms conventionally assigned to these two taxa are evaluated, and new names for forms that are sufficiently distinctive to merit subspecific or specific status are proposed.

However, for many forms, there is insufficient information to decide whether the form is a new species or subspecies, or an unusual variant of another species. In most cases, the material examined is collected from deeper water, with relatively few examples available. The decision as to which distinctive forms are separate species or subspecies is somewhat subjective at this time. In this manuscript, we have generally taken an approach in which only very distinctive forms that are well defined are given new specific or subspecific names.

In describing new species and subspecies, we have deliberately taken a narrow set of specimens as the

type material; it is possible that even forms that only differ subtly and are quite similar are, in fact, separate species. It seems wise to limit the type material to the narrowest possible variation and geographic range since the possibility that there will prove to be three or even ten times as many species as are being recognized below from the material examined cannot be eliminated.

We also intend this initial evaluation, based on shell morphology, to facilitate the assessment of relationships between the various forms using a molecular approach. Since the required live-collected material is generally not available for molecular studies, a systematic morphological evaluation of conchological characters should help focus collection efforts of the appropriate specimens for analysis. We anticipate that the molecular work will include the identification of genes encoding venom components; such genes have been useful in assessing relationships between species in *Conus* (Olivera, 2002). The prospect of systematic collection efforts of live material by the Paris Museum in the near future may provide an unparalleled opportunity to collect the live specimens needed for the requisite molecular analysis.

We first discuss those species that are morphologically most distant from *Gemmula*, namely the *L. indica*-like forms, followed by an analysis of the *L. unedo*-like forms.

Overview of *Lophiotoma indica*-like forms

Lophiotoma indica is the largest shallow-water form in the genus, but specimens assigned to this species are morphologically heterogeneous. This heterogeneity may arise in part because *L. indica* is quite variable, but in addition, several different species have been lumped under this taxon. The description of Kilburn (1983) on the general problematic taxonomy of the Turridae particularly applies to this group: "intense regional speciation has produced a high percentage of often poorly studied endemics". The *L. indica* species group comprises a confusing series of seemingly interrelated forms; the treatment that follows is a conservative evaluation of the available material. As more material is collected, and a more thorough characterization of the various forms becomes available, it seems probable that more species and subspecies will be recognized.

The various forms that are often labeled in collections and in publications as *L. indica* can be divided into two groups on the basis of protoconch morphology: all shallow-water forms appear to have a blunt paucispiral protoconch. However, there are deep-water forms which may or may not be taxonomically distinct that also have a blunt paucispiral protoconch. In addition, several forms conventionally assigned to this species have a polygyrate protoconch, and can therefore be distinguished from other *L. indica*-like morphs based on this character. All of the latter are collected off-shore, and although they have been previously assigned to *L. indica*, the difference in protoconch morphology provides a firm basis for separating these from *L. indica* and other related forms with paucispiral protoconchs.

In the treatment that follows, all forms with blunt paucispiral protoconchs are included in Group I. Among the forms assigned to *L. indica* (and sometimes misidentified as *Lophiotoma unedo*) that have blunt paucispiral protoconchs, we propose a new subspecies; in addition, four distinctive forms in the *L. indica* complex of uncertain taxonomic status are defined. In Group II, we include the *L. indica*-like forms with polygyrate protoconchs; four new species are proposed and several distinctive forms of uncertain taxonomic status are described.

Group I species: *Lophiotoma indica*-like forms with blunt paucispiral protoconchs

Even when all forms with polygyrate protoconchs are excluded from *L. indica*, this complex still encompasses a bewildering variety of forms as illustrated in Figs. 1 and 2.

Within the *L. indica* complex, we recognize two subspecies as is discussed below. In the eastern Indian Ocean, Indo-Pacific arc (New Guinea to the Philippines), and Japan, the "typical form" *Lophiotoma indica indica* (Röding, 1798) is found. We propose a new subspecies, *Lophiotoma indica queenslandica*, for specimens collected in the southeastern edge of the range from Queensland, Australia to Fiji. Four additional forms in the *L. indica* complex are described which require further evaluation.

Fig. 1A. *Lophiotoma indica indica* from the Philippines, variation series.
A1 is the melanistic variety from Murcielagos Bay, Misamis Occidental, northern Mindanao Island, Philippines. A7 is an albinistic example (form *bulowi*) trawled off Negros Island, Philippines. A4 is from Cuyo Island, Palawan, collected by divers in shallow water. A2, A3, A5, and A6 were trawled in deeper water from various Philippine localities.

Fig. 1B. *Lophiotoma indica queenslandica*.
The holotype is shown in B1 and B2. B3, B4, and B5 are paratypes 1, 6, and 7, respectively, all live-collected specimens trawled off Queensland, Australia. B6 and B7 are dead-collected specimens from the Swain Reefs, paratypes 2 and 3, respectively (Appendix).

***Lophiotoma indica indica* (Röding, 1798)**

Description (adapted from Powell, 1964)

Adult shells up to 100 mm in height, elongate-fusiform with a tall spire, and a long straight anterior canal. Whorls, about 14 with a blunt, smooth paucispiral protoconch (1 to 1 1/2 whorls) with a half whorl of strong axial ridges. A strong, narrowly-rounded, smooth peripheral carina is located below medium whorl height. At the subsutural fold, there is a strong, smooth spiral cord at its lower extremity, with a weaker cord and several threads above it. Between 1 to 3 smooth primary spiral cords are present between the periphery

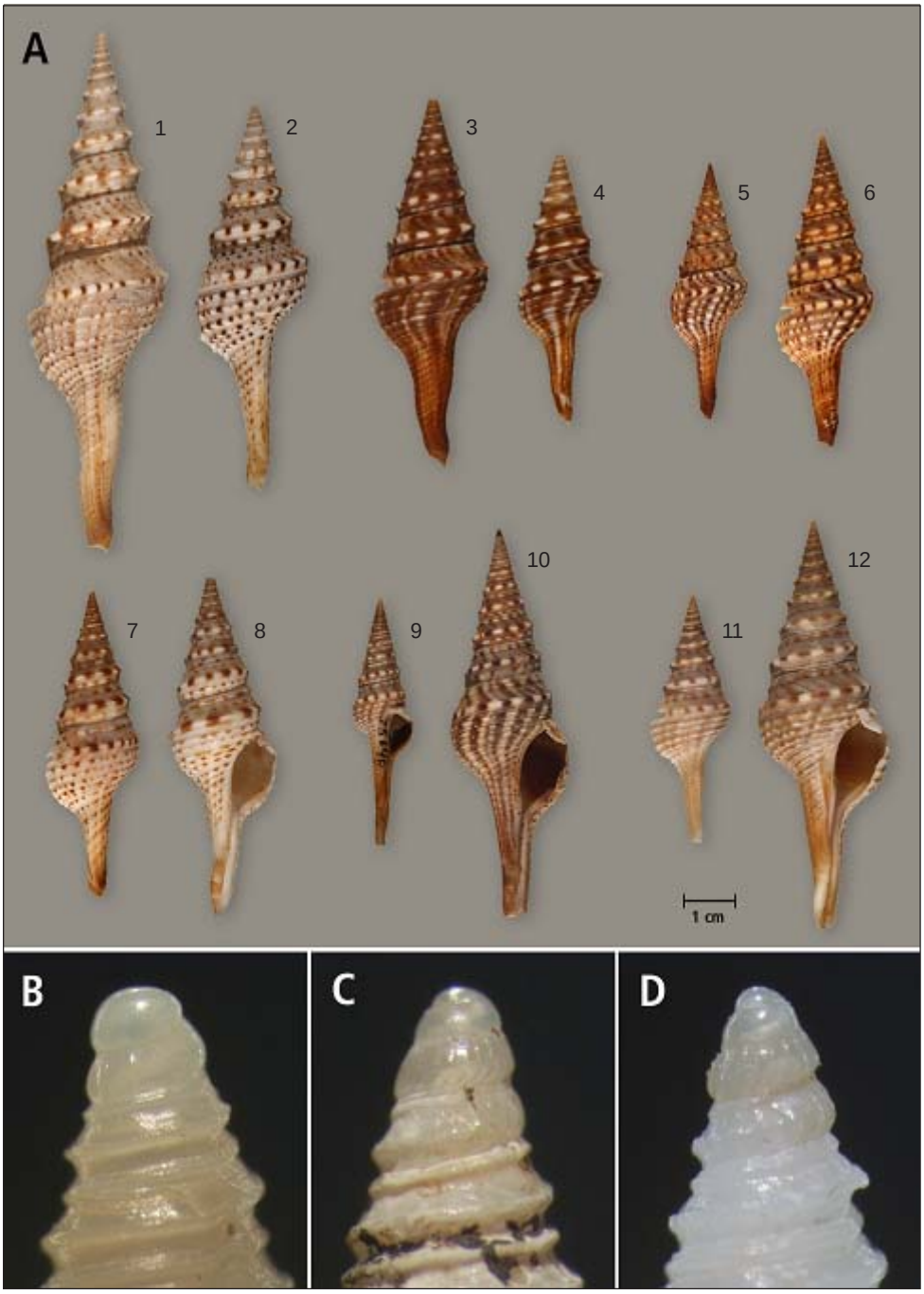

Fig. 2A. Distinct forms within the *Lophiotoma indica* complex.

A1 and A2 are *L. indica indica*, typical forms. A3 and A4 are *L.c.f. indica*, variant/form 1, from South India ("Arabian Sea form"). A5 and A6 are *L.c.f. indica*, variant/form 2, from Exmouth Gulf, Western Australia. (Bottom row) A7 and A8 are *L.c.f. indica*, variant/form 3, thin shallow-water form from Broome, western Australia. A9 and A10 are *L.c.f. indica*, variant/form 4, from Cagayan Province, northeast Luzon, Philippines (Los Angeles County Museum #75648). A11 (holotype) and A12 (paratype 6) are *L. indica queenslandica*, trawled off the Queensland coast.

Figs. 2B, 2C, and 2D. Comparison of protoconchs.

Fig. 2B. *Lophiotoma indica queenslandica* (Swain Reefs, Australia).

Fig. 2C. *Lophiotoma bisaya* (Aligway, Philippines).

Fig. 2D. *Lophiotoma friedrichbonhoefferi* (Aligway, Philippines).

Photos, 25x using a DP-10 Olympus digital camera on an Olympus SZX9 stereomicroscope. Photomicrographs by Nancy Kurtzeborn.

and the lower suture, with 18 to 20 primary spinal cords in the body whorl from the periphery to the end of the anterior canal. The entire surface is crowded with smooth spiral threads of varying strength. The color pattern is profusely spotted, with dark round maculations on a white, grayish-white or brownish-white background. The maculations are confined to the primary spiral cords, but diffuse vertically in many specimens, presenting a sinuous eggshell pattern that varies in strength, giving the shell pattern a generally marbled effect. The peripheral maculations are always the strongest. The tip of the anterior canal often has a brownish tint, with the brownish cast extending over the entire canal in some specimens.

The recently collected specimens of the "typical form" of *L. indica* shown in Fig.1 are from the Philippines, north to Japan and south to Queensland. However, this form occurs in the Indian Ocean, since the type is reported to be from Tranquebar, India (R. Kilburn, personal communication). Even within the typical form, considerable variation in color, pattern, and shape is observed—some of this variation appears to be a function of depth. In the central Philippines, *L. indica* has been trawled by fishermen at depths of over 50 m; the deeper-water material tends to be narrower and often lighter in color (Fig. 1). At intermediate depths, the typical form is less narrow, and shallow-water morphs from the Philippines have broader, more robust shells. A range of diverse forms, likely all variants of *L. indica indica*, are shown in Fig. 1A.

Atypical forms, probably variations of *Lophiotoma indica indica*

Melanistic form

In northern Mindanao and the Visayas Islands, Philippines, a slender melanistic form has been collected; one locality verified by trawlers is Murcielagos Bay, off Misamis Occidental, north-central Mindanao (Fig. 1A, specimen 1).

Albinistic form ("form bulowi")

Several morphs in the *L. indica* complex have a tendency to become albinistic. Albinistic specimens from the Philippines, which we include in *L. indica indica*, tend to have a broader canal than other forms of *L. indica* (Fig. 1A, specimen 7).

***Lophiotoma indica queenslandica*, new subspecies**

Most specimens have been collected from Queensland, Australia offshore that appear distinctive enough from any other form in the complex to justify at least subspecific separation. The unusual depth at which specimens are collected and the known geographic range also separate this form from *L. indica indica*. Future work may justify separation into different species.

Description

L. indica queenslandica has a blunt paucispiral protoconch (Fig. 2B), typical of the *L. indica* complex, and 12-13 teleoconch whorls. Each whorl has highly characteristic sculpture and markings between the suture and the periphery. There are two rows that are broadly maculated in brown: one set of maculations is centered around the periphery, which comes to a sharp apex in most specimens; the second row of maculations is subsutural and is centered around a cord that is usually well displaced from the suture. Otherwise, the sculpture consists of very fine spiral threads (both the peripheral apex and the cord that is maculated in the subsutural region are generally lighter in color than the background except for the broad brownish maculations). The body whorl has a grayish-brown background below the periphery, with a transition to a brownish base and siphonal canal. There are about 5-6 spiral cords within the area of the grayish-brown background and a larger number in the siphonal canal. The body whorl is quite rounded, particularly in the suite of specimens from the Swain Reefs, giving the entire shell a generally more bulbous, less pagoda-form appearance than other forms in the *L. indica* complex. In the region from the suture to the periphery, only a subsutural cord and the periphery are maculated; the multiple cords in the region between the suture and the periphery are not maculated. Some specimens tentatively assigned to *L. indica queenslandica* have strong axial markings.

Type material

The holotype and some paratypes are shown in Fig. 1B. The holotype will be deposited in the Muséum National d'Historie Naturelle (MNHN), Paris, France. Paratypes will be deposited at the National Museum of Natural History (USNM), Washington, D.C.; the Academy of Natural Sciences (ANSP), Philadelphia,

PA; the Field Museum of Natural History (CFM), Chicago, IL; the American Museum of Natural History (AMNH), New York, NY; the Los Angeles County Museum of Natural History (LACM), Los Angeles, CA; and the Western Australian Museum, Perth. Specific measurements and data for the holotype and paratypes are given in the Appendix. Two of the paratypes, collected in the Swain Reefs area, were trawled between 90-105 fathoms.

Discussion

L. indica queenslandica can be differentiated from *L. indica indica* by its generally more bulbous shape, by the background brown or grayish-brown color (in *L. indica indica* the background is generally white or light grayish white), and most strikingly, the markings on the spiral ribs. In *L. indica queenslandica*, the markings on the spiral ribs are lighter and tend to run axially in both the cords and in the intercord regions; in typical *L. indica indica*, a pattern of boldly, regularly maculated spiral cords is generally observed. Many of the *L. indica queenslandica* paratypes included in the type series for the species were freshly dead-collected specimens from Swain Reefs—we have included these as paratypes because these have the most specific locality collection data (Appendix); however, because these specimens were dead collected, they are lighter pinkish brown in color than the grayish brown or reddish brown of live-collected specimens. Most of the live-collected specimens were from commercial dealers, and the precise collection data could not be definitively established, but were said to have been trawled in Queensland, offshore in deeper water.

We note that a recent publication figured a specimen reportedly collected in Japan (Okutani, 2000) that appears to be *L. indica queenslandica* identified as *L. indica*. Some specimens in collections assignable to this species are labeled "Taiwan"—however, many shells labeled "Taiwan", though purchased in Taiwan, were actually collected off Australia. If the northern Pacific localities are verified, it would provide support for *queenslandica* being a separate species, rather than a subspecies of *indica*.

Distinctive forms in the *Lophiotoma indica* complex of uncertain taxonomic status

Several very distinctive morphs are part of this species complex. These are compared to typical *L. indica indica* and *L. indica queenslandica* in Fig. 2. These forms are described from a west to east gradient.

L.c.f. indica, variant/form 1;
Arabian Sea form

This form can be differentiated from typical *indica* by its generally darker background, and broader shell with a proportionally shorter and broader canal. The peripheral carina is more prominently raised than in the typical form and shows a greater contrast in color pattern than is found in the rest of the shell (the background in the peripheral keel is distinctly whiter). A pattern of continuous dark axial flames in the body whorl is seen in most specimens, with each flame being much wider than in the typical variety. The subsutural fold has two equally strong, smooth spiral cords in contrast to one strong lower one in typical *L. indica*. This variant is shown in Fig. 2A, specimens 3 and 4.

Most specimens of this form available to the author were obtained from fishing vessels in South India, and were probably collected by trawlers off Kerala. The form may be found further west to the Arabian Peninsula (Bosch et al., 1995). Although the specimen figured from the Gulf of Oman in the book by Bosch is consistent with this form, it appears to be dead collected. None of the specimens observed had an intact protoconch; therefore, it is possible that this is a Group II form. The distinctive shell morphology and the geographic distribution of this form are consistent with its being separable at least at a subspecific level. However, more specimens need to be examined to understand the relationship of this form to *L. indica indica* and *L. indica queenslandica*, as well as to some of the other morphs described below.

L.c.f. indica, variant/form 2;
western Australian form

In western Australia, a distinct form that is smaller but more robust than typical *L. indica indica* is found (Fig. 2A, specimens 5 and 6). One verified locality where this form has been collected is Exmouth Gulf; specimens were trawled in deeper water. The shells are much darker and smaller than typical *L. indica*, dominated by strong, dark brown axial markings rather than the maculations on the spiral cords.

L.c.f. indica, variant/form 3;
northwestern Australian form

A series of unusually light shells, collected in shallow water (intertidally in Broome, Australia) have a broader spire and relatively shorter canal with much larger brown maculations in the periphery, compared to typical *L. indica indica* (Fig. 2A, specimens 7 and 8).

L.c.f. indica, variant/form 4;
northeastern Luzon form

Two specimens of a broad gray form that is distinct from all other *L. indica*-like forms found in the Philippines are in the Los Angeles County Museum of Natural History collection (#756481). These are shown in Fig. 2A, specimens 9 and 10. The larger specimen (Fig. 2A, specimen 10) is broader in outline, with less constricted sutures than other forms of *L. indica*. Furthermore, the body whorl is light grayish, strongly maculated at the peripheral cord with an axial pattern that follows the growth line and continues through the body whorl to the canal in continuous zebra-like streaks. The canal has a brownish background color in most specimens. The subsutural region has a well-maculated cord, splitting into two cords separated by a canal in the body whorl. The juvenile specimen is very similar in general sculpture and coloration to some specimens of *L. indica queenslandica*, except that in overall shape it is more slender than comparably sized specimens of that species. This form also has affinity with the Arabian Sea form described from southern India. These specimens bear the label "1-5 fathoms on sand and coral bottom, Escarpa Point, Cagayan Province, northeast Luzon Island (collected 22 June 1964, Norton Collection)."

One possibility to be considered further is that the *L. indica queenslandica* is in fact a distinct species, and that both this form and the Arabian Sea form (variant/form 1) are variants of that species rather than of *L. indica*.

Group II species: *Lophiotoma indica*-like forms with polygyrate protoconchs

The shells of species included in Group II are generally similar to forms in the *L. indica* complex in Group I, and can be difficult to separate if protoconchs are not intact. However, all forms in Group II do not have the blunt paucispiral protoconch typical of forms in Group I, but have polygyrate protoconchs (Figs. 2C and 2D). We describe four new species that belong to this group, *Lophiotoma friedrichbonhoefferi*, *Lophiotoma bisaya*, *Lophiotoma tayabasensis*, and *Lophiotoma dickkilburni*, which are illustrated in Fig. 3. The first three forms described as new species from the Philippines comprise a discrete range of sizes: the relatively small *L. friedrichbonhoefferi* (35-50 mm), the medium-sized *L. bisaya* (60-75 mm), and the large *L. tayabasensis* (80-110 mm). These, as well as related variants, are illustrated in Figs. 3 and 4.

Lophiotoma friedrichbonhoefferi, new species

Description

This distinctive form, illustrated in Fig. 3, is smaller and narrower than other Group II species, and has relatively larger and fewer maculations. The polygyrate protoconch (Fig. 2D) distinguishes it from *L. indica* and other Group I forms. In specimens where the spire is not corroded, the first postnuclear whorl shows a weakly gemmate structure that is visible in Fig. 2D. Most mature shells range in size from 35-50 mm (Appendix). In addition to the polygyrate protoconch of ca. 3.5 whorls, there are about 11 teleoconch whorls. The spire is boldly maculated at both the peripheral rib and in the subsutural region; the subsutural cord is strong, and in later whorls is split into two, separated by a narrow canal. The area from the strong subsutural

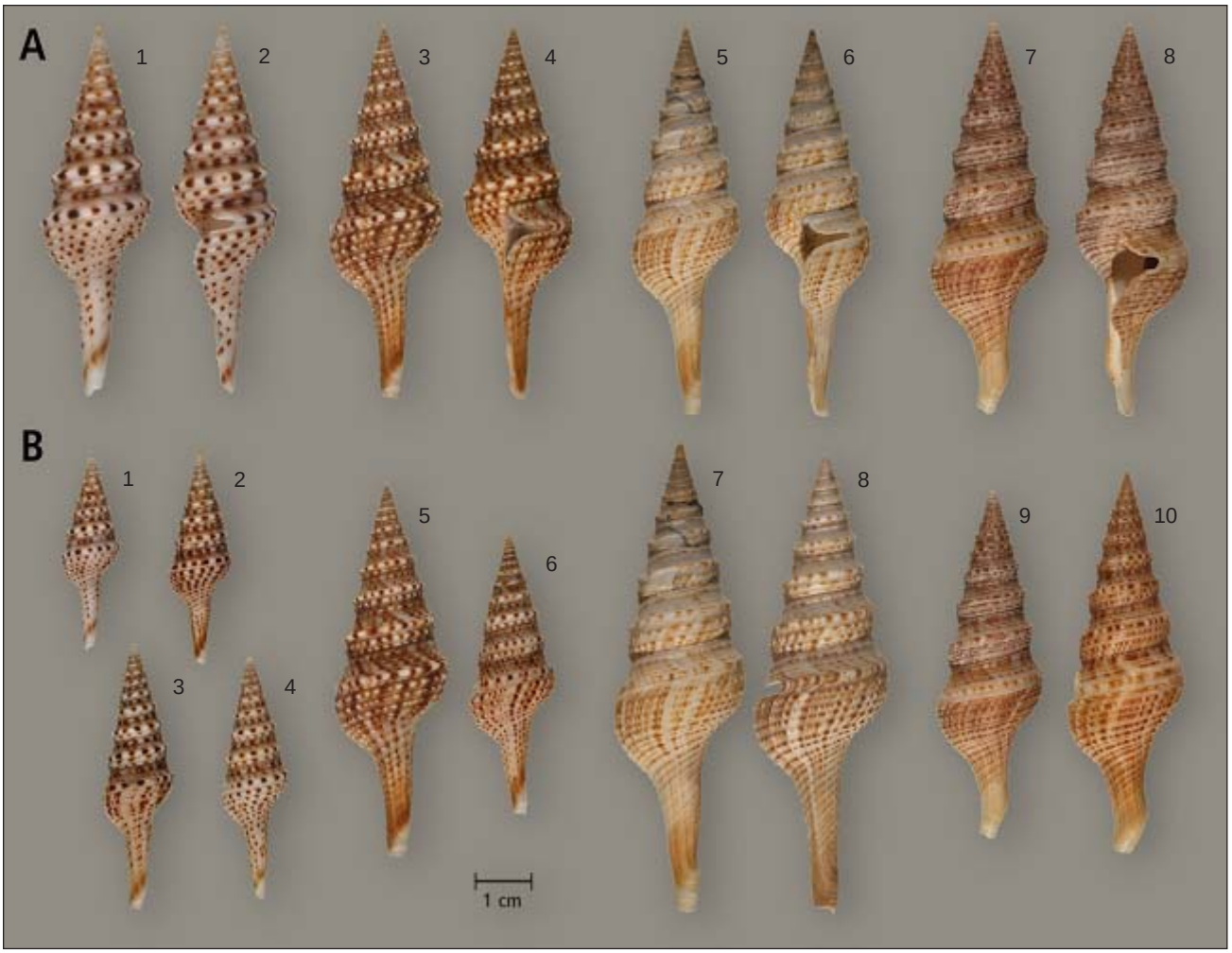

Fig. 3A. Specimens illustrated not to scale, to be approximately the same size. Dorsal and side view of *Lophiotoma friedrichbonhoefferi* (A1 and A2); *Lophiotoma bisaya* (A3 and A4); *Lophiotoma tayabasensis* (A5 and A6); and *Lophiotoma dickkilburni* (A7 and A8).

Fig. 3B. All specimens are shown to scale. B1 (holotype), B2 (paratype 1), B3 (paratype 8) and B4 (paratype 9) are *Lophiotoma friedrichbonhoefferi*; B5 (holotype) and B6 (paratype 26) are *Lophiotoma bisaya*; B7 (holotype) and B8 (paratype 26) are *Lophiotoma tayabasensis*; while B9 (holotype) and B10 (paratype 1) are *Lophiotoma dickkilburni*.

cord to the periphery is flat and almost perpendicular to the axis of the shell. The color of the shell is white with a light pinkish or purplish tone; the body whorl and base have about six primary cords that are more or less regularly maculated in the same purplish brown color as the peripheral cord and the subsutural region; these smaller maculations on the primary cords tend to be parallel to each other and to the growth line of the aperture. On the relatively long siphonal canal, the pattern of regular maculated ribs continues; there are about seven primary cords with additional weaker cords in some specimens. Anterior to these cords is a distinctive purplish-brown band and the very tip of the siphonal canal is pure white. The maculations on *L. friedrichbonhoefferi* are bolder, and there is more contrast with the white background than in most related forms.

Most specimens of this form examined were from Aligway Island off N. Mindanao, said to be collected by small trawls at depths of 30-100 fathoms. Two dead-collected specimens, one relatively well preserved, in the Paris Museum (MNHN) are assignable to *L. friedrichbonhoefferi*. These are labeled, “13° 53’ N–

120° 09' E, Musorstom St. 56, 134 m, from near Lubang Island, Philippines" (Appendix). The polygyrate protoconchs are reasonably well-preserved in both specimens, which have been included in the type series. Thus, the species is found from northern Mindanao to Lubang Island, off western Luzon in the Philippines.

Type material

The holotype will be deposited at the Philippine National Museum, Manila. Paratypes will be deposited at MNHN, Paris; AMNH, New York; USNM, Washington; CFM, Chicago; Natal Museum, South Africa; LACM, Los Angles; and ANSP, Philadelphia. Data on the types are given in the Appendix.

This species is named for a truly creative pioneer in several fields of science, Friedrich Bonhoeffer. The author has been a grateful beneficiary of Friedrich Bonhoeffer's creativity, scientific insight and warm friendship.

***Lophiotoma bisaya*, new species**

Description

Lophiotoma bisaya has a paucispiral protoconch and 12-13 teleoconch whorls in typical mature specimens. The subsutural fold usually has a strong cord that is maculated, that often splits into two cords in the body whorl, with 2-3 similarly maculated primary cords between the subsutural and the peripheral cord. On the body whorl, there are usually 6 primary cords and 7-9 maculated cords on the canal. At the anterior end of the canal, there are approximately four additional cords with progressively decreasing intensity of maculation; the most anterior generally located in a distinct dark brown band. The tip of the siphonal canal is white and lacks any primary cords. The maculations are brown to maroon-brown, and in some specimens, there are axial patterns that result in a darker base color between the maculated cords; however, other specimens have no axial markings and the pattern on the body whorl is restricted to regular maculations on the primary cords. From northern Cebu, Bohol, and Aligway Island, specimens have a siphonal canal that is generally very straight, with the maculated cords giving way to a dark brown band, followed by the characteristic white tip (a feature that is also characteristic of *L. friedrichbonhoefferi*, as well as most specimens of *L. unedo*).

Type material

The holotype will be deposited at the Philippine National Museum, Manila. Paratypes will be deposited at MNHN, Paris; AMNH, New York; USNM, Washington; CFM, Chicago; LACM, Los Angles; and ANSP, Philadelphia. Data on the types are given in the Appendix.

Discussion

The shell pattern of the body whorl of *L. bisaya* is one of closely-spaced spiral cords, finely maculated with small squarish brown maculations; the slightly maroon tinge of these maculations gives Philippine forms of *L. bisaya* a generally different color cast from *L. indica*. *L. friedrichbonhoefferi* can be differentiated from *L. bisaya* by the whiter background, fewer and bolder maculations, and generally smaller size of the former. Although there are some members of the *L.* (*Unedogemmula*) *unedo* complex that are very similar morphologically to *L. bisaya*, *L. bisaya* does not have the massive subsutural structure that is characteristic of Philippine specimens of *L. (Unedogemmula) unedo*. In *L. bisaya*, between the maculated subsutural cord and the periphery are typically 2-3 primary cords, decorated with maroon-brown maculations similar in intensity to the maculation on the cords on the body whorl. In *L. friedrichbonhoefferi*, the subsutural cord and periphery are strongly maculated—maculated cords in between are either completely absent or present only in the body whorl (always with much weaker maculations than in the subsutural cord). Philippine specimens of *L. unedo* typically have a concave, deeply excavated region with fine unmaculated cords between the upper suture and the periphery.

Compared to specimens of *L. indica indica*, Philippine specimens of *L. bisaya* have a more horizontal shoulder, perpendicular to the rest of the whorl, giving each whorl a distinctly squarish appearance. Furthermore, the peripheral keel is much more depressed (in most specimens of *L. indica*, the peripheral keel comes to a

sharp edge). The peripheral carina has a whiter background than the remainder of the whorl, and in some specimens the white area is extended, both above and below the actual sinus cord itself. A definitive characteristic is that *L. bisaya* has a polygyrate protoconch of approximately three whorls (Fig. 2C), while all forms of the *L. indica* complex have a blunt paucispiral protoconch.

L. bisaya appears to be closely related to *L. friedrichbonhoefferi* described above, as well as to *L. dickkilburni* as described below. Shells of *L. bisaya* are generally smaller than *L. tayabasensis* (mature specimens 60-75 mm vs. 80-110 mm for *L. tayabasensis*); the maculations are a distinct maroon-brown color as opposed to the straw-brown maculations of *L. tayabasensis*. Although there are some specimens of *L. bisaya* that begin to approach *L. tayabasensis* in shape and size, the differences in color, the generally squarish shape of the whorls, and the distinct dark maculations on the sinus cord in *L. bisaya* (as opposed to curved yellowish-brown markings on *L. tayabasensis*) will generally distinguish the two species.

Atypical varieties of *L. bisaya*

Unbanded variety

A variation of *L. bisaya* apparently collected by trawlers working out of Maqueda and Carigara Bays in Samar Island and Tayabas Bay in South Luzon Island is illustrated in Fig. 4, specimen 2—these specimens are very similar to the type material, except that they lack the sharp demarcation provided by the dark brown band at the siphonal canal between the white anterior tip and the posterior brownish canal. A specimen in the Los Angeles County Museum (LACM 75534) from Tayabas Bay (trawled at a depth of 22 fathoms in May 1965 by J. Norton) has excellent preservation of the polygyrate protoconch.

South Indian variety

A more distinctive form, also probably a variation of *L. bisaya*, that has a proportionally longer siphonal canal with generally lighter color streaks in the body whorl and canal has been collected in South India (Fig. 4, specimen 3); the protoconchs were not preserved in any of the specimens examined.

***Lophiotoma tayabasensis*, new species**

This distinctive form is likely to be found in collections labeled *Lophiotoma unedo* (or *Unedogemmula unedo* or *Gemmula unedo*), and sometimes *Lophiotoma indica*. Most specimens in collections were collected by trawlers in Tayabas Bay, Luzon, Philippines, in the late 1950s and the 1960s; this form is illustrated in the monograph by Springsteen and Leobrera as *Gemmula unedo* (Springsteen & Leobrera, 1986; Plate 76, #3). The misidentification of this previously unnamed Philippine form probably came about because, for many years, this was the only large form of the Turrinae at all similar to *L. unedo* routinely collected in Philippine waters. The species appears to be common offshore, from southern Luzon to northern Mindanao. Recent specimens have been collected in the Cebu-Bohol region by trawlers out of Lapu-Lapu City, Mactan.

Description

This is one of the largest Philippine turrids, adult specimens reaching over 105 mm (Appendix). *L. tayabasensis* has fine, regular straw-brown maculations along the spiral cords; the underlying axial streaks of yellow-brown to straw-brown vary considerably in intensity, and can be the dominant pattern in some specimens. The subsutural area typically has two cords in the later whorls, well-separated with the one further from the suture, strong and more boldly marked. There are 1-3 more maculated cords between the subsutural area and the peripheral keel. The sinus is deep and the peripheral keel is relatively flattened in the body whorl, with curved brown maculations that are parallel to the edge of the sinus. A characteristic feature of this species is that in many specimens, the early teleoconch whorls have sinus cord maculations that are more continuous and in earlier whorls of the spire, the sinus cord can be a uniform amber brown.

Below the peripheral sinus cord, there are 9-13 spiral cords on the body whorl that are finely-marked with

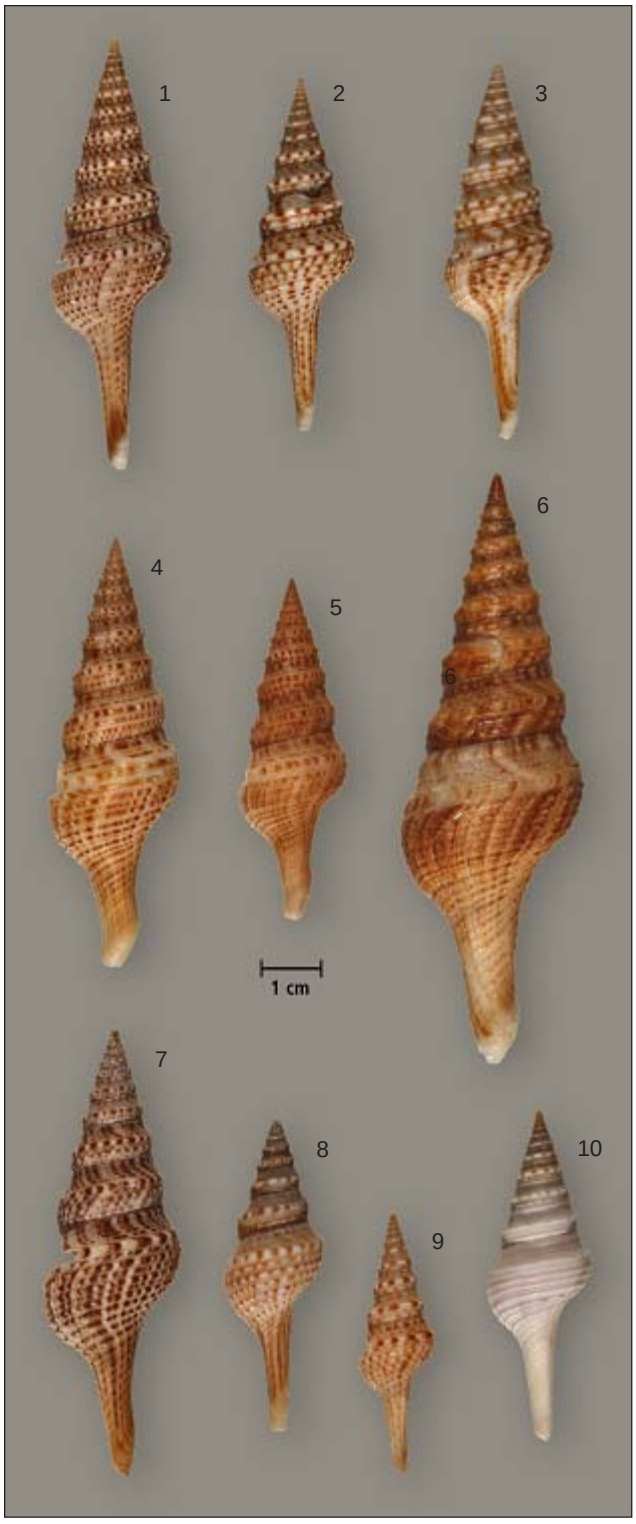

Fig. 4. An illustration of various forms related to *Lophiotoma bisaya* and *Lophiotoma dickkilburni*.

(Top row) Variations of *L. bisaya*. Specimen 1, typical form from Aligway, Philippines; specimen 2, *L. bisaya* variant from Tayabas Bay; and specimen 3, *L. bisaya* variant collected from South India.

(Middle row) *L. dickkilburni*. Specimen 4, paratype 1 from Mozambique; specimen 5, holotype from South Africa; specimen 6 is a south Indian specimen tentatively assigned to L. *dickkilburni*.

(Bottom row) Variant/forms related to *L. dickkilburni*. Specimen 7, *L.c.f. dickkilburni*, variant/form 1, dark mottled variety from Mozambique; specimens 8 and 9, *L.c.f. dickkilburni*, variant/form 2, longer canal form from Natal, South Africa (specimen 8) and from Pondicherry (specimen 9), India; specimen 10, *L.c.f. dickkilburni*, variant/form 3, albinistic form from Angoche, Mozambique.

brown, squarish maculations; at the siphonal canal, the spiral cords continue, but there is a transition to less prominent maculations (and in some specimens the maculations are completely obsolete). To varying degrees, the siphonal canal has a darker brown background which may either cover the entire canal, or be restricted to the anterior half; in almost all specimens, the very tip of the siphonal canal is significantly lighter in color. However, there is no distinctive dark brown border region characteristic of specimens of *L. friedrichbonhoefferi* or *L. bisaya*. In most specimens, the protoconch and early postnuclear whorls are either absent or extremely corroded; this form lacks gemmules in later whorls. The protoconch was not preserved in any specimens examined, but appears to be polygyrate from the few specimens with corroded remnants of the protoconch. One specimen showed evidence for weak gemmules in the first teleoconch whorl.

Type material

The holotype will be deposited at the Philippine National Museum, Manila. Paratypes will be deposited at MNHN, Paris; AMNH, New York; USNM, Washington; CFM, Chicago; LACM, Los Angles; and ANSP, Philadelphia. Data on the types are given in the Appendix. The species is named for the type locality, Tayabas Bay, as well as the old Philippine province of Tayabas on Luzon Island, a traditional name for a long coastal province on Luzon Island.

Discussion

The lack of a massive subsutural cord distinguishes this species from most Philippine specimens of the *L. unedo* complex; instead of a strongly concave region between the suture and the periphery, in *L. tayabasensis* the immediate subsutural area is slightly raised but otherwise the subsutural area has spiral cords that are decorated with light brown or purplish-brown maculations as in the rest of the body whorl, and the region is not deeply excavated or horizontal compared to the rest of the whorl, but instead is gently sloping towards the periphery. The continuous brown color of the sinus cord in the earlier spire whorl is another distinguishing characteristic. The species can be easily differentiated from *L. friedrichbonhoefferi, L. bisaya,* and other Group II species by its large size, more lightly colored maculations on the primary spiral cords, and more bulbous shape.

***Lophiotoma dickkilburni*, new species**

Most of the specimens assigned to this species were collected in South Africa and Mozambique; a few dead-collected specimens from South India are possibly assignable to this taxon as well. The specimens examined show significant variability, and a larger series from a wider geographic range needs to be examined; it is probable that there is more than one Group II species in the western Indian Ocean. We have deliberately restricted our description and the type series to one specific form from South Africa and Mozambique. The relationship between the various species needs to be more definitively established.

Description

This form has a polygyrate protoconch and 13-14 teleoconch whorls. The subsutural fold has two cords that are close together, and tends to form a distinct terrace, particularly in the earlier whorls. Between the subsutural fold and the periphery there are usually three primary cords. In addition to the peripheral cord, the body whorl has 10-12 primary cords that are maculated in more or less parallel fashion with a variable number of cords continuing on the canal. The cords become weaker and disappear on the anterior end of the canal.

An additional characteristic of many specimens is that on the later whorls, there is a white area surrounding the peripheral cord that is lighter in background color than the rest of the body whorl. The maculations are generally lighter brownish in color, with the color of the siphonal canal progressively lighter anteriorly. The anterior end of the siphonal canal is often curved towards the aperture end.

Type material

The holotype will be deposited at the MNHN, Paris. Paratypes will be deposited at MNHN, Paris; the Natal Museum, South Africa; AMNH, New York; USNM, Washington; CFM, Chicago; LACM, Los Angles; and ANSP, Philadelphia. Data on the types are given in the Appendix.

This species is being named for Richard (Dick) Kilburn, a preeminent authority on the taxonomy of turriform gastropods and of South African molluscs. Dr. Kilburn has been most generous in sharing his vast knowledge of turrids, and has been an invaluable resource for this work.

Discussion

A large specimen collected in South India (Fig. 4, specimen 6) seems to be conspecific with *L. dickkilburni*. *L. dickkilburni* appears most closely related to *L. bisaya*, but there appears to be a number of consistent differences. The tip of the siphonal canal in all specimens of *L. bisaya* examined from the type locality is white with a distinct darker brown border. The area from the suture to the periphery is much flatter in many *L. bisaya* specimens, a feature that gives the spire of *L. bisaya* a more pagoda-form aspect, instead of the more gradual curvature observed in *L. dickkilburni*. Finally, a significant fraction of *L. dickkilburni* specimens have a curved siphonal canal, a feature not observed in *L. bisaya*. In general, the cords of *L. dickkilburni* are more finely maculated than *L. bisaya*; thus, the typical number of maculations

per whorl on the peripheral cord of *L. bisaya* varies from 14-17, while in *L. dickkilburni* it is over 20 (generally around 25).

The material from South India suggests that variants of both *L. dickkilburni* and *L. bisaya* may occur there. Specimens 3 and 6 of Fig. 4 are both from southern India; they do not appear to be conspecific, with one tentatively assigned to *L. bisaya* (specimen 3) and the other to *L. dickkilburni* (specimen 6).

Distinctive variants/forms possibly related to *Lophiotoma dickkilburni*

Several distinctive forms that may or may not be conspecific with *L. dickkilburni* are shown in Fig. 4.

L.c.f. dickkilburni, variant/form 1

This form is larger and more heavily reticulated than *L. dickkilburni*; specimens examined were collected in Mozambique. This differs from the type series of *L. dickkilburni* in having a darker purplish-brown color and a less prominent subsutural cord.

L.c.f. dickkilburni, variant/form 2

Another form possibly related to *L. dickkilburni* are slender *Lophiotoma indica*-like specimens that have a purplish-brown background color, with long siphonal canals, collected in the South Africa/ Madagascar region. Similar specimens have been found in India (Fig. 4, specimens 8 and 9). In specimens the author has seen from the Indian Ocean, the protoconchs have been eroded—these are invariably simply labeled "*Lophiotoma indica*" (although they are distinct from the forms described under Group I above). There are a series of specimens morphologically similar collected by the MNHN, Paris Museum, from Makassar, Indonesia; although the color is slightly different—the specimens have a yellowish-brown instead of purplish-brown background—the sculpture and general shape are similar. These specimens have eroded protoconchs, but what remains suggests a polygyrate protoconch with an indication of gemmules on the first teleoconch whorl, observations consistent with these specimens being Group II forms. Whether these are related to *L. dickkilburni* or any of the other Group II species described above, or whether these forms comprise a geographically widely distributed separate species can only be established when more material is examined. Apparently, all of the specimens available to the author were dredged in deep water. The South African specimen had a label indicating that it was dredged off the Natal Coast at 200 m; the Makassar specimens from Indonesia were collected at a depth of 220 m.

L.c.f. dickkilburni, variant/form 3

Specimens from Mozambique in which the shell is largely white (with some residual faint maculations, particularly in the earlier whorls) may also be related to the forms above. Although the protoconch has not been preserved in any of the specimens examined, the general shape of these specimens differs from the similarly white "bulowi form" that belongs with the Group I species, but which is much more slender. The general shape of these specimens is much more similar to *L. dickkilburni*. However, curiously the aperture of *L. dickkilburni* and related forms that all have a darker exterior color is whitish, while the aperture of these seemingly somewhat albinistic specimens is dark. These specimens are apparently being sold by dealers in Mozambique material as "*Lophiotoma indica*, albinos" or "*Lophiotoma indica*, form bulowi," but at this time seem more likely to be a local endemic in the *L. dickkilburni* complex.

Groups III and IV species: Overview of the "*Lophiotoma unedo*" complex

All forms included in Groups III and IV have been identified in recent publications (and in most collections) as *Lophiotoma unedo*, or alternatively *Gemmula* (*Unedogemmula*) *unedo*—this name is occasionally applied to some of the species in Group II as well. This is one of the most confusing groups of the larger Turrinae. The larger spectrum of specimens available has revealed some general patterns.

In Powell's treatment of "*Gemmula unedo*," all of the specimens that he actually figured were from Japan (Powell, 1964), and the description of the species was largely based on Japanese specimens. In the period before 1964, the great majority of specimens available of this Group III complex were collected at depths of about 50 fathoms from southern Japan. Powell observed: "the peripheral carina is weakly gemmate in the first few postnuclear whorls, although in some specimens the beading may persist to the penultimate whorl"; later, in the formal description: "the earlier postnuclear whorls bear distinct gemmules in the peripheral carina and in a few instances these persist over most of the remaining whorls."

The analysis of a wider suite of specimens from a broader geographic area indicates two distinct classes of specimens, based on whether the peripheral carina has gemmules in the earlier postnuclear whorls (Group III), or whether the gemmules persist to most of the remaining whorls (Group IV). We believe that this character is reliable for separating almost all specimens into two taxonomically distinct groups. Over the entire range of the complex, there are representatives of both Groups III and IV, including the Japanese specimens assigned to *L. unedo*. The broader biogeographic survey indicates that the two groups are distinct from each other at all localities, with the morphological differences between the "early" (Group III) and "mostly" gemmate specimens (Group IV) more marked in non-Japanese material. This is particularly true in Australia, where there is not only a more striking morphological differentiation, but some biogeographic segregation of the two groups (III and IV) as well. The name *Pleurotoma* (*Turris*) *unedo* appears from Kiener's figure to apply to one of the "early" gemmate forms (Group III), and not to the "mostly" gemmate class (IV). The same appears to be true of the form *Pleurotoma* (*Turris*) *invicta*.

Group III: *Lophiotoma (Unedogemmula) unedo* and related forms with early postnuclear gemmate whorls

Group III forms comprise *Lophiotoma unedo* and related forms that typically have gemmules similar to *Gemmula* spp. on the first 3-4 postnuclear whorls, followed by a transition zone of 2-3 whorls where the gemmules become less distinct and may look like undulations in the peripheral keel. Most Group III forms are conventionally assigned to *L. unedo*; several other species such as *Lophiotoma hastula* (Reeve, 1843), a small very distinct species, and *Lophiotoma deshayishii* (Doumet, 1839) also fit the description above for Group III species, but they are sufficiently distinctive from *L. unedo* or *L. indica* that they have long been recognized as different taxa, and will not be further discussed here. The forms assigned to *L. unedo* in most collections and publications also include Group IV forms as noted above, but these are separable by the criteria described. However, even among "early gemmate" forms, there is still a very confusing array of morphologically diverse forms.

Most material labeled "*Lophiotoma unedo*" in collections and recent books is the large Japanese form. Kiener's type of the species is probably from Indonesia and is one of the forms more poorly represented in most present-day collections; this form was not discussed nor figured when Powell wrote his monograph on the Turrinae. The author feels that there is uncertainty as to whether the typical Japanese form is conspecific with the forms from Indonesia that are most similar to the type illustration. Although this is the form figured as *L. unedo* in most publications, the Japanese form is at the minimum atypical (when compared to the available Kiener figures) and may not even be the same species. We recognize one Group III form, *Lophiotoma capricornica*, new species, as a local endemic collected offshore in Queensland; the presence of fairly typical *L. unedo* in the same general locality justifies this separation.

Lophiotoma (*Unedogemmula*) *unedo*

Lophiotoma unedo is a confusing taxon; even when all of the "mostly gemmate" forms are removed, a wide variety of forms are potentially assignable to *L. unedo*, extending geographically from southern Japan to New South Wales, and from Fiji to southern India and the Arabian Peninsula. Kiener's type specimen, which apparently has not been located (R. Kilburn, personal communication), is probably from Indonesia.

Description

Shell large, fusiform with a deeply "U"-shaped posterior sinus. Adult specimens have 12-13 teleoconch whorls in addition to the polygyrate protoconch (that is generally broken or corroded in most specimens). There are about three postnuclear whorls that are gemmate, and an additional 2-3 that are transitional (where the gemmules are bisected and get progressively weaker). On the spire whorls, there is a maculated subsutural rib (or fused pair of ribs), followed by a concave area with 4-5 unmaculated threads and a peripheral keel with two ribs, also strongly maculated. On the last whorls before the body whorl, 1-2 additional primary cords are emergent. On the body whorl, there are distinctive zones: the strongly maculated subsutural region, followed by an unmaculated or much more lightly maculated concave region, the maculated periphery, a darker area with 4-5 smaller maculated cords which comprise most of the body whorl. From the base through much of the siphonal canal, there is a generally lighter zone with 5-8 primary cords. The tip of the canal is usually white, bordered by a dark brown area, generally significantly darker than the rest of the canal. The canal is broad and proportionally shorter than in other closely related forms. There are well-developed, raised revolving threads visible within the aperture. The broader angle of the spire, the relatively shorter and wider canal, and the raised threads in the aperture are features that distinguish the forms that we assign to *L. unedo* from other forms in the complex.

A number of specimens from Indonesia seem close to Kiener's type figure. These are generally thinner shells —the example shown in Fig. 5 (specimen 2) is from Makassar, Indonesia. Similar shells but lighter in color with more prominent subsutural cords have been collected in Aligway Island, and by the French expedition to Lubang Island, Philippines, in 180-200 m. These appear to be the closest morphological variant to the original Kiener illustration.

Variations

Most recently collected specimens that we assign to this species have much thicker shells than the typical form. In some specimens, the subsutural rib is massive, and the sculpture of spire whorls is dominated by the subsutural rib and the immediately adjacent peripheral keel of the preceding whorl, both maculated (Fig. 5, specimen 1). Smaller specimens with massive subsutural cords have been collected by trawlers off Kerala, India. Some Australian specimens examined seem intermediate between other forms of *L. unedo* and the description of *Unedogemmula binda* from New South Wales. The type of *binda* has the same well-developed, raised revolving threads visible within the aperture, and a "more obtusely rounded periphery with a weaker sinus rib and a shallower shoulder concavity, as well as more numerous basal spirals". Some Australian specimens have more numerous basal spirals on the body whorl than other forms of *unedo*, but do not have the rounded periphery of the *binda* holotype specimen. Until more material is available, we regard *binda* as an extreme form of *Lophiotoma unedo* from southeastern Australia.

L.c.f. unedo, variant/form 1, "Typical Japanese form"

The Japanese specimens that Powell figured as *L. unedo* are quite different from the Kiener type, and may or may not be conspecific. Since this form is so well represented in collections, we discuss it in more detail than other varieties.

Description (adapted from Powell, 1964)

Adult shell, 75-105 mm in height, solid, fusiform with a tall spire, and long anterior canal. Spire a little more than the height of the aperture + canal; spire angle 30-35. Sculptured, with two narrow, sharply raised spiral cords submargining the suture, followed by a bimarginate sinus rib which forms the peripheral angle at a little below median whorl height, then 2-3 primary spiral cords emergent between the sinus rib and the lower suture. On the base and neck there are about 17 primary spirals. On the concave shoulder area, there are from 4-7 crisp secondary spirals. All the interspaces carry from 1-3 spiral threads. Whorls, 12-13, exclusive of a multispiral narrowly conic smooth protoconch of 3-3.5 whorls, terminating in a half whorl of brevic

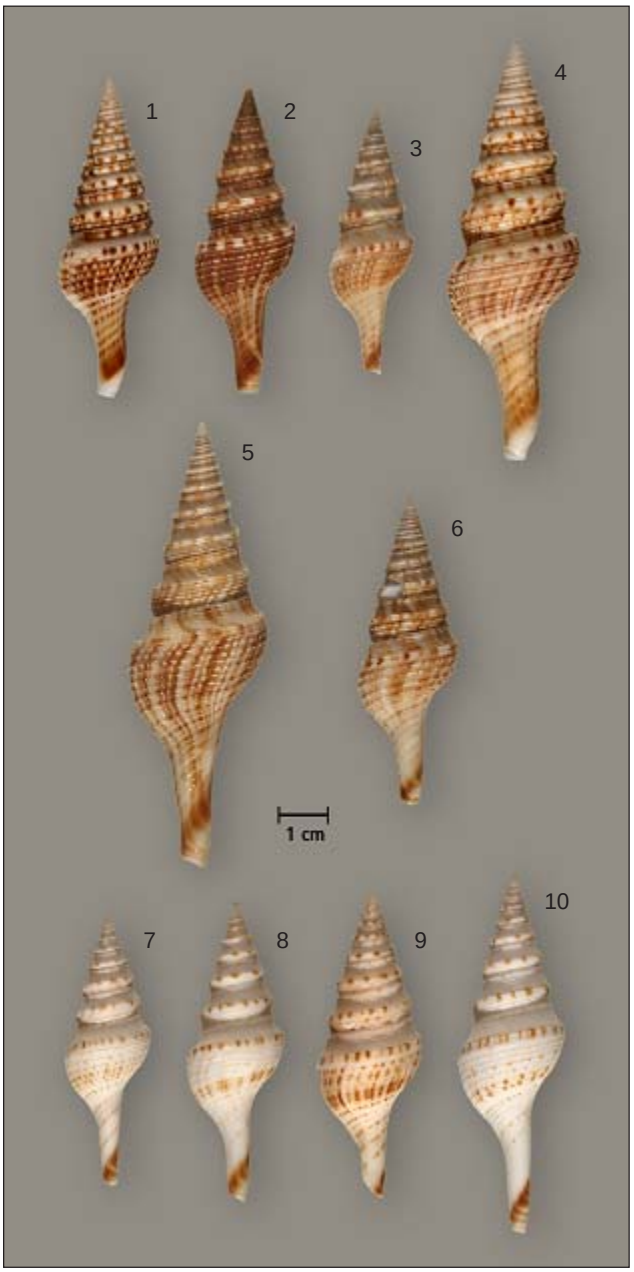

Fig. 5. Group III forms of *Lophiotoma*.

(Top row) *L. unedo*, different forms—specimen 1, variety with massive subsutural cords, Pamilacan Island, Bohol, Philippines; specimen 2, typical form, Makassar, Indonesia; specimen 3, Kii, Japan; specimen 4, large thick variety from Sindangan, Zamboanga del Norte, Philippines.

(Middle row) *L.c.f. unedo*, variant/form 1 ("typical Japanese form")—specimen 5, from Tosa Bay, Japan; specimen 6, from the Philippines.

(Bottom row) *L. capricornica*— specimen 7, holotype; specimen 8, paratype 6; specimen 9, paratype 2; and specimen 10, paratype 1. All specimens of *L. capricornica* were trawled in deep water off Queensland, probably in the Capricorn Islands.

axials. The postnuclear whorls bear distinct gemmules on the peripheral carina. Color pattern consisting of small reddish-brown dots, diffused into slightly larger maculations around the subsutural collar and the sinus rib, the whole loosely and irregularly connected axial by flexious, pale reddish-brown streaks that follow the successive grow lines. Brown color in interior, aperture white. In occasional specimens, the sinus rib carries a third but weaker spiral than the two margining ones. Operculum leaf-shaped with an apical nucleus. Most specimens of this form are described from southern Japan at depths of 50 fathoms. A few specimens of this variant ("Japanese form") are labeled as being collected from northern Australian localities; these are all specimens from commercial dealers, and the localities need to be verified. However, until there is a more reliable characterization of these forms, we feel that it would be premature to separate them at the subspecific or specific level, or to conclude that they are conspecific.

***Lophiotoma capricornica*, new species**

This form seems most closely related to the "typical Japanese form" described above. Both have a more slender shell, with a proportionally longer aperture. Like *L. unedo*, as well as *L.c.f. unedo*, variant/form 1 ("typical Japanese form"), there is the typical white tip and brown marking bordering the white-tipped canal. However, *L. capricornica* is much thinner and distinctly different in its sculpture.

Description

The shell is much whiter, thinner, and narrower than other related Group III forms conventionally assigned to the *L. unedo* complex, with 10-11 whorls. The subsutural area is defined by a rib that is faintly maculated some distance from the suture, followed by a slightly concave region with 3-4 white primary

threads. The peripheral keel has two cords and narrow brown axial markings. The primary cords are relatively fine and are mostly white. There is an area of two cords at the base that are more highly maculated than the other spiral cords on the body whorl. The remainder of the base and the canal is white except at the tip where a dark diagonal brown marking, typical of many forms in the *L. indica*/*L. unedo* complex, is found. In most specimens, this diagonal dark brown band is striking against the very white color of the background and the relatively sparse maculations in the rest of the shell.

All of the specimens examined were collected off Queensland, and trawled by fishing boats between 40-120 fathoms. Most were reportedly trawled near Lady Musgrave Island. Freshly collected specimens of *L. capricornica* have an attractive silky appearance. The species does not appear to have any raised lines inside the aperture, as described for other forms of Group III *Lophiotoma*.

Type material

The holotype will be deposited at the MNHN, Paris. Paratypes will be deposited at AMNH, New York; USNM, Washington; Western Australian Museum, Perth; CFM, Chicago; LACM, Los Angles; and ANSP, Philadelphia. Data on the types are given in the Appendix.

Group IV: "Mostly Gemmate" *L. unedo*-like forms

The Group IV forms have gemmules beyond the early postnuclear whorls, typically up to the penultimate whorl. These comprise a confusing set of morphologically diverse deep-water forms, and there is almost certainly more speciation in the group than will be formally recognized here. Some varieties in this group are very similar to the species in Group III, but distinguishable by the presence of gemmules on the peripheral carina of most whorls. A characteristic feature is that markings on the peripheral carina are restricted to the area between gemmules; these can be very regular in the earlier spire whorls, but invariably become irregular (and sometimes absent) in the last two whorls. Another general feature of all forms in this group is the presence of irregular maculations in the subsutural area.

Forms in this group have been collected in Japan, the Philippines, western Australia, New Caledonia, Madagascar, and Reunion. There is considerable morphological diversity, and how the various forms are related to each other requires additional analysis of more specimens. We describe a new species that is represented by many specimens collected from the central Philippines, *L. panglaoensis*, and have deliberately restricted the type material to a narrow morphological range from a narrow geographic locality. Three other distinctive forms described below may or may not be conspecific with *L. panglaoensis*. The Group IV specimens from deep water off Madagascar appear sufficiently distinct to merit separation at the species level, and are of particular interest since they suggest a close relationship between Group IV *Lophiotoma* and certain *Gemmula* spp., and thus provide the basis for a hypothetical evolutionary scenario (Discussion). Although this group is relatively poorly represented in most collections, the deep water expedition carried out by the Paris Museum, and gill-net collecting in the central Philippines suggest that Group IV forms are common at depths of 200-600 m, and that there may be a large number of yet-undiscovered species belonging to this general division of *Lophiotoma*.

Lophiotoma panglaoensis, new species

Description

Most specimens examined are medium-sized for the genus (45-65 mm); the protoconch is not preserved in any of the type specimens. There are 10-11 teleoconch whorls. The subsutural region has an irregularly maculated spiral cord (split into two in some specimens). A white concave area with about five white spiral cords separates the subsutural region from the peripheral carina. The peripheral carina has two cords running parallel and is characterized by the presence of numerous gemmules up to the penultimate whorl in most specimens. There is a distinctive brownish stain (varying from orange-brown to purplish-brown) in the interstices between the gemmules (which are whitish); this is typically on the edge of the gemmule away from the

aperture. The stain between the gemmules is more regularly spaced in the earlier whorls, becoming more irregular, particularly in the body whorl. The frequency and intensity of interstitial gemmule coloration shows considerable variation; these can be much lighter in some specimens, and even absent. On the later teleoconch whorls, there are between 1-3 primary cords emergent. These whorls have axial brown markings, that originate at the interstitial brown area of the peripheral rib and run parallel to the growth line. In the body whorl, there are approximately 13-16 primary cords that continue to the siphonal canal with secondary threads in between; in many specimens, the base and posterior canal are generally lighter in color than the region of the body whorl next to the peripheral canal. The very tip of the canal is whitish, with a diffuse brownish band bordering it. The holotype and some paratypes are shown in Fig. 6A, top row, and Fig. 6B, specimens 1 and 2.

Type material

The holotype and paratypes 1-10 were collected off Panglao Island, Bohol, Philippines, by tangle nets in about 200 fathoms (the major commercial product of this fishery is *Murex alabaster*, an attractive ornamental species). One specimen in the Los Angeles County Museum, collected by James Norton in July 1966, belongs to this series (paratype 11). This specimen, LA CMNH 75849 was collected between 52-60 fathoms on sand and mud bottom, east of Talaga, Batangas Bay, southwest Luzon, Philippines. The other paratypes include a series (12-14) collected from Lubang Island, off Mindoro by the MNHN, Paris. Thus, the type series includes specimens from the central Philippines (Panglao Island) to southwest Luzon Island.

Discussion

The type material was deliberately restricted to specimens that closely resemble the holotype specimen collected off Panglao Island. A specimen in the collection of the American Museum of Natural History from Tosa, Japan appears to be conspecific with *L. panglaoensis*, strongly suggesting that the species occurs to southern Japan. The distribution of shell morphology found in the specimens from Lubang expeditions of the Paris Museum suggests that there may be two distinctive forms of *L. panglaoensis*, or two sympatric species. The Lubang form that appears to be typical *L. panglaoensis* (paratypes 12-14) was collected between 190-210 m; some morphologically distinct specimens (see *L.c.f. panglaoensis*, variant/form 2 below) were apparently collected in the same general area. The material from Panglao is presumably from even greater depths; most Panglao Island specimens are thinner, more whitish and slender compared to the shallower Lubang Island material.

All of the type material for *L. panglaoensis* is in the smaller size range of Group IV forms; some forms belonging to this group are the largest and heaviest *Lophiotoma* yet found, particularly the western Australian material. The forms potentially related to *L. panglaoensis* are summarized below.

Distinctive forms related to *L. panglaoensis*

Several forms collected in the same central Philippines region as *L. panglaoensis* are potentially variants of *L. panglaoensis*, but were deliberately excluded from the type material because of the possibility that they may be taxonomically distinct; two of the most distinctive forms, *L.c.f. panglaoensis*, variant/forms 1 and 2, are described below. The western Australian material (*L.c.f. panglaoensis*, variant/form 3) is very distinctive, but at this time it is not possible to judge whether it is separable at the species or subspecific level, or an unusually large albinistic variety, conspecific with *L. panglaoensis*.

L.c.f. panglaoensis, variant/form 1, broad thin form

This is an extremely thin shell, much finer but with a broader spire than the type material, which is shown in Fig. 6A, specimen 5.

L.c.f. panglaoensis, variant/form 2

This form has much darker, larger purplish-brown interstitial markings than the typical *L. panglaoensis*,

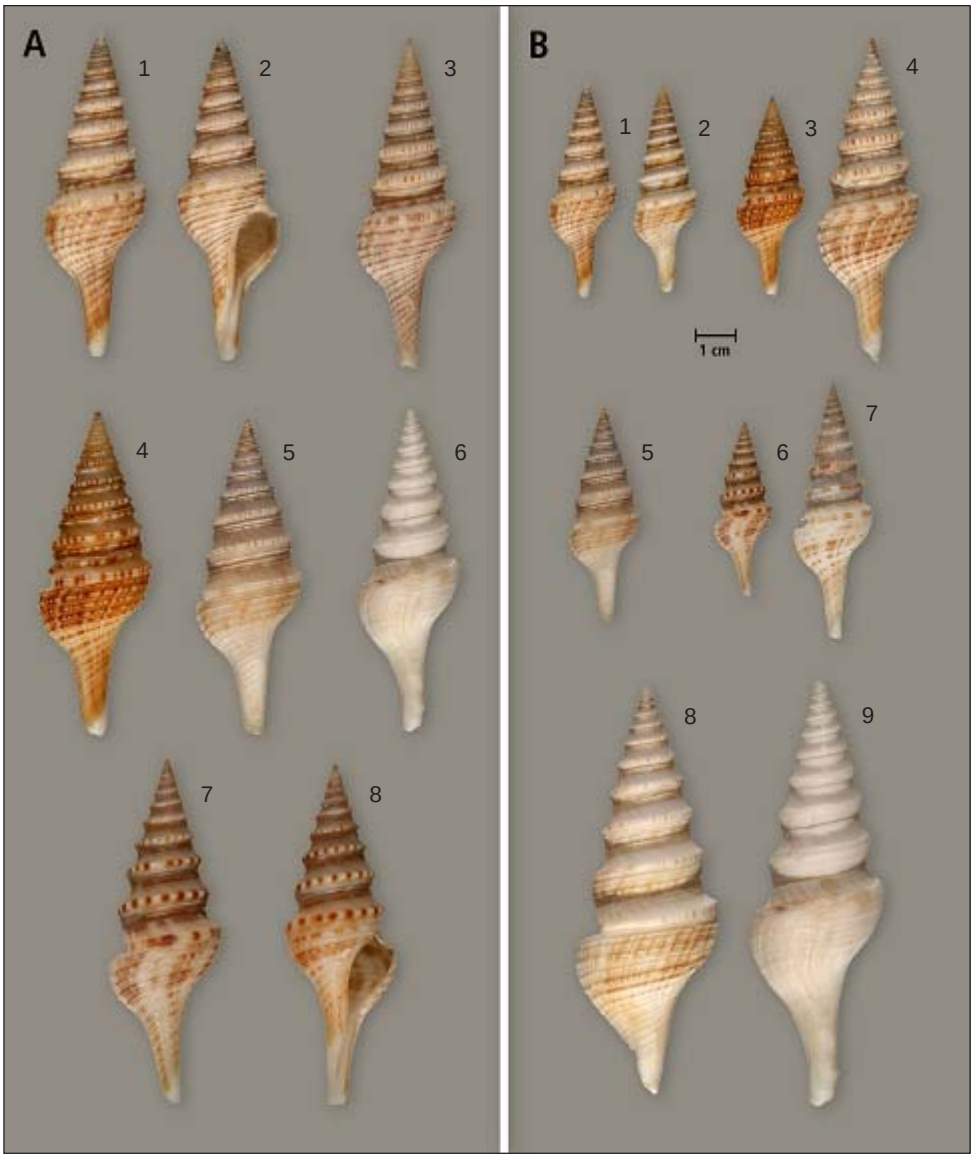

Fig. 6. Group IV *Lophiotoma* species and distinctive variants.
Fig. 6A. (All specimens figured approximately the same size, not proportional to natural size). A1-3 *Lophiotoma panglaoensis*, new species. A1 and A2 are the holotype, A3 is paratype 12. A4-6 Distinct variant/forms potentially related to *L. panglaoensis*. A4 is the dark brown form of *L.c.f. panglaoensis*, variant/form 2; A5 is the broad thin form of *L.c.f. panglaoensis*, variant/form 1; and A6 is the western Australian form of *L.c.f. panglaoensis*, variant/form 3. A7-8 *L. madagascarensis*, two views of the holotype.

Fig. 6B. The same set of forms (with some different specimens) illustrated showing relative size. B1-4: B1 (holotype) and B2 (paratype 4) are *L. panglaoensis*; B3 and B4 are *L.c.f. panglaoensis*, variant/form 2, extreme morphs. Note the much more prominent spots between gemmules in the peripheral carina compared to typical *L. panglaoensis*. B5-7 *L.c.f. panglaoensis*, variant/form 1 (same specimen as in A5). B6 and B7 are *L. madagascarensis*. B6 is the holotype from Madagascar, B7 is a variety from Reunion. B8-9 *L.c.f. panglaoensis*, variant/form 3, both collected off western Australia by scampi fishermen in very deep water. B9 is from the American Museum of Natural History collection (AMNH 223170).

with thicker, sturdier shells, deeper brown in background color in the body whorl and much broader (Fig. 6A, specimen 4 and Fig. 6B, specimens 3 and 4). Shells of this form can be much larger than typical *L. panglaoensis* (Fig. 6B) and are apparently also found in Japan. In some museum collections, such specimens are labeled "*Unedogemmula unedoides*"; it appears that this is a manuscript name by Kuroda that was never

published. This form can be morphologically very similar to some specimens of *L. unedo*, but can be distinguished by the persistence of gemmules to the penultimate whorl. It is possible that there is more than one taxon that we have included in this group.

L.c.f. panglaoensis, variant/form 3

A number of large *Lophiotoma* specimens were collected in deep water, typically 300-400 m off western Australia by scampi fishermen. Most of these differ from the typical *L. panglaoensis* in being larger, generally lighter in color (many specimens are pure white), and in the absence of strong subsutural sculpture. As described above, there is variation in coloration even in typical *L. panglaoensis*, but the much larger average size and the absence of sculpture in the subsutural region distinguishes most of the western Australian material from typical *L. panglaoensis*. A few western Australian specimens (Fig. 6B, specimen 8 for an example) have the general outline of *L. panglaoensis* (albeit broader and larger); on these specimens, light interstitial maculations can be seen. However, the majority of specimens are much larger, whiter in color, and have a much weaker subsutural cord than typical *L. panglaoensis* (Fig. 6A, specimen 6, and Fig. 6B, specimen 9). We think it likely that the western Australian form deserves at least subspecific separation from *L. panglaoensis*. There is considerable morphological variation in the western Australian material, and it is conceivable that these comprise more than one species.

***Lophiotoma madagascarensis*, new species**

In addition to *L. panglaoensis* and the distinctive forms described above, there is a Group IV species collected in the western Indian Ocean in relatively deep water. This form is quite distinct from all of the other variations and forms described above, and appears to be clearly separable from *L. panglaoensis*.

Description

The protoconch is polygyrate, and is followed by 10 teleoconch whorls. There are two thin subsutural cords irregularly maculated followed by approximately 5 fine white threads, with the subsutural maculations extending out to the threads to a varying extent in different specimens. The peripheral carina has gemmules, and between the gemmules, the cord is stained regularly in the earlier whorls with a deep purple-brown color. On the body whorl, the gemmules become obsolete and the maculations on the peripheral cord become very irregular in most mature specimens. There are 13-14 primary cords on the body whorl with 1-2 threads in between each primary cord. The ground color is a light off-white, with the very tip of the canal somewhat whiter than the rest of the body whorl. The spiral cords are sparsely and irregularly maculated with the same purplish-brown color as the periphery, and are organized axially on the body whorl giving an intermittent pattern of purplish brown that is most intense between the third and fifth primary cord from the peripheral carina, and becomes much lighter at the base and siphonal canal. Most of the specimens examined were collected off Madagascar, in 300-460 m.

A specimen collected in Reunion from an expedition in 1982 in 450-480 m (MD32/Reunion, St. CP179, 21° 03 S 55° 10 E) is more finely sculptured than the specimens from Madagascar, but is likely to be conspecific with *L. madagascarensis*, with the maculations on the peripheral carina narrower and less prominent than in the Madagascar specimens. The protoconch is polygyrate and there are 13 teleoconch whorls, with the last two lacking gemmules.

Discussion

L. madagascarensis can be distinguished from *L. panglaoensis* by the thinner shell, the more triangular shape of the whorls resulting in a broader spire angle coupled with a constricted suture, and by the bolder maculations on the peripheral carina. Examples of this species are illustrated in Fig. 6A, bottom row, and Fig. 6B, specimens 6 and 7.

DISCUSSION

Larger *Lophiotoma* specimens are generally identified either as *Lophiotoma indica* or *Lophiotoma*

(*Unedogemmula*) *unedo* in most publications and collections. In this work we have examined all forms that were accessible to us, which are conventionally assigned to the two taxa. A total of 21 distinctive forms can be differentiated morphologically; all of these have previously been identified as "*indica*" or "*unedo*". Of the 21 forms, in the opinion of the author, at the present time nine are sufficiently distinctive to separate at the species level (seven new species are described above), and one new subspecies is proposed. The assignment of the 11 remaining forms needs further evaluation; molecular data may be particularly useful in these cases.

Any assessment of the evolutionary relationships between various forms of the *Lophiotoma* spp. described in this manuscript must be clearly regarded as preliminary. However, there is a clear gradient from *Gemmula*-like to true *L. indica*-like forms. Thus, the deep-water forms related to *L. panglaoensis* (Group IV) are the most *Gemmula*-like of this series; the forms in Group III related to *L. unedo* are intermediate in having the first few postnuclear whorls gemmate, followed by a transitional region with the larger whorls having gemmules largely absent (this group roughly corresponding to *Unedogemmula*). Forms such as *L. friedrichbonhoefferi* (Group II) represent a further transition, in having relict gemmules in the first postnuclear whorl. Finally, there are the forms in Group I that all have blunt paucispiral protoconchs with gemmules absent from all postnuclear whorls (a group that corresponds to Powell's concept of *Lophioturris*). The gradient from *Gemmula*-like to *Lophiotoma*-like forms roughly parallels the bathymetric range of these forms. The more highly gemmate forms such as *L. panglaoensis* are collected in deeper water, and only the Group I forms such as *L. indica* are found in shallow water (in certain cases in intertidal habitats). Like all generalizations in biology, there are exceptions: *L. indica queenslandica* is a Group I form that is apparently only found in deeper water.

This range of forms from *Gemmula*-like to *Lophiotoma*-like suggests a working hypothesis for the evolution of the larger Turrinae. The longer geological history of *Gemmula*, and its much wider biogeographic distribution (with living forms in the Caribbean and Eastern Pacific, and a richer early Tertiary fossil record) compared to the two other major groups of Indo-Pacific Turrinae (*Turris* and *Lophiotoma*, that only have a fossil record back to the Miocene) makes a *Gemmula*-like ancestor likely for both *Lophiotoma* and *Turris*.

There are several reasons to suggest that the closest group within *Gemmula* to this branch of *Lophiotoma* is the species complex related to *G. kieneri*. The stained interstices between gemmules that is characteristic of Group IV species (*L. madagascarensis* and *L. panglaoensis*), as well as the irregularity of maculations on the subsutural cord are features shared by *L. madagascarensis*, *L. panglaoensis*, and *G. kieneri*. Some unusual specimens of *G. kieneri* even show the irregular maculations in both the peripheral carina and the primary cords on the body whorl characteristic of Group IV *Lophiotoma*.

A putative common ancestor of the *L. madagascarensis*/*L. panglaoensis* Group IV complex and *G. kieneri* may have resembled certain forms in the *G. kieneri* complex. It is notable that the specimens of *G. kieneri* that are at the extreme edge of the range, such as northern Mozambique and New Caledonia, are much more similar to the form in Hawaii given the name *Gemmula interpolata* (Powell, 1966), a species closely allied to *G. kieneri*. A comparison of these forms with *L. madagascarensis* is shown in Fig. 7. It seems reasonable to suggest that an ancestral form similar to these morphs within the *G. kieneri* complex, as well as the deep-water *L. madagascarensis* could have been the progenitor of both the *G. kieneri* complex of species (including *G. kieneri* and *G. interpolata*) as well as the Group IV *Lophiotoma* species discussed above. Some specimens of *L. madagascarensis* show a strong affinity for some Group III forms, particularly *L. capricornica*. Thus, deriving Group III from the putative *Gemmula* ancestor would involve a more extensive loss of gemmules from the peripheral carina with adult development.

The Group II species above, with forms like *L. bisaya* and *L. friedrichbonhoefferi*, were postulated in the first paper of the series as being a potential ancestral link from *Gemmula* to certain types of *Turris* species (such as *Turris pagasa* (Olivera, 1999)). Thus, one could imagine that the evolution of both *Lophiotoma* and *Turris* from a *Gemmula*-like ancestor may have involved ancestral forms similar to living Group II, III,

Fig. 7A. Series illustrating one branch of *Gemmula* related to Group III and Group IV *Lophiotomas*.
The specimens are not figured to scale in Panel A. From left to right: A1 *L.c.f. unedo*, variant/form 1 ("typical Japanese form"); A2 *L. capricornica* from Queensland, Australia; A3 *L. madagascarensis* variety, Reunion; A4 *L. madagascarensis*, holotype, Madagascar; A5 *G. interpolata*, Oahu, Hawaii; and A6 *G. kieneri*, Mozambique variety.

Fig. 7B. Some of the same species shown to scale with additional varieties of some of the species illustrated. From left to right: B1 *L.c.f. unedo*, variant/form 1, "typical Japanese form" (Group III); B2 *L. capricornica*, Queensland, Australia (Group III); B3 *L. madagascarensis* (Group IV) Madagascar; B4 *L. madagascarensis* variety (Group IV), Reunion; B5 and B6 *G. interpolata*, Oahu, Hawaii (note that the shape of these specimens is not dissimilar from some of the Group III *Lophiotomas*); B7, B8, and B9 are various varieties of *G. kieneri* taken from Mozambique, Philippines, and Japan, respectively.

and IV forms discussed above. Although a progression would appear logical from *Gemmula* spp. with gemmules, to Group IV/III forms with gemmules in some whorls, to Group II/I forms with gemmules mostly absent, we suspect that most Group II/I forms are more likely independently derived from a different *G. kieneri*/*interpolata*-like ancestor. The regular body maculations of some forms of *G. interpolata* are consistent with this branch of *Gemmula* being most closely related to Group I and II *Lophiotomas* as well. Clearly, further characterization of the biology, anatomy, and molecular biology of the living species will provide data that would be relevant to an examination of this general evolutionary scheme for the Turrinae. This hypothesis makes several predictions: (1) that *G. kieneri*/*G. interpolata* will prove to be genetically closer to *L. madagascarensis*/*L. panglaoensis* and even *L. friedrichbonhoefferi* than any other clade in *Gemmula*;

and (2) that these particular *Gemmula* may even be genetically more allied to the group of *Lophiotoma* species that is the subject of this paper than to some other forms presently included in *Gemmula*. Thus, this is an evolutionary hypothesis that in principle can be evaluated as more detailed morpho-anatomical, molecular and biochemical data become available for the relevant taxa.

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APPENDIX (prepared by Nancy Kurtzeborn).

Summary of types of new *Lophiotoma* species and subspecies.

Species	Measurement (mm)			Locality
	Height	Width[a]	Aperture[b]	
Lophiotoma indica queenslandica, new subspecies				
Holotype	47.3	15.6	19.1	Queensland, Australia
Paratype #1	62.8	19.3	36.6	Cape Moreton, Queensland, Australia
Paratype #2	67.0	21.2	41.8	Swain Reefs, Queensland, Australia
Paratype #3	41.6	14.2	24.7	Swain Reefs, Queensland, Australia[1]
Paratype #4	57.0	19.0	32.8	Queensland, Australia
Paratype #5	60.8	19.3	35.2	Queensland, Australia
Paratype #6	77.4	25.1	42.8	Queensland, Australia
Paratype #7	72.9	24.7	42.3	Queensland, Australia
Paratype #8	64.8	21.0	37.2	Australia
Paratype #9	42.7	15.2	24.5	Queensland, Australia
Paratype #10	36.8	12.4	21.8	Australia
Paratype #11	53.3	16.9	30.8	Queensland, Australia
Paratype #12	68.0	22.1	41.0	Cape Moreton, Queensland, Australia
Paratype #13	63.5	20.4	35.9	Swain Reefs, Queensland, Australia
Paratype #14	68.5	22.8	34.7	Swain Reefs, Queensland, Australia
Paratype #15	71.7	24.6	44.8	Swain Reefs, Queensland, Australia
Paratype #16	75.0	22.9	46.3	Swain Reefs, Queensland, Australia
Paratype #17	68.5	21.1	38.1	Swain Reefs, Queensland, Australia[2]
Lophiotoma freidrichbonhoefferi				
Holotype	35.8	10.8	18.9	Aligway Island, Philippines
Paratype #1	39.0	11.4	20.0	Aligway Island, Philippines
Paratype #2	35.6	10.4	18.9	Aligway Island, Philippines
Paratype #3	39.0	11.6	20.1	Aligway Island, Philippines
Paratype #4	35.4	10.3	19.0	Aligway Island, Philippines
Paratype #5	41.8	12.2	21.6	Aligway Island, Philippines
Paratype #6	31.0	10.2	16.1	Aligway Island, Philippines
Paratype #7	47.7	13.4	24.5	Aligway Island, Philippines
Paratype #8	44.1	12.3	23.7	Aligway Island, Philippines
Paratype #9	48.2	13.1	24.3	Aligway Island, Philippines
Paratype #10	52.3	14.5	26.8	Aligway Island, Philippines
Paratype #11	35.9	11.1	18.5	Aligway Island, Philippines
Paratype #12	34.7	10.7	18.8	Aligway Island, Philippines
Paratype #13	28.7	11.3	20.0	Aligway Island, Philippines
Paratype #14	36.6	10.9	18.5	Aligway Island, Philippines
Paratype #15	31.9	9.7	16.9	Aligway Island, Philippines
Paratype #16	18.7	6.6	10.0	Aligway Island, Philippines
Paratype #17	37.8	11.3	19.4	Aligway Island, Philippines
Paratype #18	36.0	11.1	17.7	Aligway Island, Philippines
Paratype #19	35.2	10.5	17.7	Aligway Island, Philippines
Paratype #20	34.6	10.6	17.4	Aligway Island, Philippines
Paratype #21	32.7	9.9	17.0	Aligway Island, Philippines
Paratype #22	33.6	10.1	17.6	Aligway Island, Philippines
Paratype #23	30.6	9.9	16.3	Aligway Island, Philippines
Paratype #24	29.9	9.5	15.4	Aligway Island, Philippines
Paratype #25	24.2	8.1	13.0	Aligway Island, Philippines
Paratype #26	35.6	10.7	18.1	Aligway Island, Philippines
Paratype #27	35.7	11.5	18.6	Aligway Island, Philippines
Paratype #28	36.6	10.4	19.1	Aligway Island, Philippines
Paratype #29	34.2	10.6	17.4	Aligway Island, Philippines
Paratype #30	30.8	10.1	16.7	Aligway Island, Philippines
Paratype #31	33.0	10.3	17.5	Lubang Island, Philippines (MNHN)[3]
Paratype #32	24.9	8.3	13.4	Lubang Island, Philippines (MNHN)[3]

Species	Measurement (mm)			Locality
	Height	Width[a]	Aperture[b]	
Lophiotoma bisaya				
Holotype	67.9	21.0	35.6	Aligway Island, Northern Mindanao, Philippines
Paratype #1	51.3	16.2	25.9	Aligway Island, Northern Mindanao, Philippines
Paratype #2	54.5	16.1	27.5	Aligway Island, Northern Mindanao, Philippines
Paratype #3	59.1	16.6	31.7	Aligway Island, Northern Mindanao, Philippines
Paratype #4	58.1	19.4	32.2	Aligway Island, Northern Mindanao, Philippines
Paratype #5	64.9	19.5	33.7	Aligway Island, Northern Mindanao, Philippines
Paratype #6	47.1	14.6	24.4	Aligway Island, Northern Mindanao, Philippines
Paratype #7	70.7	20.2	37.9	Aligway Island, Northern Mindanao, Philippines
Paratype #8	63.3	18.8	33.4	Aligway Island, Northern Mindanao, Philippines
Paratype #9	80.8	23.8	40.0	Aligway Island, Northern Mindanao, Philippines
Paratype #10	61.2	18.2	33.5	Aligway Island, Northern Mindanao, Philippines
Paratype #11	73.6	22.6	37.2	Aligway Island, Northern Mindanao, Philippines
Paratype #12	61.3	17.7	32.9	Aligway Island, Northern Mindanao, Philippines
Paratype #13	71.4	21.3	37.3	Aligway Island, Northern Mindanao, Philippines
Lophiotoma tayabasensis				
Holotype	85.0	24.8	44.7	Tayabas Bay, Philippines
Paratype #1	73.3	22.0	40.4	Tayabas Bay, Philippines
Paratype #2	83.8	25.5	46.5	Tayabas Bay, Philippines
Paratype #3	99.2	28.4	52.3	Probably from Tayabas Bay, Philippines
Paratype #4	94.7	27.4	49.5	Probably from Tayabas Bay, Philippines
Paratype #5	88.1	27.7	49.1	Probably from Tayabas Bay, Philippines
Paratype #6	92.8	27.7	48.7	Probably from Tayabas Bay, Philippines
Paratype #7	98.1	28.4	54.5	Probably from Tayabas Bay, Philippines
Paratype #8	76.8	23.4	42.6	Tayabas Bay, Philippines
Paratype #9	93.8	27.7	46.5	Probably from Tayabas Bay, Philippines
Paratype #10	96.3	28.9	52.8	Probably from Tayabas Bay, Philippines
Paratype #11	93.1	28.0	47.5	Probably from Tayabas Bay, Philippines
Paratype #12	95.4	27.8	48.3	Probably from Tayabas Bay, Philippines
Paratype #13	87.3	27.1	47.5	Probably from Tayabas Bay, Philippines
Paratype #14	98.8	29.8	53.6	Probably from Tayabas Bay, Philippines
Paratype #15	86.9	26.4	45.5	Between Mactan and Bohol Island, Philippines
Paratype #16	65.4	19.2	37.6	Between Mactan and Bohol Island, Philippines
Paratype #17	106.9	31.7	57.5	Probably from Tayabas Bay, Philippines
Paratype #18	91.0	27.7	48.2	Probably from Tayabas Bay, Philippines
Paratype #19	87.2	26.7	47.0	Probably from Tayabas Bay, Philippines
Paratype #20	87.1	27.3	47.9	Sindangan, Dipolog, Philippines
Paratype #21	85.6	25.5	45.5	Probably from Tayabas Bay, Philippines
Paratype #22	93.6	28.0	51.3	Probably from Tayabas Bay, Philippines
Paratype #23	76.6	22.8	40.6	Between Mactan and Bohol Island, Philippines
Paratype #24	97.0	28.5	52.6	Between Mactan and Bohol Island, Philippines
Paratype #25	61.7	20.1	34.7	Between Mactan and Bohol Island, Philippines
Paratype #26	83.2	23.9	45.9	Between Mactan and Bohol Island, Philippines
Paratype #27	74.8	22.0	40.1	Between Mactan and Bohol Island, Philippines
Paratype #28	69.0	22.0	39.8	Between Mactan and Bohol Island, Philippines
Lophiotoma dickkilburni				
Holotype	63.4	19.2	30.1	Tongaat, Natal, South Africa
Paratype #1	69.8	21.4	34.5	Angoche, Northern Mozambique
Paratype #2	56.0	18.0	27.2	Tongaat, Natal, South Africa
Paratype #3	46.2	16.0	23.4	Tongaat, Natal, South Africa (broken)
Paratype #4	43.8	13.2	11.6	Tongaat, Natal, South Africa
Paratype #5	53.9	17.9	19.0	Tongaat, Natal, South Africa

Species	Measurement (mm)			Locality
	Height	Width[a]	Aperture[b]	
Paratype #6	69.6	20.3	34.3	Mozambique (AMNH 162582)[4]
Paratype #7	73.0	24.3	35.8	Mozambique (AMNH 162582)[4]
Paratype #8	54.2	18.1	28.3	Natal, South Africa (AMNH 174780)[5]
Lophiotoma capricornica				
Holotype	60.7	19.3	33.9	Queensland, Australia
Paratype #1	73.3	21.3	41.9	Queensland, Australia
Paratype #2	60.9	21.1	33.5	Queensland, Australia (canal damaged)
Paratype #3	64.0	19.2	34.5	Queensland, Australia
Paratype #4	54.3	17.6	29.7	Queensland, Australia
Paratype #5	58.2	19.1	32.6	Queensland, Australia
Paratype #6	54.7	17.6	31.8	Queensland, Australia
Lophiotoma panglaoensis				
Holotype	54.2	17.2	27.9	Panglao, Bohol Island, Philippines
Paratype #1	60.1	18.5	31.2	Panglao, Bohol Island, Philippines
Paratype #2	46.5	15.1	22.3	Panglao, Bohol Island, Philippines
Paratype #3	59.3	18.5	28.4	Panglao, Bohol Island, Philippines
Paratype #4	52.7	16.5	25.1	Panglao, Bohol Island, Philippines
Paratype #5	45.2	15.0	22.9	Panglao, Bohol Island, Philippines
Paratype #6	54.2	17.2	26.2	Panglao, Bohol Island, Philippines
Paratype #7	49.5	15.5	25.6	Panglao, Bohol Island, Philippines
Paratype #8	73.6	24.7	38.8	Panglao, Bohol Island, Philippines
Paratype #9	64.2	21.2	34.1	Panglao, Bohol Island, Philippines
Paratype #10	64.8	20.4	34.7	Panglao, Bohol Island, Philippines
Paratype #11	46.6	14.9	23.8	SW Luzon Island, Philippines (LACM 75849)[6]
Paratype #12	49.6	15.7	25.0	Lubang Island, Philippines (MNHN)[7]
Paratype #13	36.8	11.8	18.5	Lubang Island, Philippines (MNHN)[7]
Paratype #14	46.1	14.4	22.5	Lubang Island, Philippines (MNHN)[8]
Lophiotoma madagascarensis				
Holotype	44.7	15.0	23.4	Madagascar (MNHN)[9]
Paratype #1	42.8	13.9	22.1	Madagascar (MNHN)[9]
Paratype #2	54.4	18.6	28.8	Madagascar (MNHN)[9]
Paratype #3	64.9	19.8	32.5	Madagascar (MNHN)[10]
Paratype #4	54.9	18.4	28.4	Madagascar (MNHN)[11]
Paratype #5	59.1	19.4	29.8	Madagascar (MNHN)[11]
Paratype #6	66.1	21.4	32.9	Madagascar (MNHN)[11]
Paratype #7	63.5	21.0	33.0	Madagascar (MNHN)[11]
Paratype #8	63.2	20.3	32.0	Madagascar (MNHN)[11]
Paratype #9	65.2	21.7	32.8	Madagascar (MNHN)[11]
Paratype #10	60.8	19.2	30.3	Madagascar (MNHN)[11]
Paratype #11	67.7	22.3	32.0	Madagascar (MNHN)[11]
Paratype #12	59.0	19.8	29.4	Madagascar (MNHN)[11]
Paratype #13	55.9	18.6	28.3	Madagascar (MNHN)[11]
Paratype #14	60.8	19.6	30.8	Madagascar (MNHN)[11]
Paratype #15	61.9	20.2	30.6	Madagascar (MNHN)[11]
Paratype #16	65.1	20.8	34.1	Madagascar (MNHN)[11]
Paratype #17	62.1	21.0	31.6	Madagascar (MNHN)[11]
Paratype #18	65.5	19.6	32.5	Reunion[12]

[a]Width of shell at its widest point.
[b]Length from posterior of aperture to anterior tip of siphonal canal.

[1]S7E Swain Reefs, Australia 5/98; trawled 104-105 fathoms between 22°35' S 153°16' E and 22° 26' S 153° 22' E.
[2]Swain Reefs, Australia 6/98; trawled in 91 fathoms 22° S to 22° 18' S.
[3]Musorstom St. 56, Lubang Island, Philippines; 134 m 14° 00' N 120°20' E.
[4]20 miles off mouth of Limpop River, Mozambique; 200-300 m, mud bottom.
[5]Off Tugela River mouth, Natal, South Africa; 100 fathoms, mud bottom.
[6]East of Talaga, Batangas Bay, Batangas Province, SW Luzon Island, Philippines; 52-67 fathoms on sand and mud bottom.
[7]Musorstom St. 10; 187-205 m 14° N 120° 19' E.
[8]Musorstom 2-Philippines St. CP66, Lubang Island, Philippines; 192-209 m 14° 00' N 120°20' E.
[9]Madagascar; 300 m Dragage 3 Sables calco-quartzeux 12°36.0' S 48° 17.3' E.
[10]SW Madagascar, Campagne crevettiere 1986, St. 117; 370 m 22°15' S 43°07' E.
[11]SW Madagascar, Campagne crevettiere 1986, St. 57; 460 m 22°26' S 43°06' E.
[12]MD32/Reunion 1982, St. CP179; 450-480 m 21°03' S 55°10' E.