EXPLORING NOVEL TAXONOMIC CHARACTER SETS IN THE MOLLUSCA: THE *CRIBRARULA CRIBRARIA* COMPLEX (GASTROPODA: CYPRAEIDAE) AS A CASE STUDY

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Chapter 6

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ABSTRACT

The goal of this dissertation is to explore novel and non-traditional taxonomic characters that may be useful for mollusks, and combine them with radular and shell characters to carry out a taxonomic review of the genus *Cribrarula* (Cypraeidae). Shells in this genus have conspicuous dorsal spots, but like other cowries, lack sculpture, spines, and other shell characters commonly used in gastropod taxonomy. For these reasons, cowrie shells are considered uninformative.

The study of dorsal spots (DS) and related characters suggest that at least in this complex, the dorsal spots may represent a record of the mantle papillae. If the hypothesis is correct, then DS may provide information on the soft parts that previously was only available from the study of live or preserved specimens. Each species in the complex has a species-specific range of DS, marginal spots, and allied characters, thus suggesting that they may be useful in distinguishing species in the complex.

The odontophore cartilage provides support for the radula and attachment for the muscles responsible for feeding. Although intimately connected to the radula and known since the 1800's, the taxonomic value of the odontophore has been overlooked. A study of odontophore variation in the family Cypraeidae proposes the structure as a novel taxonomic character, potentially applicable to most mollusks.

The *Cribrarula cribraria* Linnaeus, 1758 complex is reviewed, and twelve species and six subspecies are recognized on the basis of multivariate analyses of shell characters, the radula, odontophore, and geographic distribution. The shell, radula,

odontophore and distributional maps are illustrated for each taxon. The nominal species, *cribraria*, ranges from East Africa to the Central Pacific, and several populations are distinctive enough to be recognized as subspecies. The other eleven species are restricted to narrower ranges along the periphery of the distribution of *cribraria*.

During the review of *Cribrarula*, a new species from New South Wales was described as *C. gravida* Moretzsohn, 2002.

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CHAPTER 1

TAXONOMY OF THE FAMILY CYPRAEIDAE (MOLLUSCA: GASTROPODA)

Introduction

The marine gastropod family Cypraeidae (the cowries) is composed of some 220 Recent species and more than 500 extinct species (Kay, 1996) with species occurring worldwide. Some species are abundant (e.g., the money cowrie, *Erosaria moneta* (Linnaeus, 1758)), and several played an important role as currency in many places in the Indo-Pacific until recently (e.g. India, China, and many Pacific Islands). Cowrie shells are glossy, usually colorful, and thus are favorites among shell collectors. The family is arguably among the best known mollusks. However, despite (or, in part, because of) the attention that cowries have received from both biologists and collectors, there remain numerous taxonomic problems within the family, among them the boundaries of both genera and species. Now that most species are probably known to science (at least shallow water species), and studies at the population-level are uncovering intraspecific variation, there is a recent trend in naming subspecies (e.g. Lorenz, 2002; see under Systematics, Chapter 6).

The main goal of this dissertation is the study of molluscan taxonomy. Traditional characters used in molluscan taxonomy include shell (conchological) and soft parts anatomy. Molecular characters such as DNA sequencing have been introduced only recently, in the late 1980's and early 1990's (e.g. Cann et al., 1987; Davis, 1994); allozymes have been used for over 30 years (e.g. Chambers, 1978; Dillon, 1984), but not widely among malacologists. Using a group of well-known gastropods, the Cypraeidae, in particular the *Cribrarula cribraria* (Linnaeus, 1758) species complex, a group of 12 putative closely related species, as a case study, I explore novel and non-traditional characters that may help shed light on molluscan taxonomy and evolution. Although widely used in taxonomy, cowrie shells are usually regarded as uninformative, and unable to provide the fine-scale resolution necessary for taxonomic discrimination (Meyer, 1998). One of the purposes of this dissertation is to explore alternative characters that might be useful in distinguishing species in mollusks, and to verify if cowrie shells indeed lack shell characters as generally believed.

In Chapter 2, I explore non-traditional shell characters that may be useful in separating species in the *C. cribraria* complex. The most striking shell feature in the complex is the conspicuous dorsal spotting. The study of hundreds of shells shows that each species in the complex has a species-specific range of dorsal spots (DS). Observations of live specimens and of photographs of live specimens suggest that there is a correspondence between DS and dorsal papillae, projections of the mantle that covers the shell in cowries. DS and allied characters may provide information on the soft parts, previously only available from the study of live or preserved specimens.

A recent paper (Holznagel, 1998) proposed a simple method of cleaning radulae by digesting the tissues with a protease, and suggested that the supernatant could be used for molecular studies. When cowries in the *C. cribraria* complex were digested to obtain a clean radula and DNA, another structure, not mentioned in Holznagel (1998)'s paper and rarely in any paper on radulae, was found to withstand protease action. This structure turned out to be a long-known but neglected structure, the odontophore cartilage. Many classical anatomical works illustrate the odontophore in place, supporting the radula. A few recent studies (e.g. Ponder and Lindberg, 1997; Haszprunar, 2000) use the odontophore as a phylogenetic character, but the taxonomic utility of the structure has been neglected. I observed unexpected variation in the odontophore in the *C. cribraria* complex. That prompted an exploration of odontophore variation in the Cypraeidae (Chapter 3), and using the available extensive collections of Kay and Bradner (Bradner and Kay, 1996), about one third of the species in the family was sampled. The results are promising, and suggest odontophores are a source of potentially informative new characters for molluscan taxonomy. The odontophore is present in most mollusks, except bivalves and a few other small groups that secondarily lost the radula or odontophore as in the Conidae, so the structure potentially can be useful across most of the phylum.

Chapter 4 is a short "method" paper, which describes a simple method to prepare cowrie radulae for SEM mounting. This method allows ample time for the manipulation of cleaned radulae, and produces radulae with little distortion, suitable for taxonomic comparison. Although the method was tested only with cowrie radulae, it may also work with radulae of other groups with similar radular size range (6 to 30 mm). The method was used to prepare the radulae illustrated in chapters 5 and 6.

Chapter 5 is the description of a new species of *Cribrarula* from New South Wales, Australia, *Cribrarula gravida* Moretzsohn, 2002, based on shell, radular and odontophoral characters, as well as its disjunct distribution (Moretzsohn, 2002b).

A taxonomic review of the genus *Cribrarula* Strand, 1929 is presented in Chapter 6. The review of the literature was as thorough as possible, and a comprehensive list of synonyms is given, as well as descriptions and illustration of the shell, radula and odontophore, a morphometric analysis of shell characters, and a key to the 12 species and 6 subspecies recognized. Comparison tables and distributional maps are also presented. Lorenz (2002) elevated one subspecies (*C. cribraria exmouthensis* (Melvill, 1888)) to species, and proposed several new subspecies in the genus, based on shell characters, and molecular data from an unpublished source (Meyer, in press). However, until additional information and Meyer's molecular data become available, I do not recognize any of the taxa in the *Cribrarula* group proposed by Lorenz (2002).

Finally, Chapter 7 presents a discussion on the utility of the different taxonomic characters and methods presented in the other chapters, and provides some directions for future research needed to advance our understanding of molluscan taxonomy.

Biogeography

Most cowries occur in shallow tropical waters, but a few species occur at latitudes to 40ºN and 40ºS. Among the six major cowrie biogeographical provinces generally recognized, the Indo-West Pacific is by far the most diverse, with some 65% of the Recent species (circa 130 spp.). The other provinces tend to have a much smaller number of endemic species: Atlantic-Mediterranean-West Africa (10 spp.); Caribbean (6 spp.); East Pacific (9 spp.); Australia (13 spp.), and South Africa (14 spp.) (Fig. 1.1) (Taylor, 1979; Kay, 1985).

This dissertation focuses on the *Cribrarula cribraria* (Linnaeus, 1758) species complex, a group of twelve apparently closely related species. The nominal species, *C. cribraria*, has a wide Indo-West Pacific distribution; the other species have considerably smaller ranges at the periphery of the distribution of *C. cribraria*, with some species restricted to groups of islands (e.g. *C. gaskoinii* (Reeve, 1846) in Hawaii, and *C. garciai* Lorenz and Raines, 2001, apparently restricted to Easter Island). *C. cribraria* is very variable morphologically, and has several geographically isolated populations that have been described as subspecies (Chapter 6).

Cowrie taxonomy

The systematics of the Cypraeidae began with Linnaeus (1758, 1767), who recognized 42 species in one genus, *Cypraea*, in the material available in Europe at the time. A second genus, *Cypraeovula*, was proposed (Gray, 1824) to accommodate a group of endemic South African cowries. In succeeding decades, other genera and species were recognized (Jousseaume, 1884; Cossmann, 1903; etc, in Kay, 1985), and the number of recognized genera of living cypraeids eventually reached 61 (Steadman and Cotton, 1946), when Allan (1956) asked:

> "What happened to the original genus *Cypraea* of Linnaeus, that once included all the cowries? This has become divided and subdivided into genera and subgenera to such a degree that *Cypraea* is now a monotypic genus in the family, possessing only *Cypraea tigris* Linnaeus as its species."

In the first in-depth comparative study of cowrie anatomy, Kay (1957a) recognized four patterns of radular morphology within the Cypraeidae, but combining the radular features with other anatomical characters, she identified only two groups. Because these groups crossed the generic boundaries recognized by most authors, Kay (1957b, 1960a) proposed that all species of living cowries *sensu* Linnaeus be retained in the Linnaean genus *Cypraea* until anatomical, other characters, and more taxa were better understood. Today, more than 40 years later, with detailed information on a large number of taxa available, Kay (Bradner and Kay, 1996) has a less conservative approach, recognizing 31 genera of living cowries in 13 groups based on radular morphology. This arrangement shows a remarkable consistency with the generic arrangement proposed by Schilder and Schilder (1971).

At the species level, the "pendulum of cowrie taxonomy" also swings between the opinions of lumpers and splitters. Helfer (1946) and Donohue (1965) illustrate this point when they show that the number of species accepted by the Schilders varies from paper to paper in their own work, as well as in the work of other authors. The Schilders in essence separate (and name) geographically separate demes of apparently single polymorphic species as distinct groups at intraspecific levels, that is, subspecies, clines, infraspecies, and morphs. The German Schilders (e.g.1922-1971) were considered splitters (Donohue, 1965); Burgess (1970, 1985), Kay (1957b, 1960a), Wilson (1993, 1998) and others were considered lumpers (Schilder, 1963). More recently, another German, Lorenz, is again swinging the pendulum towards the splitter camp, proposing numerous species and subspecies (e.g. Lorenz, 1997, 2002).

Life history

The life history of a cowrie begins when sperm from a male fertilizes the eggs within the body of a female cowrie. The female deposits the fertilized eggs in ovoid or triangular capsules with parchment-like walls that are attached to the substrate in a gelatinous mass (Taylor, 1975). Spawnings of 100 to 1000 egg capsules, each with 200 to 500 ova inside are reported (Ostergaard, 1950; Kay, 1960; Renaud, 1976). Unlike most gastropods, the female cowrie remains on the egg mass until the veliger larvae hatch (in about 11 to 18 days for tropical cowries, and up to six weeks in temperate species (Wilson, 1985)). Veligers have a small conical shell with 2 1/2 to 5 1/2 cancellate whorls, and four-lobed velum that bears minute cilia (Taylor, 1975). Planktonic life as a veliger is supposedly the norm in cowries, although direct development is known in at least a few groups (the *Cypraeovula* complex in South Africa (Liltved, 1989) and the *Zolia* complex in Southern Australia (Wilson and Summers, 1966; Wilson, 1985, 1988)).

Once the planktotrophic veliger larva begins to metamorphose and shell growth begins, it sinks to the ocean bottom. The mantle adds calcium carbonate to the shell, and as it grows spirally it changes shape, becoming oliviform and is termed a "bulla" (Fig. 1.2). At this stage, the juvenile shell is very thin, cream or brown in color, with a few spiral bands called "embryonic bands" (e.g. Lorenz and Hubert, 2000, but a misnomer, because these bands occur in the juvenile, not the embryo). The larval shell or protoconch is visible early in the juvenile shell, but the body whorl in the adult usually covers the previous shell, and as a result, the protoconch becomes buried in the shell (Kay, 1985).

When the animal reaches maturity, the outer lip of the shell turns toward the columella, and both labral and columellar lips begin to thicken. Then, differently from most gastropods, the cowrie shell stops growing significantly in size. For this reason cowries are said to have determinate growth (Vermeij and Signor, 1992). However, the mantle continues to add nacre and the shell takes on its characteristic gloss and color pattern. As more nacre is added, teeth form on the labral and columellar lips, and the shell thickens. When fully developed, the adult cowrie shell typically has a long, narrow aperture framed by thick lips bearing teeth. Externally the shell is almost bilaterally symmetrical; internally, it remains spiral.

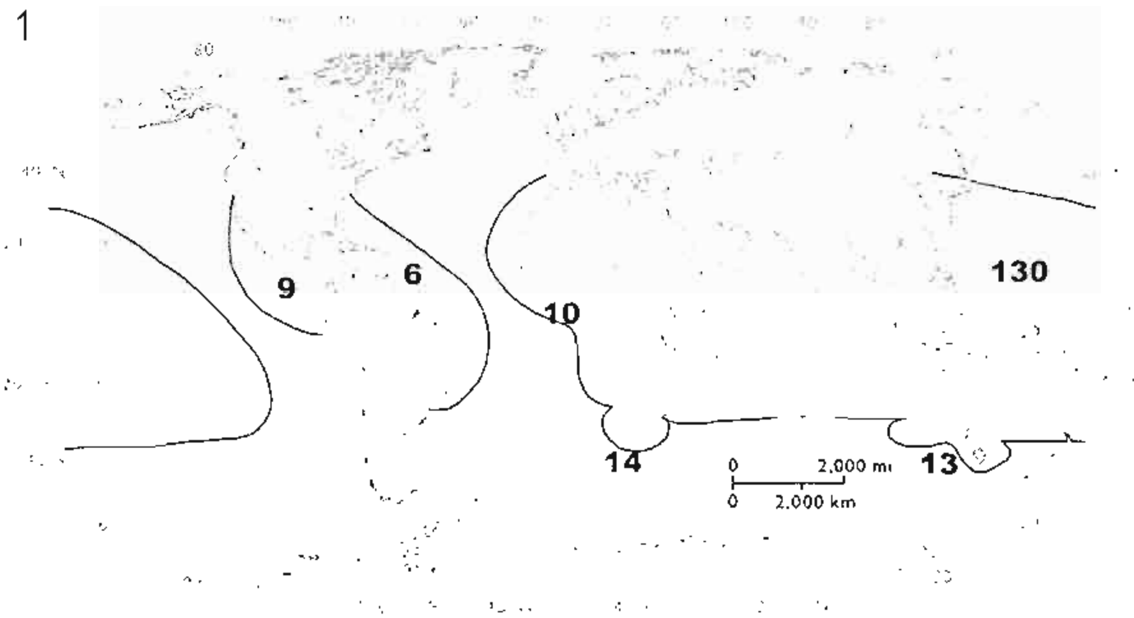
Several authors suggest shell size as indicative of sexual dimorphism in some cowries (e.g., Orr, 1959; Schilder and Schilder, 1961, 1962), the female usually with a larger shell than the male, but males being larger than females in other species (Schilder and Schilder, 1962). In *C. gaskoinii*, sexual dimorphism was observed not only in shell size, but also in radula and odontophore features (Chapter 6), the shell of the female being typically larger than that of the male (personal observation).

Some cowries are herbivores, apparently grazing primarily on seaweeds; others feed on sponges. There is anecdotal information on cowries feeding on a variety of invertebrates (Kay, 1985). Hayes (1983) reports that the Hawaiian endemic *C. gaskoinii* feeds almost exclusively on one species of orange-red sponges (*Prianos* sp.), and proposes that the distribution of the cowrie may be heavily influenced by the presence of the sponge. Total sponge cover in Hayes' study site (off Puako, Hawaii Is.) was only 2%, but 47.7% of the occurrences of *C. gaskoinii* were on the sponges.

Figure captions

Figure 1.1. Major cowrie provinces with the number of species supposedly endemic to each province (based on Taylor, 1979, and Kay, 1985). The number of species considered valid today is slightly higher because of species described since the 1980's, but the pattern of cowrie diversity remains similar. (Map modified from www.nationalgeographic.com/xpeditions)

Figure 1.2. Growth series in *Blasicrura alisonae* (Burgess, 1981) showing the changes in shell shape as the cowrie matures. The four shells on the left are thin-shelled juveniles in the "bulla" stage, and the shell on the right is that of an adult. Note the wide and toothless aperture and the protoconch in the juvenile shells, and the narrow and toothed aperture in the adult shell.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CHAPTER 2

HOW DID THE COWRIE GET ITS SPOTS?

– AND WHY THEY MAY BE INFORMATIVE

Abstract

Cowrie shells are generally considered uninformative because they lack several of the characters commonly used in gastropod taxonomy. Shells in the *Cribrarula cribraria* complex have distinct dorsal spots (DS) patterns, as well as other shell characters such as the dorsal line angle, which may be useful in distinguishing the species. This paper explores those and other non-traditional shell characters and concludes that cowrie shells may be more taxonomically informative than previously believed. The hypothesis that DS correspond to dorsal papillae of the mantle is also proposed. If the hypothesis is correct, then the shells in the *C. cribraria* complex can tell a story about the animal that produced them.

Introduction

Paraphrasing Kipling (1902)'s famous leopard story is the story of another spotted animal, the cowrie (family Cypraeidae).

The protoconch is hidden in adult cowrie shells, which are smooth and involute, lack sculpture, texture, spines and other taxonomic characters commonly present in other gastropods. Additionally, presence and thickness of calluses vary widely even intraspecifically, and may be the result of environmental conditions such as depth, wave energy, and other factors (e.g. Orr, 1959; Renaud, 1976). Color patterns are often used to distinguish species in cowries, but are also variable. Therefore, cowrie shells are generally considered uninformative (e.g. Meyer, 1998). In other families, shell characters are also considered by some authors too plastic to be useful (e.g. Kool, 1993; Robertson, 1996).

The characters traditionally used in cowrie taxonomy include: shell size, apertural teeth, radula, and coloration. Molecular characters are still in their infancy for mollusks in general. A recent search (late January 2003) at GenBank showed only four nucleotide sequences from cypraeids. However, there is a large phylogenetic project on the Cypraeidae under way (The Cowrie Genomic Database Project - http://www.flmnh.ufl.edu/cowries/) using mitochondrial DNA (16S rRNA and cytochrome oxidase I (COI)) (Meyer, in press), but results are not yet.

Conchological, radular, odontophoral and molecular characters (mtDNA COI) were used to investigate the relationships in the *Cribrarula cribraria* (Linnaeus, 1758) species complex (Moretzsohn, in prep.) (Gastropoda: Cypraeidae); shell morphometric analyses, as well as the radular and odontophoral data will be reported elsewhere (Moretzsohn, in review B) [Chapter 6].

The purpose of this chapter is to explore novel and non-traditional shell characters such as dorsal spots and allied characters in the *Cribrarula cribraria* (Linnaeus, 1758) complex, and to see if these characters might be useful in separating species. Additionally, I propose that the dorsal spots on the shell of *C. cribraria* represent a record of the mantle papillae at the time the dorsal pattern was laid by the mantle.

Color pattern formation in cowries

In most shelled mollusks, the outer fold of the mantle border is the region responsible for the secretion of the shell (Hyman, 1967). Cowries, on the other hand, have mantles that, when fully exposed, cover the whole shell. In adult specimens the entire internal surface of the mantle secretes the shell as thin layers of $CaCO_3$ interspaced with a protein matrix. The presence or absence of pigment, the translucency or opacity, and the thickness of each layer determines a three-dimensional color pattern that can be quite complex (Savazzi, 1998). For example, the color pattern seen in *Barycypraea fultoni* (Sowerby, 1903) (Fig. 2.2), is nearly impossible to replicate in most gastropods, which have two-dimensional color patterns.

In contrast, the adult color pattern formation is relatively simple in the cribraria complex, consisting of thin, uniformly pigmented dorsal layers, with oval unpigmented windows (dorsal spots) through which the white or cream juvenile shell can be seen. The lack of pigmented layers cause the dorsal spots to be depressed in relation to the surrounding background, resembling the effect of coats of thick paint (Savazzi, 1998).

Hypothesis

Dorsal spots (DS) are typical of all species in the cribraria complex, and there are species-specific patterns of dorsal spotting, such as size, density (number of spots), shape, color and clarity of the spots, as well as the color of the nacre between the spots (also referred to as dorsal color).

Based on personal observations and photographs of live animals (Fig. 2.1), and observations by others of live animals in tanks and in the field (C. Meyer, pers. comm., 1999), I propose the following hypothesis: dorsal spots on shells in the *Cribrarula cribraria* complex represent a record of the dorsal papillae at the time the dorsal pattern was laid. Furthermore, there is a one-to-one correspondence between the papillae and DS, and perhaps also between the shape and diameter of DS and those of the papillae.

Materials and methods

A total of 1298 shells supposedly belonging to all twelve species in the *Cribrarula* cribraria complex were studied at eight museums, and borrowed from an additional five museums and five private collections for study (see acknowledgements). A suite of 61 shell characters was studied (Appendix 6.1); the complete suite of characters was recorded for about one third of the specimens (379), while the remainder varied from almost complete to a few basic measurements. In this paper, only dorsal spots and allied characters (Table 2.1) are discussed. Discussion of additional shell characters and multivariate analyses of shell characters will be presented elsewhere (Moretzsohn, in review B) [Chapter 6].

The number of DS was counted directly on 234 shells and on photographs showing the dorsal view of the same shells, to calculate a linear regression between DS_{shell} and DS_{photo}, and to estimate DS from photographs alone. This was necessary because some DS are not seen in dorsal view because of shell curvature. The 234 shells used to estimate the correction factor represented nine of the twelve species in the complex. DS counts from shells that were eroded, albino, partially albino or juvenile were not included in the calculation of the regression because of unfeasibility or errors in counting spots. The dorsal view is perhaps the most widely represented view of cowrie shells in the literature. Using the regression formula, photographs from the literature or posted on the Internet could be used to estimate species-specific ranges of DS in the *cribraria* complex.

Table 2.1. Dorsal spots and related shell characters

Dorsal spots (DS) – number of DS
Marginal columellar spots (CS) – number of CS
Labral spots (LS) – number of LS
Dorsal line (DLT) thickness - (0) none; (1) thin; (2) medium; (3) thick
Dorsal line angle (DLA) – approximate angle in degrees
Ring around DS (Ring) - (0) no ring; (1) dark ring around spot
DS distinctive (DSD) - (0) no dorsal spot; (1) distinct; (2) indistinct; (3) smeared.
Dorsal coat overlay (DCO) - (0) no dorsal coating; (1) normal; (2) overlay, misregistration; (3) melanistic

Results

Measurements and counts are shown in Table 2.2. Figures 2.4 to 2.10 show boxplots of the shell characters and the range of variation in each species in the *Cribrarula cribraria* complex.

Table 2.2. Average values and standard deviations (parenthesis) for the dorsal spot and related characters for each taxon in the *Cribrarula cribraria* complex (N = number of specimens measured)

Taxon (N)	DS	CS	LS	DLT	DLA	Ring	DSD	DCO
astaryi (10)	46.4 (9.8)	17.8 (5.5)	23.0 (4.8)	1.9 (0.6)	38.0 (4.8)	0.6 (0.5)	1.0 (0)	1.1 (0.3)
cribellum (28)	50.1 (12.4)	8.2 (6.5)	10.2 (7.0)	2.0 (0.7)	38.5 (6.4)	0 (0)	1.0 (0.2)	1.0 (0)
catholicorum (10)	62.8 (12.2)	3.4 (6.7)	7.8 (3.1)	2.6 (0.8)	60.8 (12.0)	0.1 (0.3)	1.1 (0.3)	1.1 (0.3)
crib. comma (52)	54.3 (9.5)	0.7 (2.7)	1.7 (3.3)	1.8 (0.5)	30.6 (9.6)	0 (0)	1.2 (0.4)	1.0 (0.2)
crib. cribraria (136)	49.7 (13.1)	0.3 (2.0)	0.5 (1.8)	1.9 (0.5)	32.8 (12.0)	0 (0.1)	1.1 (0.3)	1.2 (0.6)
crib. exmouthensis (19)	41.7 (7.8)	0 (0)	0 (0)	2.1 (0.3)	24.5 (6.0)	0 (0)	1.4 (0.7)	1.1 (0.2)
crib. ganteri (15)	53.8 (15.7)	2.9 (5.9)	3.2 (4.2)	1.9 (0.5)	33.2 (9.9)	0 (0)	1.3 (0.7)	1.5 (1.1)
crib. gaspardi (11)	34.9 (13.1)	0 (0)	0 (0)	1.8 (0.4)	34.1 (7.7)	0 (0)	1.0 (0)	1.3 (0.9)
crib. melwardi (15)	28.5 (28.5)	0 (0)	0 (0)	1.7 (0.5)	38.5 (8.3)	0 (0)	0.7 (0.5)	1.0 (0)
cumingii (19)	33.5 (9.0)	16.1 (3.8)	17.7 (5.0)	1.4 (0.7)	40.3 (11.5)	0.8 (0.4)	1.0 (0.3)	0.9 (0.2)
esontropia (16)	69.3 (19.0)	25.3 (8.8)	16.4 (8.4)	1.8 (0.7)	33.8 (6.2)	0 (0)	1.0 (0)	1.0 (0)
fallax (9)	49.2 (9.4)	0 (0)	0 (0)	2.4 (0.5)	39.4 (10.2)	0 (0)	1.8 (1.0)	1.2 (1.1)
garciai (2)	51.0 (5.7)	29.0 (4.2)	33.0 (4.2)	1.0 (0)	45.0 (0)	1.0 (0)	1.0 (0)	1.0 (0)
gaskoinii (50)	65.4 (16.9)	28.0 (14.5)	25.1 (14.4)	2.6 (0.5)	56.6 (8.6)	0.1 (0.3)	1.2 (0.6)	1.0 (0)
gravida (1)	88	0	0	2	40	0	2	1.0
pellisserpentis (1)	40	22	17	0	60	0	1	1.0
taitae (6)	41.2 (14.6)	10.5 (4.4)	14.0 (2.2)	1.7 (0.8)	40.0 (6.1)	0 (0)	1.3 (0.5)	1.0 (0)

Using the DS counted on a photograph, the following linear regression formula estimates the number of DS on the shell:

$$DS_{shell} = 0.823 * DS_{photo} - 0.851 \quad (R2 = 0.90, N = 234; \text{Fig. } 2.3).$$

Dorsal spots

The shells of *Cribrarula taitae* (Burgess, 1993) and *cumingii* (Sowerby II, 1832) had the lowest average number of DS (36.0 and 50.3 respectively) and those of *esontropia* and *gaskoinii* the largest average number of DS (99.0 and 83.6 respectively). Shells of *cribraria melwardi* (Iredale, 1930) are frequently completely or partially albino, but some may have as many as 65 spots, the average was 36.0 DS; shells of *cribraria comma* (Perry, 1811) and *cribraria cribraria* (Linnaeus, 1758) had averages of 67.6 and 67.4 respectively (Fig. 2.4).

Intraspecific variation of DS number in *cribraria* (Fig. 2.5) reveals that shells from the West Indian Ocean on average had the highest number of spots, followed by shells from the Malayan, East Indian Ocean, and Central Pacific provinces, although the difference is not significant for the last three provinces. Two shells from the Polynesian province had an unusually high number of DS for *cribraria.* Some shells from the Malayan province had no or few DS, which was the case of albino shells of *melwardi* from Queensland.

Examination of shells of *cribraria* under the dissecting microscope shows a subtle relief in the DS. This corroborates the observations Burgess (1993) and Savazzi (1998) about depressed dorsal spots on shells in the *cribraria* complex.

Personal observations of live specimens of *cribraria* from Guam, and *gaskoinii* (Reeve, 1846) from Hawaii, as well as photographs of live cowries in the *cribraria* complex corroborate the observations of Meyer (pers. comm., 1999) that there is a one-to-one correspondence between DS and papillae in species in the *cribraria* complex.

Marginal spots

Most species in the *cribraria* complex have shells with marginal spots, but they are absent in *fallax* (Smith, 1881), *gravida* Moretzsohn, 2002, and rare in *cribraria* (Moretzsohn, 2002b; Moretzsohn, in review B). The number of marginal spots varies widely within the *cribraria* complex (Fig. 2.6 and 2.7). Shells of *gaskoinii* had the highest number of both CS and LS, followed by *esontropia* (Duclos, 1833), *astaryi* Schilder, 1971, *cumingii, cribellum* (Gaskoin, 1849) and *taitae.* Shells of *catholicorum* (Schilder and Schilder, 1938) may have a few or no marginal spots.

Intraspecific variation of marginal spots in shells of *cribraria* is shown in Fig. 2.8 and 2.9. Most shells do not have any marginal spotting either on the columellar or the labral side. On the rare shells with marginal spotting, there is a slightly larger number of spots on the columellar margin than on the labral margin. About half of the marginally spotted shells of *cribraria* were from the West Indian Ocean; fewer spots were found in East Indian Ocean, Central Pacific and Malayan provinces in that order.

Discussion

Most molluscan shells grow by marginal accretion of calcium carbonate and incorporate shell pigments in the shell matrix controlled by a one-dimensional morphogenetic program, thus resulting in a two-dimensional graph (Meinhardt and Klinger, 1987). Meinhardt (1995) shows several morphogenetic programs that produce color patterns in molluscan shells. Juvenile cowrie shells show spiral or divaricate bands that are typical of mollusks that grow by marginal accretion (like most gastropods). In contrast, adult cowries and a few other gastropods (such as some marginellids), however, have a mantle that covers the whole shell. Upon reaching maturity, the shell grows only in thickness and in apertural characters. Savazzi (1998) demonstrates a three-dimensional color pattern in adult cowrie shells formed by uneven thickness of pigmented layers of nacre deposited by the mantle. These adult cowrie color patterns include irregular or round patches, rings or complex meshwork unlike patterns generated by one-dimensional programs.

The presence of DS on shells of species in the *cribraria* complex is a characteristic of the group: indeed, the Linnaean taxon *cribraria* derives from the Latin "cribrum" meaning sieve, because of the perforated appearance of the shell (Dodge, 1953). Shells of all other species in the *cribraria* complex have distinct DS, with perhaps the exception of *melwardi*, with shells often completely or partially albino or with neither dorsal coloration nor spots, but photographs of live albino specimens of *melwardi* (e.g. figure in Walls, 1979: 25) show the red mantle similar to that of congeneric species, bearing numerous papillae.

The DS of *cribraria* and allied species are formed by non-pigmented oval "windows" through which the white background of the dorsum is seen (Savazzi, 1998), a fact noted by Reeve in 1815 (Dodge, 1953).

Observations of juvenile and young adult shells (lip and apertural teeth just beginning to form) from museum collections suggest that the deposition of the final pigmented layer in several species in the *cribraria* complex seems to be a relatively rapid event, and while the shell is still thin (personal observation). This is corroborated by observations of live animals in aquaria and in the field that the deposition of the adult pattern can be as short as one week (C. Meyer, pers. comm., 1999).

The mantle of cowries is stationary in relation to the shell (Savazzi, 1998), meaning that the mantle always returns to the same region of the shell. Meyer (pers. comm., 1999) observed that there is a one-to-one correspondence between DS and papillae of the mantle on live specimens of *cribraria*. Savazzi (1998), however, suggests no correlation between DS and papillae. In the *cribraria* complex, and at least in *Lyncina leucodon* (Broderip, 1828) (Moretzsohn, unpublished), the correspondence between DS and papillae also seems to be real (Fig. 2.1).

Burgess (1993, and pers. comm., 1996) believes that the DS in shells of *cribraria* and related species are depressed in relation to the surrounding areas; Savazzi (1998) calls it the "thick-paint effect" because the observed relief looks like the effect of a thick paint, with the windows (DS) sunken in. Study of shells under a dissecting microscope reveals that DS are slightly depressed in shells in the *cribraria* complex.

One possible explanation for the lack of deposition of the pigmented layers sharply underneath papillae is that the papillae could affect diffusion of oxygen through the mantle, changing the pH and other chemical conditions locally to below the threshold necessary to start the morphogenetic program that produces the adult color pattern, thus preventing the deposition of the pigmented layer immediately under the papillae and vicinity. Therefore, the diameter and shape of DS in shells of *cribraria* and allied species could be roughly proportional to the diameter and shape of the papillae. Possible roles of the papillae in cowries have been suggested, such as participation in respiration, mimicry (Kay, 1985), and chemical defense against predators (Thompson, 1969), but the real role is unknown. Other characters can also be recovered from the patterns of dorsal spotting on the shells of *cribraria*, such as the spacing between spots, and the size, shape and sharpness of the DS.

Marginal spots

Rare shells of *cribraria* and those of several allied species may also have spots on the marginal calluses of the shell, but the nature of their formation and correlation with papillae is not known. The marginal spots, distinguished here as labral and columellar spots, or LS and CS, seemed to be formed by deposition of a dark pigment or, occasionally a light brown color pigment, and not by lack of pigment as in the DS. It was not possible to determine from photographs of live specimens if there is a correspondence between marginal papillae and LS or CS. Nevertheless, the number of LS or CS seems to be species-specific to each species in the *cribraria* complex (Figs. 2.6 and 2.7), and therefore, useful characters in separating these species.

Shells of *cribraria* do not have marginal spots except for specimens from the Indian Ocean, especially from East Africa, and occasional specimens from Micronesia and the South Pacific (Figs. 2.8 and 2.9). Shells of *fallax* are never spotted marginally. In contrast, shells of *gaskoinii* show as many as 70 or more brown or black spots on each margin. Shells of *esontropia* also have large numbers of CS and LS, as do shells of *astaryi* and *cumingii*. In the latter two taxa, the spots range from a few large marginal spots to several small ones. Most shells of *cribellum*, *catholicorum* and *taitae* have fewer marginal spots than those of *gaskoinii*.

Dorsal line

The dorsal line (dorsal groove, or apposition line of Savazzi, 1998) usually seen on the dorsum of the shell is the region where the two lobes of the mantle meet. Because the mantle is stationary in relation to the shell, species-specific characteristics such as the presence or absence of color pattern or even some relief may be present. Some cowrie species have a characteristically straight or slightly curved dorsal line (as in most shells in the *cribraria* complex), but the line can also be undulating or even meandering, as in *Leporycypraea mappa* (Linnaeus, 1758). The dorsal line can also be conspicuous, thick, or thin, or even inconspicuous (Fig. 2.10). Because it reflects a characteristic of the mantle, variations in the dorsal line can potentially be used as a character for phylogenetic studies.

Dorsal line angle

One character that has not been used for taxonomy is what I call the "dorsal line angle." This angle is an approximation of the angle formed between the dorsal line and the plane that includes the base of the shell, as seen from the anterior end of the shell, with the anterior canal as the vertex of the angle (Fig. 2.11). This angle represents a measurement of the proportional length or area covered by each of the two lobes of the mantle; a dorsal line angle of 90° means that both lobes are about the same size; a dorsal line angle of 45° means that the left lobe is much smaller than the right lobe.

The density of spots on each lobe of the mantle, and the size of DS on each mantle is yet another character associated with the dorsal line.

Dorsal pattern anomalies

The "unclear" dorsal pattern observed in some shells in the *cribraria* complex is the result of disturbances to the mantle during the deposition of the final dorsal pigment layer (Savazzi, 1998). Shells of two subspecies of *C. cribraria*, *comma* and *exmouthensis*, often have an "unclear" dorsal pattern (Fig. 2.12). These patterns could be the result of environmental disturbances such as the occurrence of fine sediment, or perhaps a biotic disturbance (e.g. crab attack). In some shells, the disturbance was apparently brief such that there was only a slight shift of the mantle in relation to the shell resulting in a "double exposure anomaly" (Savazzi, 1998) (Fig. 2.13). In other cases, the disturbance seems to trigger the secretion of additional layers of pigment laid in misregistration in relation to previous pigmented layers, resulting in a melanistic shell ("superimposed patterns" of Savazzi, 1998) (Fig. 2.14). The latter is often observed in shells of several cowrie species from New Caledonia, and it is supposed to be the result of environmental conditions (Chatenay, 1877). Dark rings around DS are common in shells of *C. cumingii* and *C. astaryi*; in a few shells examined, the rings were offset in relation to the DS, suggesting that the rings are deposited at a different time than the pigmented dorsal coat (Fig. 2.15).

Conclusions

Based on the observations above, I suggest that in shells of all species in the *cribraria* complex, the DS represent a record of the mantle papillae where the pigments is not deposited locally in young adults, and that DS correspond to the number of dorsal papillae. Because each species has a specific range of number of DS, this number may represent an adaptive value, and thus, maybe a useful taxonomic character. Other non-traditional shells characters, such as the dorsal line angle, may also provide insights on the soft parts previously only available from the study of live or preserved animals. The shells of some cowries may have more characters and thus, be more informative than previously believed.

Figure captions

Figure 2.1. *Cribrarula cribraria* (Linnaeus, 1758) – photograph of a live specimen in the field (Kwajalein), with the mantle fully exposed, showing the dorsal spots (DS) on the shell through the mantle. Notice the papillae rising at the center of the DS (arrows). (*Photo courtesy S. Johnson* © 2001)

Figure 2.2. *Barycypraea fultoni* (Sowerby, 1903), dorsal view, showing the complex three-dimensional color pattern.

Figure 2.3. Graph showing the regression between dorsal spots counted on a photograph of a shell (in dorsal view, DSphoto) and on a shell (DSshell).

Figure 2.4. Boxplot of number of DS showing the range of variation (Y axis) in each taxon in the *Cribrarula cribraria* complex, with taxa on the X axis.

Figure 2.5. Boxplot of number of DS in *C. cribraria* from different locations (X axis).

Figure 2.6. Boxplot of number of marginal columellar spots (CS) in the *C. cribraria* complex.

Figure 2.7. Boxplot of number of CS in *C. cribraria* from different locations.

Figure 2.8. Boxplot of number of labral spots (LS) in the *C. cribraria* complex.

Figure 2.9. Boxplot of number of LS in *C. cribraria* from different locations.

Figure 2.10. Boxplot of dorsal line thickness in the *C. cribraria* complex.

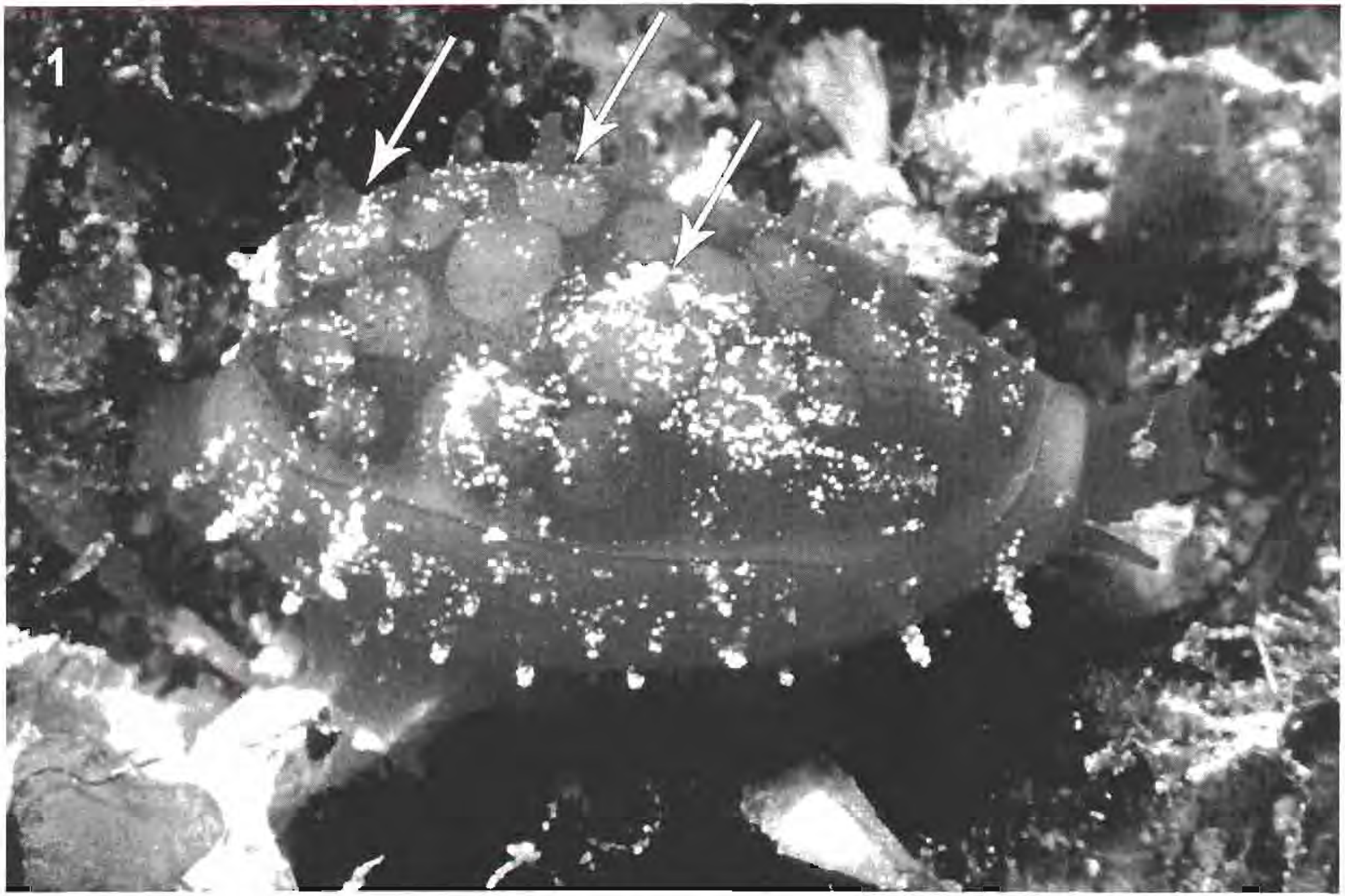
Figure 2.11. Boxplot of dorsal line angle in the *C. cribraria* complex.

Figure 2.12. *Cribrarula cribraria comma* (Perry, 1811) – example of a shell with unclear dorsal pattern.

Figure 2.13. *Cribrarula cribraria exmouthensis* (Melvill, 1888) – example of shell with "double exposure" anomaly.

Figure 2.14. *Cribrarula cribraria* (Linnaeus, 1758) – melanistic specimen from New Caledonia, showing the several additional pigmented layers.

Figure 2.15. *Cribrarula astaryi* Schilder, 1971 – example of shell showing offset dark rings in relation to DS, suggesting the rings are deposited at a different time than the pigmented dorsal coat.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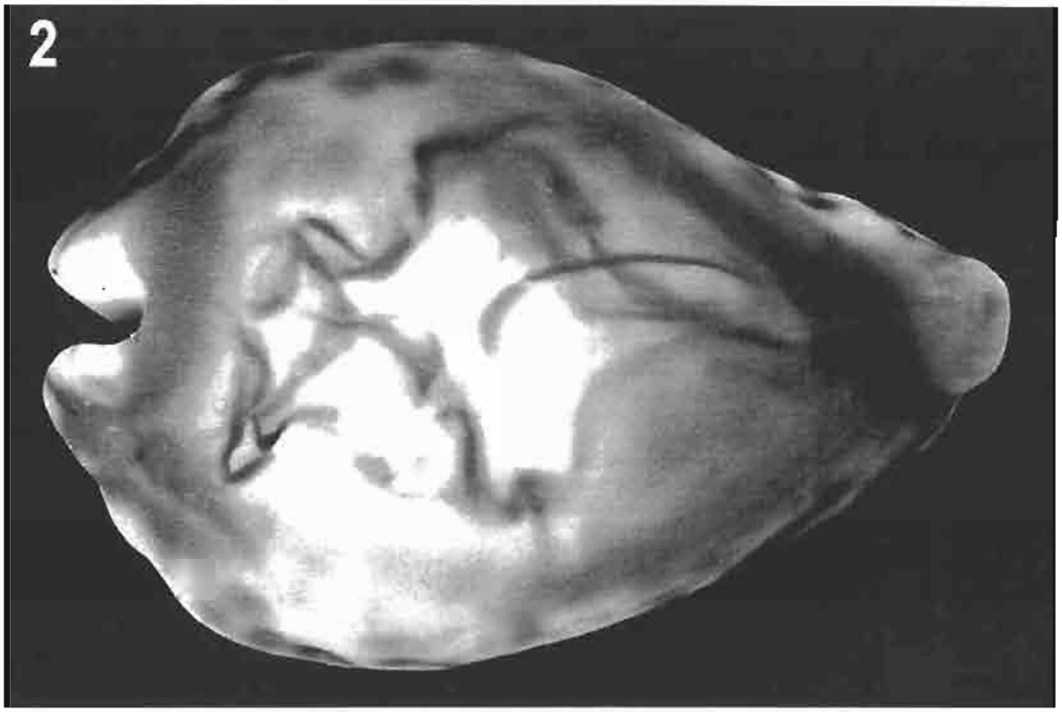
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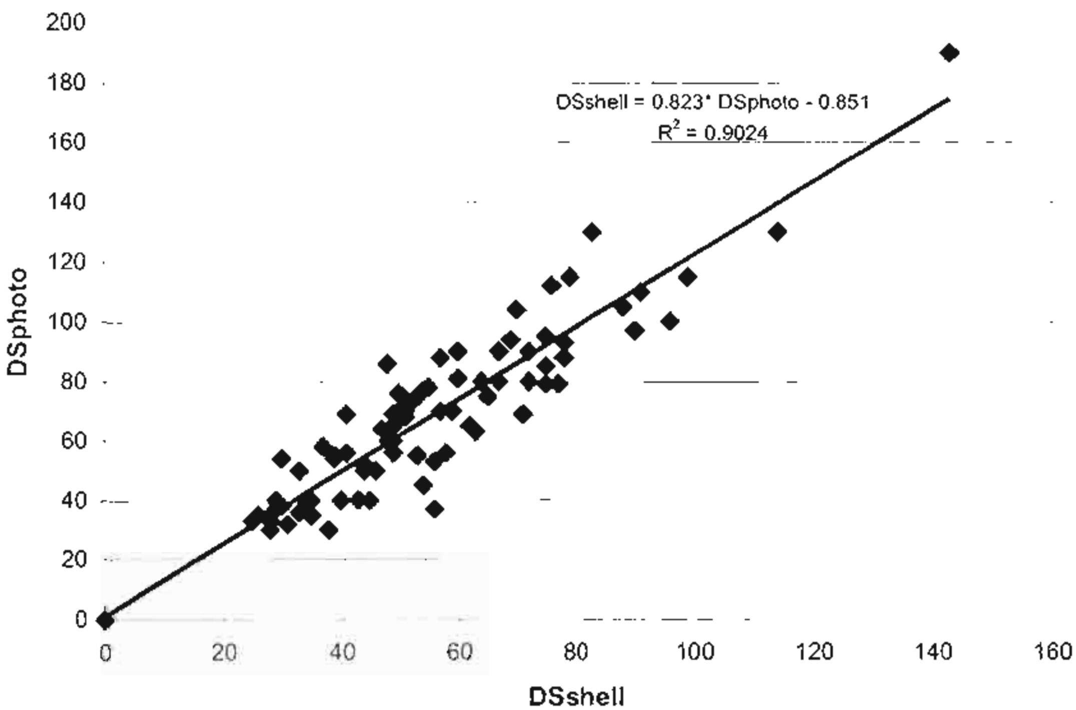
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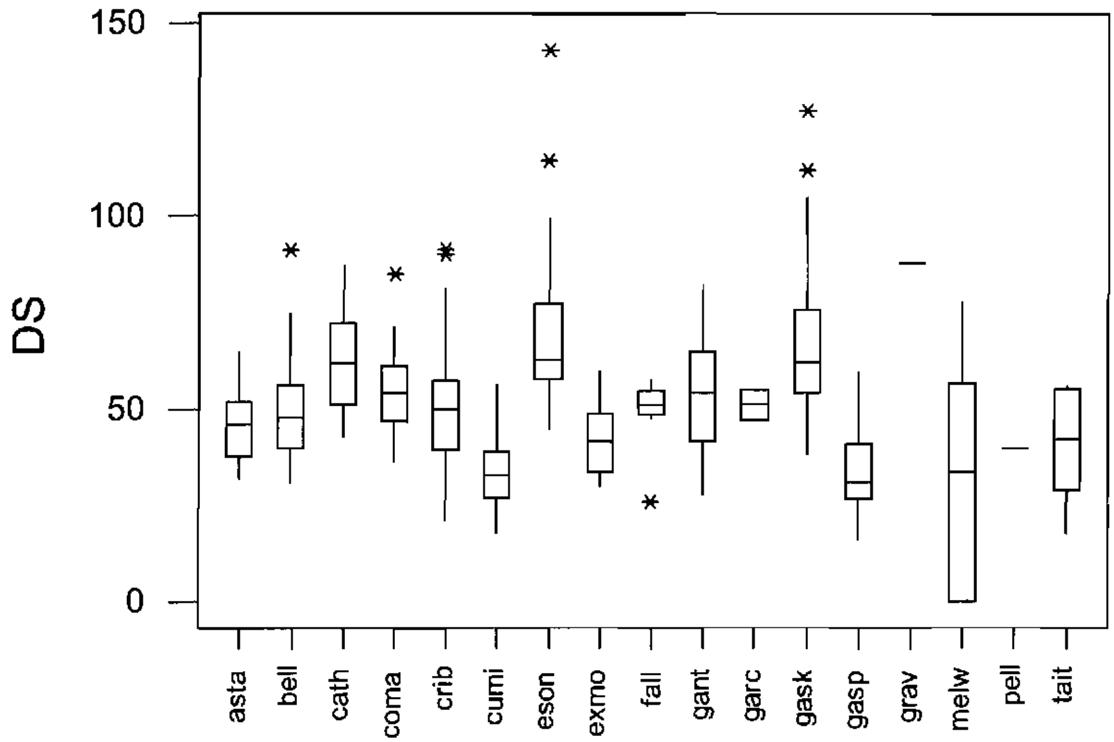

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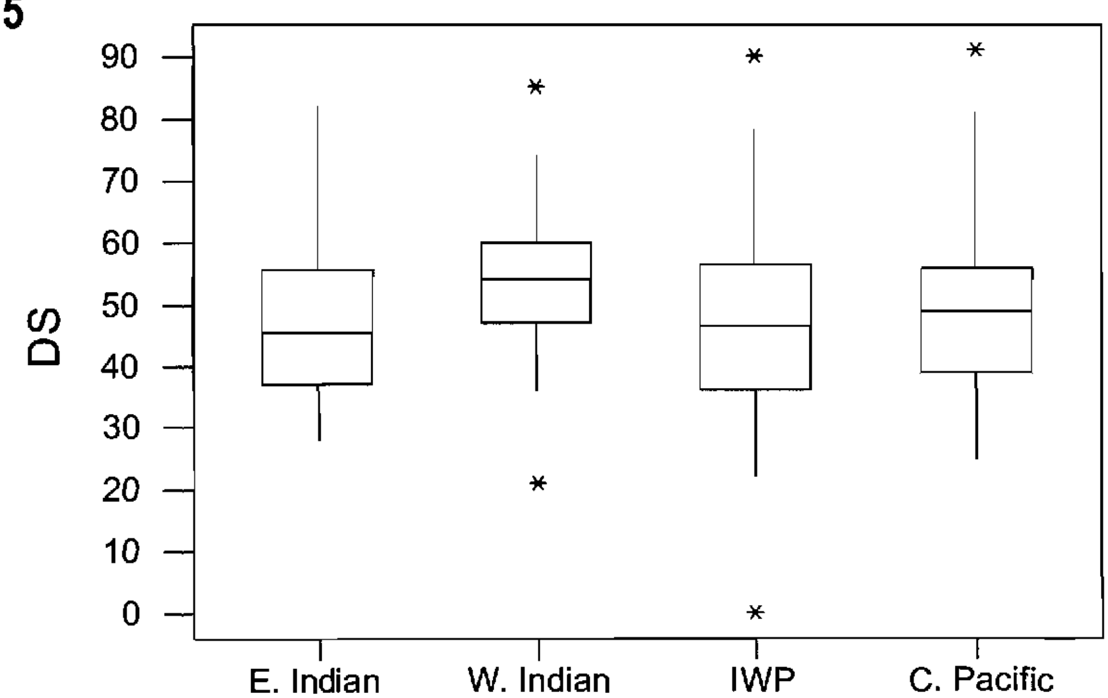

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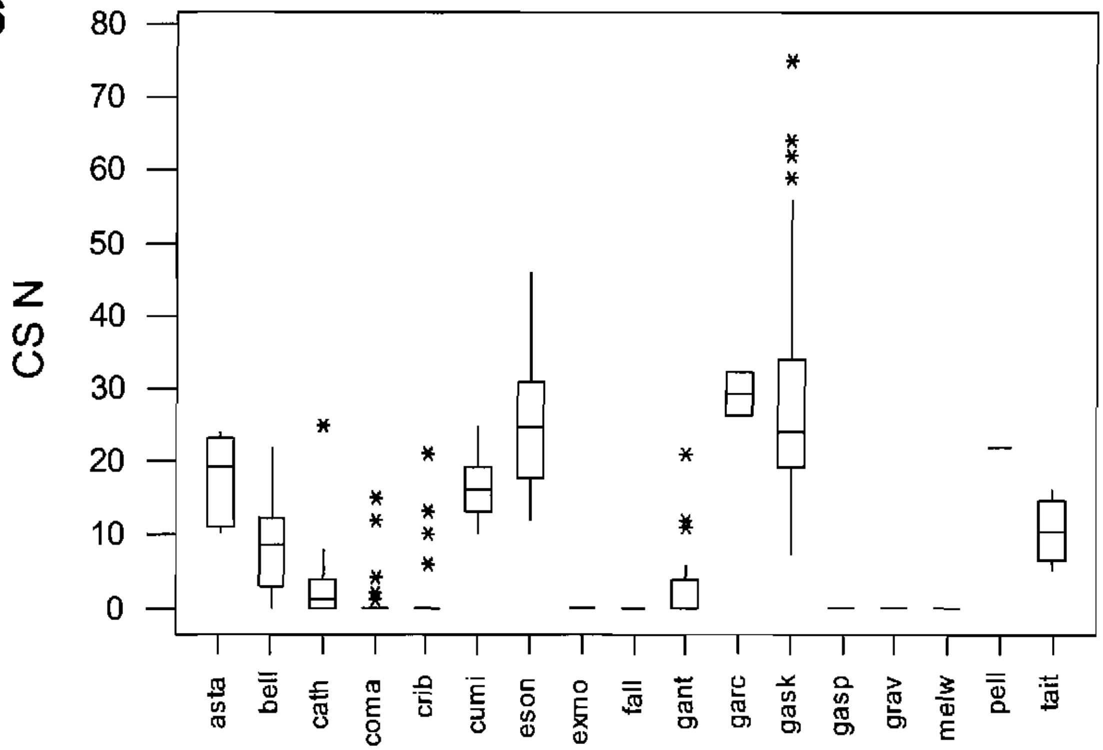
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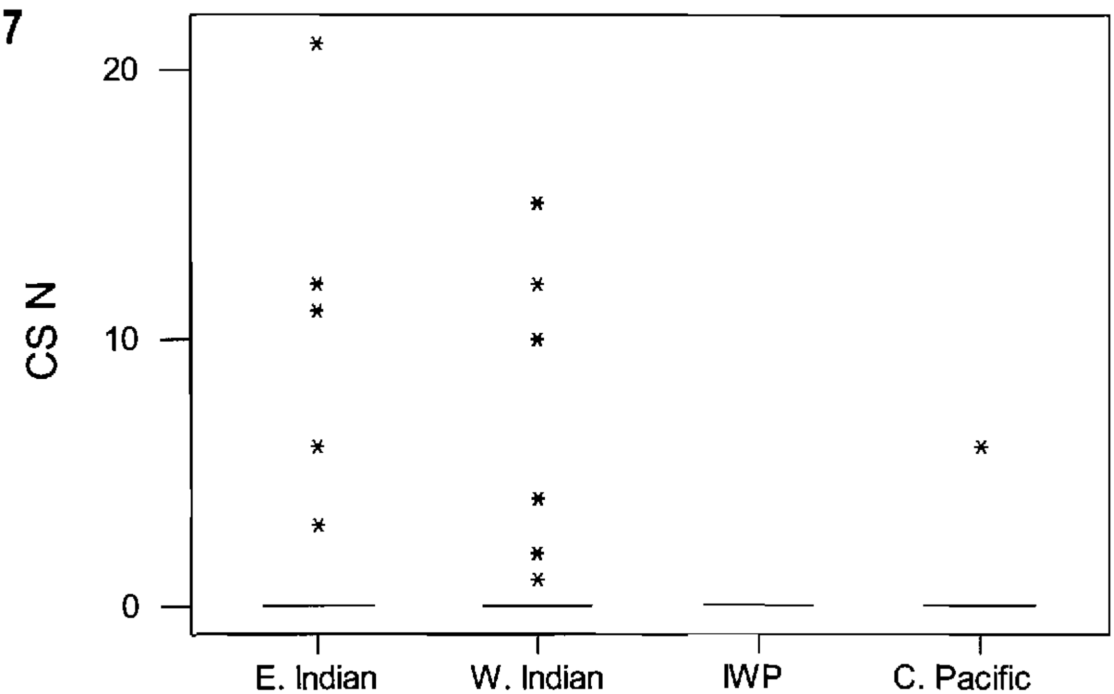
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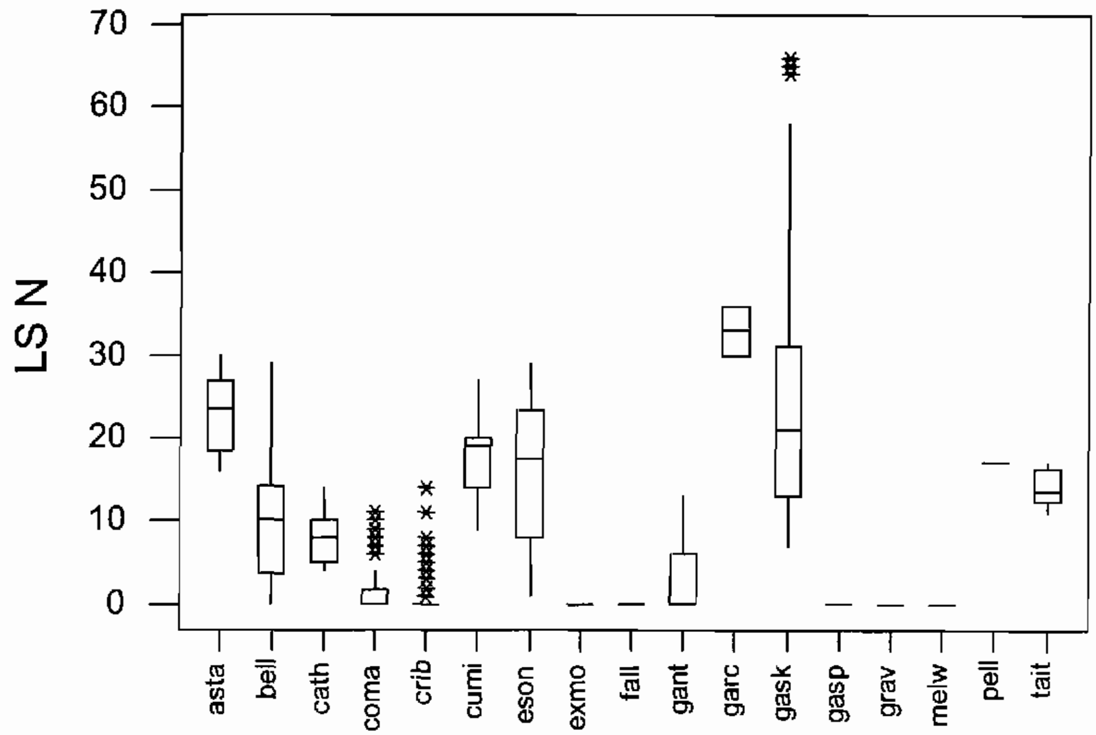
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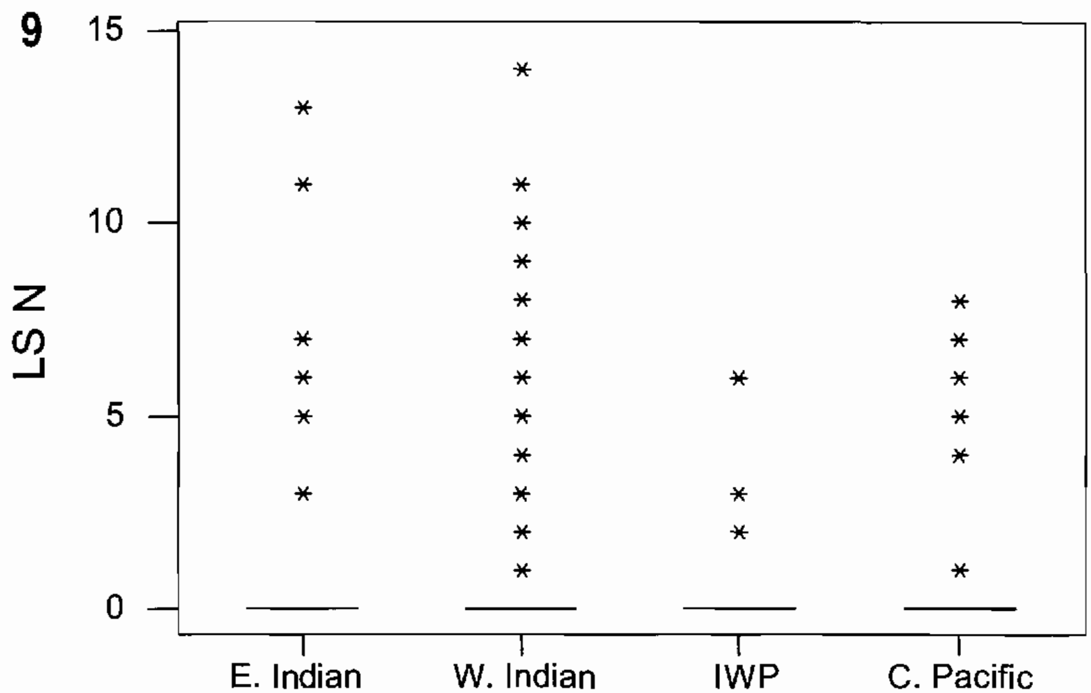
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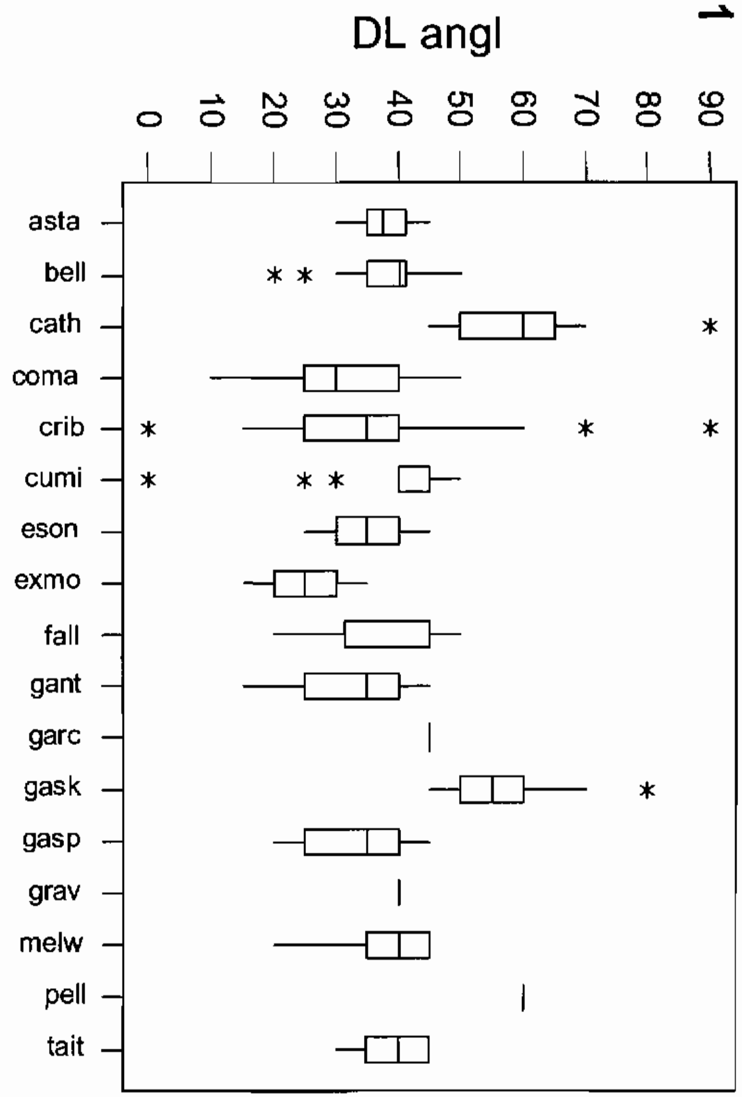
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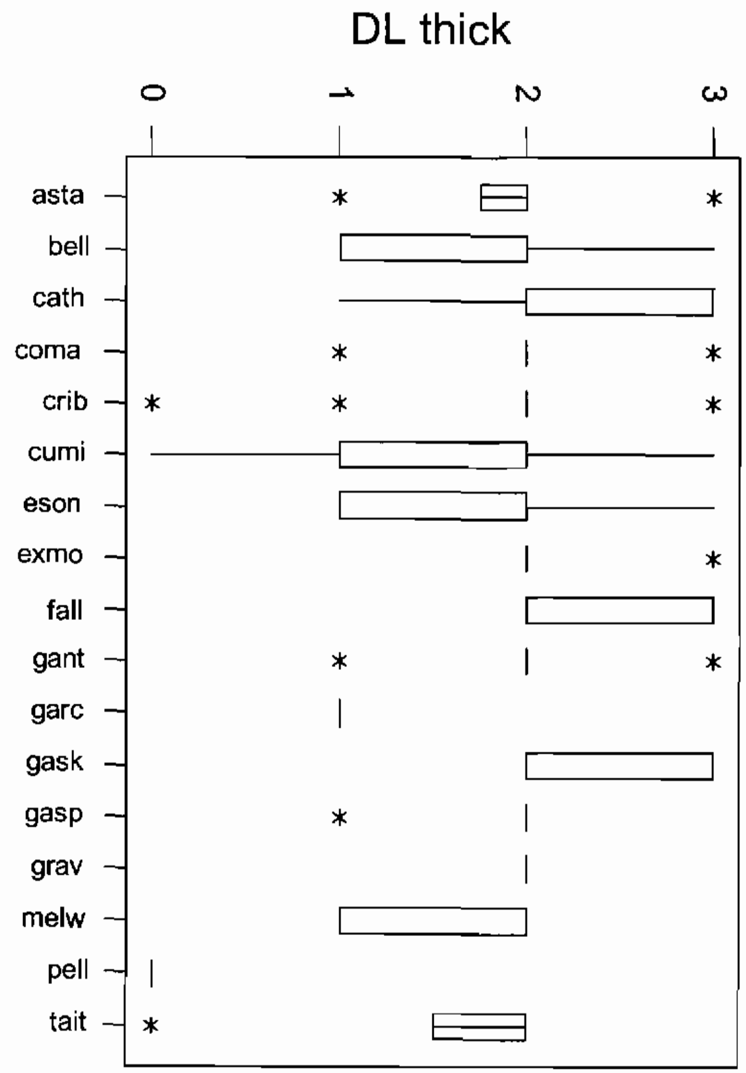
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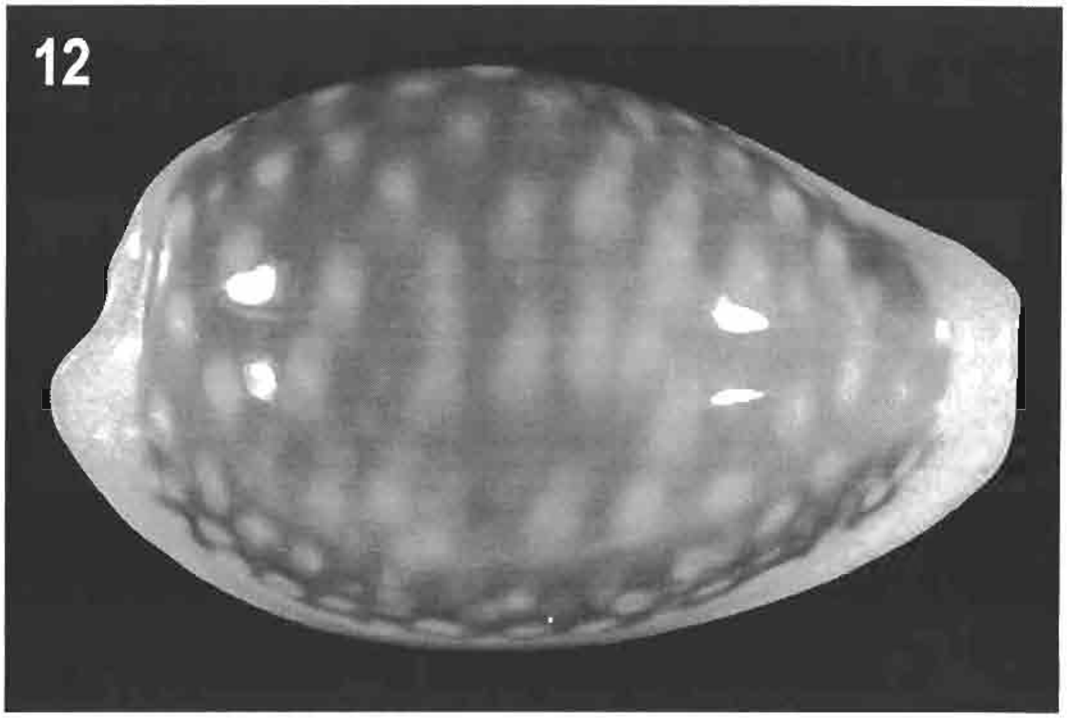
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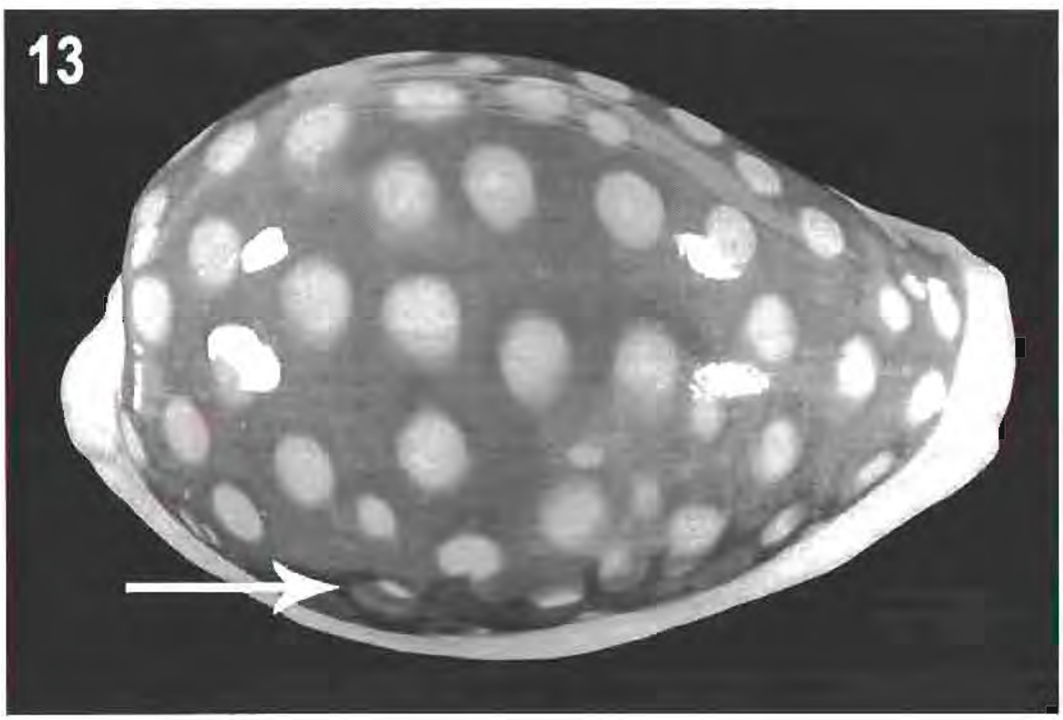
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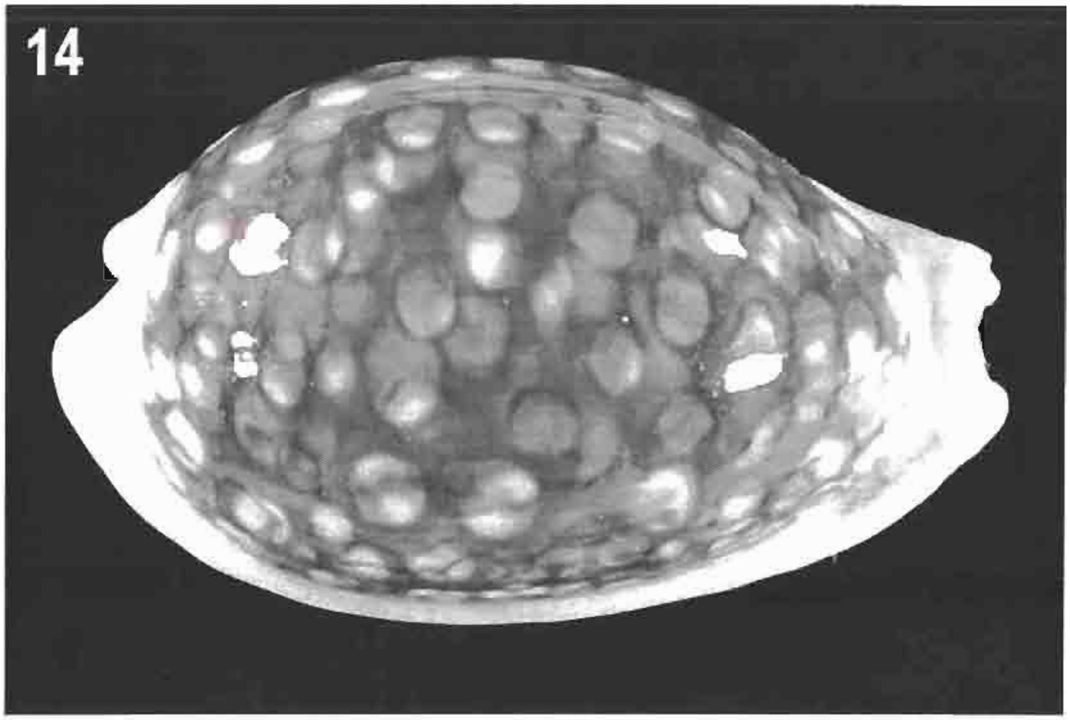
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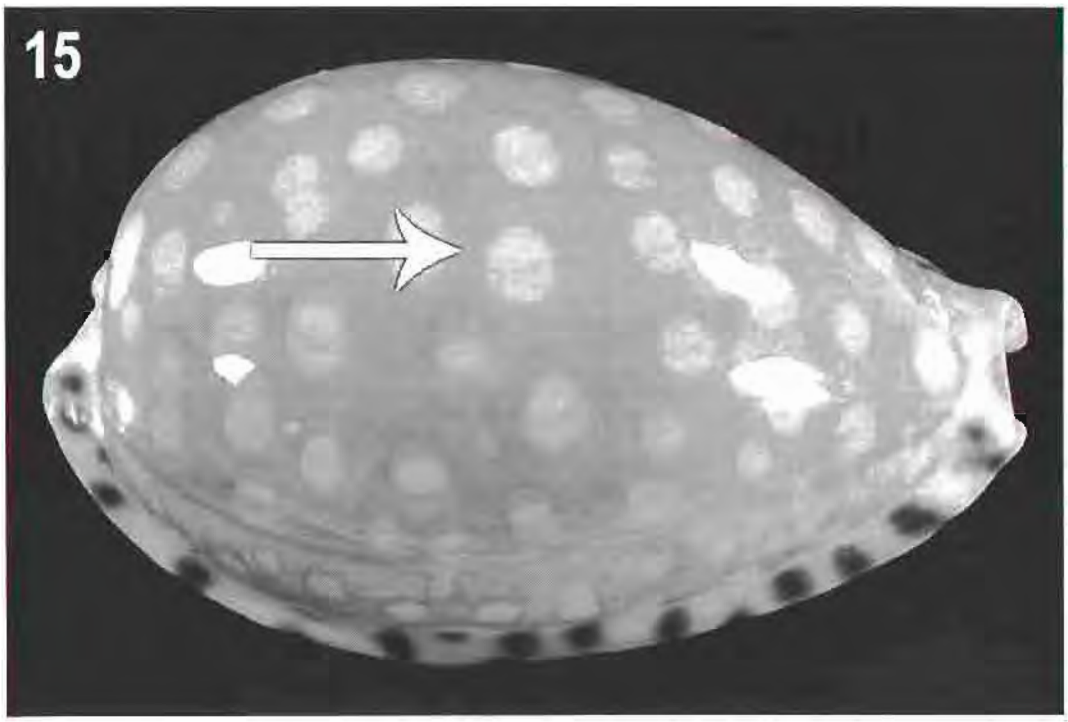
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CHAPTER 3

THE ODONTOPHORE: A "NEW RADULA" FOR MOLLUSCAN TAXONOMY? AN EXPLORATION OF ODONTOPHORE DIVERSITY IN THE CYPRAEIDAE (MOLLUSCA: GASTROPODA) [1]

Abstract

Odontophore cartilages support the radula and muscles of the buccal mass, and although intimately connected to the radula, they have been overlooked as taxonomic characters, while the radula is a standard taxonomic character in mollusks. A survey of the odontophores in 80 species in the gastropod family Cypraeidae revealed a wide variation in a number of odontophoral features, suggesting that the structure can be useful as a source of taxonomic characters. Representative odontophores of all species studied are illustrated in light microscopy, and of 70 species also in SEM.

Keywords: Odontophore cartilage; taxonomic character; diversity; Cypraeidae; SEM.

Introduction

Lack of characters that distinguish organisms, particularly the invertebrates that comprise 90% of animal species, severely limits the daunting task of assembling the catalog of life. In the Mollusca, the second largest animal phylum, taxonomy is based

[1] Manuscript currently in review (*Zootaxa*)

primarily on shell and radular characters, although many scientists consider shell characters uninformative because of convergence and plasticity (e.g. Kool, 1993; Robertson, 1996). Here I propose the use of characters of a prominent but heretofore neglected organ, the odontophore, as a source of taxonomic characters in mollusks.

Odontophore cartilages (or bolsters; odontophores henceforth) are masses of chondroid and connective tissue that support the radula and provide surfaces for the origin and insertion of the muscles that promote radular movements (Figs. 3.1-3.3) (Hyman, 1967) in all molluscan classes, except the bivalves, which lack a radula (see Aplacophora (Scheltema et al., 1994; Haszprunar, 2000), Cephalopoda (Nixon, 1998), Gastropoda (Hyman, 1967; Fretter and Graham, 1976; Voltzow, 1994), and Polyplacophora (Graham, 1973)). Members of the marine gastropod family Conidae have highly specialized toxoglossan radulae and lack odontophores (A. J. Kohn, pers. comm., 2002), and a few gastropod groups have secondarily lost the radula, e.g. most Eulimidae, but these are exceptions.

The typical cowrie odontophore consists of a pair of flattened, elongated, curved cartilages that are nearly mirror images of each other (Figs. 3.2-3.4). The two halves of the cartilage lie close to one another (Figs. 3.1-3.3). During feeding, the tip of the odontophore is protruded from the mouth by muscles running from the mouth to the posterior end of the cartilages. The radula lies over a groove formed by the dorsal surface of the two odontophore cartilages. The radula moves forward by the action of the protractors of the radula, running from the subradular membrane to the cartilages. As the radular ribbon passes over the anterior tip of the cartilage (known as bending plane, Fig.

3.5), the radular teeth, which normally are folded back, erect and splay out (Fretter and Graham, 1976: 485, fig. 183). Erect teeth then scrape the substrate, collecting food; when the movement is reversed, the teeth fold inwards and lie flat, and the food is transported into the mouth (Graham, 1973; Fretter and Graham, 1976).

A search for taxonomic characters in the marine gastropod family Cypraeidae, uncovered surprising variability in odontophores among species in the *Cribrarula cribraria* (Linnaeus, 1758) complex (Moretzsohn, in review B) [Chapter 6]. This observation prompted an exploratory study of odontophore diversity in the family. The purposes of this chapter are to describe and illustrate the unexpected odontophore variation in the cowries sampled, and to propose the odontophores as a source of informative taxonomic characters.

Material and Methods

Odontophores were obtained from specimens in the author's collection, as well as from the Kay (mostly ethanol-preserved specimens) and the Bradner collections (all specimens with dried tissue). The latter two collections were the basis for the Atlas of Cowrie Radulae (Bradner and Kay, 1996). Odontophores from 93 specimens representing 71 species of Cypraeidae and one species of Ovulidae were mounted on 19 SEM stubs. Among the 93 specimens mounted, odontophores from 16 were obtained from specimens from museum collections. The remainder were from specimens from the collections of Dr. E. Alison Kay, Dr. Hugh Bradner, or the author, and have been assigned ANSP catalog numbers ANSP 410599 to 410675. All 19 stubs will be deposited in the Academy of Natural Sciences of Philadelphia as vouchers (Winston, 1999; Ruedas et al, 2000). A complete list of the species, locality data, catalog numbers, and other pertinent information will be deposited with the stubs, as well as guides to the specimens on the stubs. The above-mentioned information is available upon request.

In this study, most odontophores were obtained by digesting the whole animal *in situ* (Moretzsohn and de Couet, in prep.) or by digesting the buccal mass with a protease. The tissues were incubated in polyethylene pouches with a buffer with Proteinase K in a shaker-incubator at 55°C and 250 RPM for up to 48 hours (or until all tissues were digested). The protease does not destroy either the chitinous radula or the sclerotized odontophores, and upon digestion, these structures are rendered clean and ready for light microscopy (LM) or scanning electron microscope (SEM) observation, and the supernatant can be used for molecular study (Holznagel, 1998). Upon study under the dissecting microscope, the odontophores were critical-point dried to preserve the original shape prior to mounting specimens onto an SEM stub.

All of the odontophores (including both halves of each pair) available were temporarily mounted unstained with water on glass slides for LM study and photographed under a dissecting microscope with a Nikon Coolpix 995 digital camera (3.3 megapixels) attached with a C-Mount to one of the eyepieces. Representative odontophores were then critical-point dried (CPD) and mounted on SEM stubs for SEM observation in a Hitachi S-800 Field Emission Scanning Electron microscope at the University of Hawai'i Biological Electron Microscope Facility (BEMF).

Digital images obtained with a digital camera through a dissecting scope, and the SEM micrographs captured digitally were edited in Adobe Photoshop 5.5 for color correction, to increase contrast for publication, as well as cropping, measurements and composition. No editing was done to purposely alter natural colors. Photodex's CompuPic 5 was also used to compose the plates. Minitab v. 12.1 was used for calculation of the basic statistics and tests of distribution.

The order of odontophores in plates loosely followed generic placement according to Lorenz and Hubert (2000). However, optimization for space (in the plates) ultimately dictated the order of appearance of the figures. An effort was made to illustrate the same specimen both in LM and SEM, but in many cases it was not possible. In those cases, the complementary (mirror image) half of the odontophore pair was used, the image flipped to maintain the same orientation.

Results

A total of 178 specimens representing 80 species in 24 genera, more than one third of the species and about two-thirds of the genera in the Cypraeidae were studied. Also sampled were one species of Eratoidae (*Trivia* sp.) and one of Ovulidae (*Jenneria pustulata* Lightfoot, 1786).

Odontophores studied varied in a number of features (Table 3. 1), including:

1) Odontophore length (OL) – range in length from 0.60 mm (*Pustularia mauiensis* (Burgess, 1967), Fig. 3.157) to 8.85 mm (*Lyncina aurantium* (Gmelin, 1791), Figs. 3.64 and 3.65). Most odontophores studied were small (mean = 2.55 mm,

StDev = 1.71, N = 79), but a few were large (Fig. 3.158). The distribution was skewed to the left (Skewness = 1.74).

2) Odontophore thickness (OT) – height, measured at the median length (Fig. 3.5). Varied from 0.15 mm (*Pustularia mauiensis*, Fig. 3.157) to 3.15 mm (*Lyncina nivosa* Broderip, 1827, Figs. 3.15 and 3.39). Most odontophores were not thick at the center (mean = 0.88 mm, StDev = 0.63, N = 79), but some were thick (or high). The distribution of OT was skewed to the left (Skewness = 1.51).

3) OT/OL ratio – The ratio OT/OH is a measure of the proportions of the odontophore; a low ratio means a long and narrow odontophore, a high ratio means a relatively short and high odontophore. The OT/OL ratio varied from 23 % (*Pustularia globulus* Linnaeus, 1758, Figs. 3.26 and 3.50) to 44 % (*Bernaya teulerei* (Cazenavette, 1846), Figs. 3.6 and 3.30) in the Cypraeidae, and 73 % in *Trivia* sp. (Fig. 3.29), in the family Eratoidae. The distribution of the OT/OL ratio was close to normal (Skewness = 0.48; mean = 32.11, StDev = 5.56, N = 78).

4) Ventral arch-odontophore height ratio (VA/OH) – This ratio describes the curvature of the odontophore, or the proportion of the height of the ventral arch (VA) to the total dorso-ventral height of the odontophore (OH). A low ratio means a nearly flat ventral arch, a high ratio a markedly curved odontophore. The VA/OH ratio varied from 12.3 % (*Zonaria arabicula* Lamarck, 1810, Figs. 3.80 and 3.81) to 37.1 % (*Purpuradusta hammondae* Iredale, 1939, Figs. 3.90 and 3.91), and its distribution was close to a normal one (Skewness = -0.28; mean = 24.5, StDev = 5.21, N = 79).

5) Odontophore length-shell length ratio (OL/SL) – The proportion of odontophore length to shell length varied from 4.6 % (*Pustularia mauiensis*) to 13.8 % (*Erosaria helvola* Linnaeus, 1758, Fig. 3.153). The distribution of OL/SL was slightly skewed to the left (Skewness = 0.95; mean = 8.13, StDev = 2.15, N = 78). Fig. 3.159 shows a plot of OL/SL versus VA/OH.

6) Color (in LM conditions) – most odontophores studied were white or off-white in LM conditions, but in some species the odontophore was distinctly colored, e.g. yellow (*Staphylaea staphylaea* (Linnaeus, 1758), Fig. 3.28) or red (*Luria isabella* (Linnaeus, 1758), Fig. 3.17).

7) Texture – as seen through the cuticle in LM. This is the appearance caused by the vacuolized chondroid tissue, the Leidig cells (Hyman, 1967). The odontophore in some cowries appears smooth (e.g. *Lyncina nivosa*, Fig. 3.15), but most show a fine texture (e.g. *Mauritia histrio* (Gmelin, 1791), Fig. 3.9), or appear spongy (e.g. *Cypraeovula edentula* (Gray, 1825), Fig. 3.18; all species in the genus *Cribrarula* , Figs. 3.24, 3.106-3.118). In a few species, such as *Pustularia globulus* (Linnaeus, 1758) (Figs. 3.26 and 3.50), the relatively large vacuolized cells give the odontophore the appearance of a bunch of grapes (especially in the SEM micrograph, Fig. 3.50).

The results above are not likely the extremes in the family, however; shape and angle of the bending plane also varied considerably. The odontophores of 82 species studied (including one species of Ovulidae and one of Eratoidae) are illustrated in Figs.

3.6-3.157. Most of the odontophores are shown in both LM and SEM. In ten species only LM figures are shown as the odontophores were either broken or lost during CPD and preparation for SEM.

Discussion

The taxonomic value of radulae was first recognized in the mid-1800s and many taxonomic groups were defined based on radular characters as early as 1863 (Bradner and Kay, 1996). Classical detailed anatomical descriptions of the buccal mass and feeding apparatus mention or illustrate odontophores in position under the radula and attached to muscles but most descriptions focus on the radula and the complex buccal musculature (e.g. Graham, 1973; Fretter and Graham, 1976, 1994; Leal and Simone, 2000; Simone, 2001). Odontophores range in number from five pairs in lower prosobranchs to a single pair (due to fusion; considered a derived condition) in higher prosobranchs, including the Cypraeidae (Hyman, 1967, Ponder and Lindberg, 1997).

Odontophores have not been used, at least in the recent literature, to distinguish species or higher ranks. This survey of the odontophores in the Cypraeidae is strong evidence that odontophores can be useful in alpha taxonomy, and perhaps also at higher taxonomic levels, as well as in phylogenetic analyses. Except for a few recent studies in which odontophores were included in phylogenetic analysis of gastropods (e.g. Ponder and Lindberg, 1997) and aplacophorans (Haszprunar, 2000), the variability and potential taxonomic usefulness of the structure have been overlooked.

In this survey, species-specific patterns or ranges of variation in odontophore features emerged. Only a single or a few specimens were sampled for most species, but in the *Cribrarula cribraria* complex several specimens were sampled per species: 46 specimens of *C. cribraria* were examined, showing that despite some intraspecific variation, there are recognizable species-specific features.

Most odontophores studied were white (in LM), but in several species there was a yellow or red cast, and a few were brightly colored (e.g. *Staphylaea staphylaea*, Fig. 3.27, or *Luria isabella*, Fig. 3.17). Libbin et al. (1992) attributed the unusual pink color of the odontophore of *Busycon canaliculatum* (Linnaeus, 1758) to high concentration of myoglobin. The presence of pigments in cowrie odontophores is unknown, but it is possible that in some species the concentration of myoglobin or other pigments may result in the colors observed.

Radulae and odontophores are molluscan synapomorphies: both are intimately associated with feeding and are probably subject to similar selective processes. Odontophores can and should be used, in addition to the radula and other available data, as sources of characters for phylogenetic analysis and systematics (Schander and Sundberg, 2001). However, despite being obtained with the radula, odontophores are discarded, thus wasting useful information. If odontophores vary within a family with relatively little feeding specialization (most cowries are herbivores), then the structure is likely to vary even more widely in groups with different feeding strategies, and thus be useful for taxonomy in other molluscan groups as well.

Anatomical characters such as reproductive organs and nervous system are usually informative but require careful dissection and interpretation. In contrast, the radula and odontophores can be procured with relative ease by simple dissection of the buccal mass, or alternatively, by digestion of the buccal mass or whole body by a protease.

Ideally, the same specimen can be studied and photographed in LM under a dissecting or compound microscope, then prepared and studied in SEM. This approach has the advantage of showing color and texture by transparency through the cuticle under LM conditions (e.g. Figs. 3.6-3.29), and the higher resolution and details of the ultrastructure in SEM (e.g. Figs. 3.30-3.51). The use of high voltage in SEM (e.g. 25 kV, as opposed to the usual 10 kV) may increase penetration of electrons through the cuticle to reveal more of the underlying honeycomb structure than at a lower voltage (Figs. 3.52 and 3.53) (T. M. Weatherby, pers. comm., 2002).

Odontophore shape and other features and proportions varied even between species in the same genus, although there were some similarities. For example, in Fig. 3.159, odontophores of *Cribrarula* spp. (represented by solid circles) sampled showed little variation in OL/SL, and more variation in VA/OH. Species of *Erosaria*, on the other hand, formed two groups that differ in OL/SL, but because the average shell length (estimated from Lorenz and Hubert, 2000) was used for specimens for which the actual shell length was not available, this result could be an artifact.

Because of limited budget, odontophores from several specimens of different species were mounted on the same stubs to save time at the SEM, reducing the need to change stubs frequently. However, this procedure brought an unforeseen problem: specimens from different museums were mounted together, and now cannot be removed from the stub because the odontophores are brittle. The solution was to donate all the stubs to the museum that had the most specimens mounted (ANSP), so that the specimens become vouchers and can be studied by other scientists. When using specimens loaned from a museum, odontophores should be mounted separately by species or by institutions, if the specimens are to be returned to the loaning museums.

Both the internal and external sides of the odontophores seem apparently flat and free from relief in LM. However, upon close inspection, especially in SEM, the external surface of the odontophore in *Macrocypraea zebra* (Linnaeus, 1758) (Fig. 3.57) and other species shows some relief, which may represent the insertion point of the odontophoral muscles. The differences between internal and external sides were not fully appreciated until the SEM study was done, and by then the specimens were already mounted on stubs. To keep the same orientation in all figures, some images were flipped horizontally. More detailed study of the external features may yield additional characters that differentiate species.

Odontophore cartilage is usually sturdy and somewhat flexible when fresh and wet, but becomes brittle after critical-point drying (CPD). Some specimens were slightly to badly damaged in this study the result of handling after CPD. A few small odontophores were lost during the CPD process because they were small, white, and therefore blended against the white cartridges used for CPD. An alternative to CPD could be hexamethyldisilazane (HMDS), which is cheaper and easier to use than CPD (just soak in HMDS for a few minutes, then air dry) (J. Leal, pers. comm., 2002), but HMDS is hazardous and may have environmental and health issues (Schöne and Bentley, 2002).

Conclusions

The odontophore characters described strongly suggest that the structure can be a useful source of taxonomic characters in the Cypraeidae, but a wider taxonomic exploration of odontophore diversity with modern imaging technologies is needed to document its variation. Also needed are a descriptive nomenclature and a coding scheme to facilitate their use in systematic and phylogenetic studies.

The odontophore could become "a new radula" as another standard character in mollusks providing additional informative characters that can be easily recovered.

Table 3.1. Odontophore characteristics per species: odontophore length (OL), odontophore thickness at center (OT); OT/OL ratio (percent); ventral arch/odontophore height (VA/OH) (percent); color; texture; shell length (SL); OL/SL ratio (percent), and number of LM and SEM photos.

Species, Author, Date	OL (mm)	OT (mm)	OT/OL (%)	VA/OH (%)	Color	Texture	SL (mm)	OL/SL (%)	Photo LM/ SEM
Bernaya teulerei Cazenavette, 1846	2.97	1.32	44.4	20.1	white	fine	45.5	6.5	6/ 30
Bistolida hirundo Linnaeus, 1758	1.31	0.38	28.6	24.7	yellow	medium	17.41	7.5	22/ 46
Bistolida kieneri Hidalgo, 1906	1.41	0.41	29	27.6	white	medium	15.13	9.3	152/ n/a
Bistolida stolida Linnaeus, 1758	2.1	0.66	31.6	24.4	gray	fine	16.52	12.7	104/ 105
Blasicrura alisonae Burgess, 1981	3.19	1	31.5	26.6	white	medium	37.3	8.5	100/ 101
Blasicrura burgessi Kay, 1983	2.54	0.72	28.4	31	white	medium	30 *	8.4	102/ 103
Blasicrura rashleighana Melvill, 1888	2.01	0.58	28.9	22.5	white	medium	19.5 *	10.3	151/ n/a
Chelycypraea testudinaria Linnaeus, 1758	4.83	2.03	40	15.2	dark yellow	smooth	100 *	4.8	8/ 32

Table 3.1. Continued. Odontophore characteristics per species.

Species Author, Date	OL (mm)	OT (mm)	OT/OL (%)	VA/OH (%)	Color	Texture	SL (mm)	OL/SL (%)	Photo LM/ SEM
Cribrarula astaryi Schilder, 1971	1.4	0.42	29.6	34.6	white	medium	20.45	6.8	106/ 107
Cribrarula catholicorum Schilder and Schilder, 1938	1.52	0.62	41	27	white	medium	19.3	7.8	108/ 109
Cribrarula cribellum Gaskoin, 1849	1.13	0.33	29.2	25.9	white	medium	15.5	7.3	110/ 111
Cribrarula cribraria Linnaeus, 1758	1.04	0.43	41	30.3	white	medium	21.3	4.9	112/ 113
Cribrarula cumingii Sowerby, 1832	0.74	0.19	26.1	30.7	white	medium	11.5	6.4	114/ 115
Cribrarula esontropia Duclos, 1833	1.28	0.41	31.8	23.5	orange	medium	19.9	6.4	23/ 47
Cribrarula fallax Smith, 1881	1.8	0.56	31.3	23.5	white	medium	31 *	5.8	116/ 117
Cribrarula gaskoinii Reeve, 1846	1.64	0.52	31.6	24.3	white	medium	20.7	7.9	24/ 48
Cribrarula taitae Burgess, 1993	0.87	0.26	29.6	25	white	medium	13 *	6.7	118/ 119
Cypraea pantherina Solander, 1786	5.59	2.06	36.9	25.8	yellow	fine	70 *	8.0	11/ 35

Table 3.1. Continued. Odontophore characteristics per species.

Species Author, Date	OL (mm)	OT (mm)	OT/OL (%)	VA/OH (%)	Color	Texture	SL (mm)	OL/SL (%)	Photo LM/ SEM
Cypraea tigris Linnaeus, 1758	4.07	1.31	32.1	28.4	white	smooth	58.55	6.9	134/ 135
Cypraeovula algoensis Gray, 1825	1.35	0.39	28.6	23.6	light yellow	fine	24 *	5.6	76/ 77
Cypraeovula castanea Higgins, 1868	2.26	0.92	40.9	21.1	white	fine	38 *	5.9	62/ 63
Cypraeovula edentula Gray, 1825	1.52	0.52	34.3	16.4	white	medium	21 *	7.2	18/ 42
Cypraeovula fuscorubra Shaw, 1909	2.78	1.08	38.7	15.4	beige	fine	33 *	8.4	60/ 61
Cypraeovula mikeharti Lorenz, 1985	1.44	0.59	41	25.9	white	fine	21 *	6.9	150/ n/a
Erosaria annulus Linnaeus, 1758	1.66	0.47	28.2	27.9	white	medium	21 *	7.9	120/ 121
Erosaria boivini Kiener, 1843	1.43	0.51	35.8	21.6	white	fine	25 *	5.7	138/ 139
Erosaria caputdraconis Melvill, 1888	3.37	0.96	28.5	29.5	light yellow	fine	25.76	13.1	122/ 123

Table 3.1. Continued. Odontophore characteristics per species.

Species Author, Date	OL (mm)	OT (mm)	OT/OL (%)	VA/OH (%)	Color	Texture	SL (mm)	OL/SL (%)	Photo LM/ SEM
Erosaria caputserpentis Linnaeus, 1758	2.65	0.78	29.4	27.2	yellow	medium	23.15	11.4	124/ 125
Erosaria gangranosa Dillwyn, 1817	2.17	0.63	29.1	21.4	white	fine	17.48	12.4	126/ 126
Erosaria guttata Gmelin, 1791	5.52	2.19	39.7	20	white	smooth	62 *	8.9	140/ 141
Erosaria helvola Linnaeus, 1758	2.97	1.14	38.4	15.5	white	medium	21.5 *	13.8	153/ n/a
Erosaria labrolineata Gaskoin, 1849	2.28	0.76	33.3	22.5	white	fine	17.47	13.0	128/ 129
Erosaria lamarckii Gray, 1825	2.12	0.89	41.8	13.7	white	fine	30.33	7.0	142/ 143
Erosaria miliaris Gmelin, 1791	4.15	1.47	35.5	24.5	red	fine	33.9	12.2	25/ 49
Erosaria moneta Linnaeus, 1758	1.64	0.47	28.9	28.1	white	medium	23 *	7.1	130/ 131
Erosaria nebrites Melvill, 1888	3.05	1.35	44	23.9	white	medium	27 *	11.3	154/ n/a
Erosaria obvelata Lamarck, 1810	1.44	0.62	43	24.3	white	large	18.5 *	7.8	155/ n/a

Table 3.1. Continued. Odontophore characteristics per species.

Species Author, Date	OL (mm)	OT (mm)	OT/OL (%)	VA/OH (%)	Color	Texture	SL (mm)	OL/SL (%)	Photo LM/ SEM
Erosaria sp.	3.3	1.21	36.7	18.8	white	fine	n/a	n/a	156/ n/a
Erosaria spurca Linnaeus, 1758	1.96	0.72	36.4	22.3	white	medium	26 *	7.5	144/ 145
Erosaria turdus Lamarck, 1810	2.71	0.97	35.7	23.8	yellow	medium	33.15	8.2	146/ 147
Erronea cylindrica Born, 1778	2.18	0.7	32.2	21.2	light yellow	smooth	18.18	12.0	92/ 93
Erronea errones Linnaeus, 1758	1.4	0.41	29.1	23.4	white	medium	18.49	7.6	84/ 85
Erronea felina Gmelin, 1791	1.33	0.37	28.2	26.2	yellow	medium	17.31	7.7	21/ 45
Erronea onyx Linnaeus, 1758	3.19	1.21	38	21.1	light yellow	fine	33.76	9.4	136/ 137
Erronea walkeri Sowerby, 1832	1.77	0.55	30.9	24.1	white	medium	30.18	5.9	86/ 87
Erronea xanthodon Sowerby, 1832	1.88	0.52	27.8	18.1	white	medium	26.74	7.0	94/ 95

Table 3.1. Continued. Odontophore characteristics per species.

Species Author, Date	OL (mm)	OT (mm)	OT/OL (%)	VA/OH (%)	Color	Texture	SL (mm)	OL/SL (%)	Photo LM/ SEM
Jenneria pustulata Lightfoot, 1786 (Eratoidae)	2.25	0.65	29.1	12.5	white	medium	20 *	11.2	27/ 51
Leporicypraea mappa Linnaeus, 1758	4.76	1.82	38.2	27.8	light yellow	smooth	76 *	6.3	58/ 59
Leporicypraea valentia Perry, 1811	6.16	2.34	37.9	26.2	reddish	smooth	86 *	7.2	10/ 34
Luria cinerea Gmelin, 1791	1.69	0.54	31.8	28.2	white	smooth	22.23	7.6	70/ 71
Luria isabella Linnaeus, 1758	1.2	0.36	30.1	25	red	medium	17.11	7.0	17/ 41
Luria isabellamexicana Stearns, 1893	2.23	0.79	35.6	20.7	white	fine	31.5 *	7.1	72/ 73
Luria tessellata Swainson, 1822	2.26	0.61	27	27.1	white	smooth	31 *	7.3	74/ 75
Lyncina aurantium Gmelin, 1791	8.85	2.67	30.1	32.6	dark yellow	smooth	95 *	9.3	64/ 65

Table 3.1. Continued. Odontophore characteristics per species.

Species Author, Date	OL (mm)	OT (mm)	OT/OL (%)	VA/OH (%)	Color	Texture	SL (mm)	OL/SL (%)	Photo LM/ SEM
Lyncina broderipii Sowerby, 1832	7.69	2.38	31	28.8	dark yellow	smooth	79 *	9.7	12/ 36
Lyncina carneola Linnaeus, 1758	1.98	0.47	23.8	28.3	white	fine	21.5 *	9.2	66/ 67
Lyncina leucodon Broderip, 1828	6.67	1.72	25.7	28.5	white	smooth	82.5 *	8.1	13/ 37
Lyncina lynx Linnaeus, 1758	2.58	0.63	24.5	32.1	light yellow	medium	30.21	8.5	14/ 38
Lyncina nivosa Broderip, 1827	7.97	3.15	39.5	24.7	beige	smooth	60 *	13.3	15/ 39
Lyncina ventriculus Lamarck, 1810	3.81	1.03	27.1	30.6	light brown	fine	49 *	7.8	16/ 40
Macrocypraea zebra Linnaeus, 1758	4.22	1.53	36.1	23.3	white	fine	70 *	6.0	56/ 57
Mauritia histrio Gmelin, 1791	3.96	1.44	36.3	25.7	red	fine	48.62	8.1	9/ 33
Neobernaya spadicea Swainson, 1823	3.53	1.17	33.3	26.6	white	fine	48 *	7.3	82/ 83

Table 3.1. Continued. Odontophore characteristics per species.

Species Author, Date	OL (mm)	OT (mm)	OT/OL (%)	VA/OH (%)	Color	Texture	SL (mm)	OL/SL (%)	Photo LM/ SEM
Notocypraea angustata Gmelin, 1791	2.65	0.81	30.5	22.7	yellow	smooth	27.6	9.6	78/ 79
Notocypraea comptoni Gray, 1847	1.71	0.45	26.2	29.2	dark yellow	medium	21.8	7.8	19/ 43
Notocypraea declivis Sowerby, 1870	2.34	0.72	30.8	27.7	reddish	fine	25.52	9.2	20/ 44
Palmadusta lutea Gmelin, 1791	0.84	0.24	28.4	20.3	white	medium	13.1	6.4	96/ 97
Palmadusta ziczac Linnaeus, 1758	0.97	0.24	24.6	30.1	white	medium	13.97	6.9	98/ 98
Purpuradusta fimbriata Gmelin, 1791	0.99	0.3	29.9	29.3	white	medium	13.28	7.4	88/ 89
Purpuradusta hammondae Iredale, 1939	1.03	0.27	26.6	37.1	white	medium	14.19	7.3	90/ 91
Pustularia cicercula Linnaeus, 1758	1.1	0.34	30.3	30.4	white	fine	18.12	6.1	148/ 149
Pustularia globulus Linnaeus, 1758	0.67	0.16	23.3	23.2	white	large	11.72	5.7	26/ 50

Table 3.1. Continued. Odontophore characteristics per species.

Species Author, Date	OL (mm)	OT (mm)	OT/OL (%)	VA/OH (%)	Color	Texture	SL (mm)	OL/SL (%)	Photo LM/ SEM
Pustularia mauiensis Burgess, 1967	0.6	0.15	24	14.4	white	large	13 *	4.6	157/ n/a
Staphylaea semiplota Mighels, 1845	1.73	0.43	25.1	26	white	medium	17.5	9.9	132/ 133
Staphylaea staphylaea Linnaeus, 1758	2.12	0.83	39	23.2	dark yellow	medium	20.3	10.4	28/ n/a
Syphocypraea mus Linnaeus, 1758	2.83	1.25	44.3	20.4	orange	fine	40 *	7.1	7/ 31
Talparia talpa Linnaeus, 1758	3.42	0.88	25.8	35.6	white	smooth	63 *	5.4	68/ 69
Trivia sp. (Eratoidae)	0.66	0.48	73	15.6	orange	fine	7.49 *	8.8	29/ n/a
Zoila jeaniana Cate, 1968	3.4 +	1.96	n/a	n/a	white	medium	69 *	n/a	54/ 55
Zonaria arabicula Lamarck, 1810	1.6	0.54	34	12.3	white	fine	22.66	7.1	80/ 81

* The average value from literature (Lorenz and Hubert, 2000) was used when shell length was not available; n/a – not available.

Figure Captions

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mm); **3.15.** *Lyncina nivosa* (Broderip, 1827) (7.97 mm); **3.16.** *Lyncina ventriculus* (Lamarck, 1810) (3.81 mm); and **3.17.** *Luria isabella* (Linnaeus, 1758) (1.20 mm).

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3.44. *Notocypraea declivis* (2.34 mm); **3.45.** *Errones felina* (1.33 mm); **3.46.** *Bistolida hirundo* (1.31 mm); **3.47.** *Cribrarula esontropia* (1.28 mm); **3.48.** *Cribrarula gaskoinii* (1.64 mm); **3.49.** *Erosaria miliaris* (4.15 mm); **3.50.** *Pustularia globulus* (0.67 mm); **3.51.** *Jenneria pustulata* (2.25 mm).

Figures 3.52 and 3.53. SEM of *Erosaria annulus* (Linnaeus, 1758) showing the same region of the external surface of the odontophore at different power settings: **3.52.** at 10 kV, and **3.53.** at 25 kV. Higher voltage increases electron penetration through the surface cuticle that covers the odontophore, thus revealing more of the honeycomb ultrastructure below the cuticle.

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Figures 3.92 to 3.105. Odontophores in LM (left) and SEM (right) (OL in mm). **3.92 and 3.93.** *Erronea cylindrica* (Born, 1778) (2.18 mm); **3.94 and 3.95.** *Erronea xanthodon* (Sowerby I, 1832) (1.88 mm); **3.96 and 3.97.** *Palmadusta lutea* (Gmelin, 1791) (0.84 mm); **3.98 and 3.99.** *Palmadusta ziczac* (Linnaeus, 1758) (0.97 mm); **3.100 and 3.101.** *Blasicrura alisonae* (Burgess, 1983) (3.19 mm); **3.102 and 3.103.** *Blasicrura burgessi* (Kay, 1981) (2.54 mm); **3.104 and 3.105.** *Bistolida stolida* (Linnaeus, 1758) (2.10 mm).

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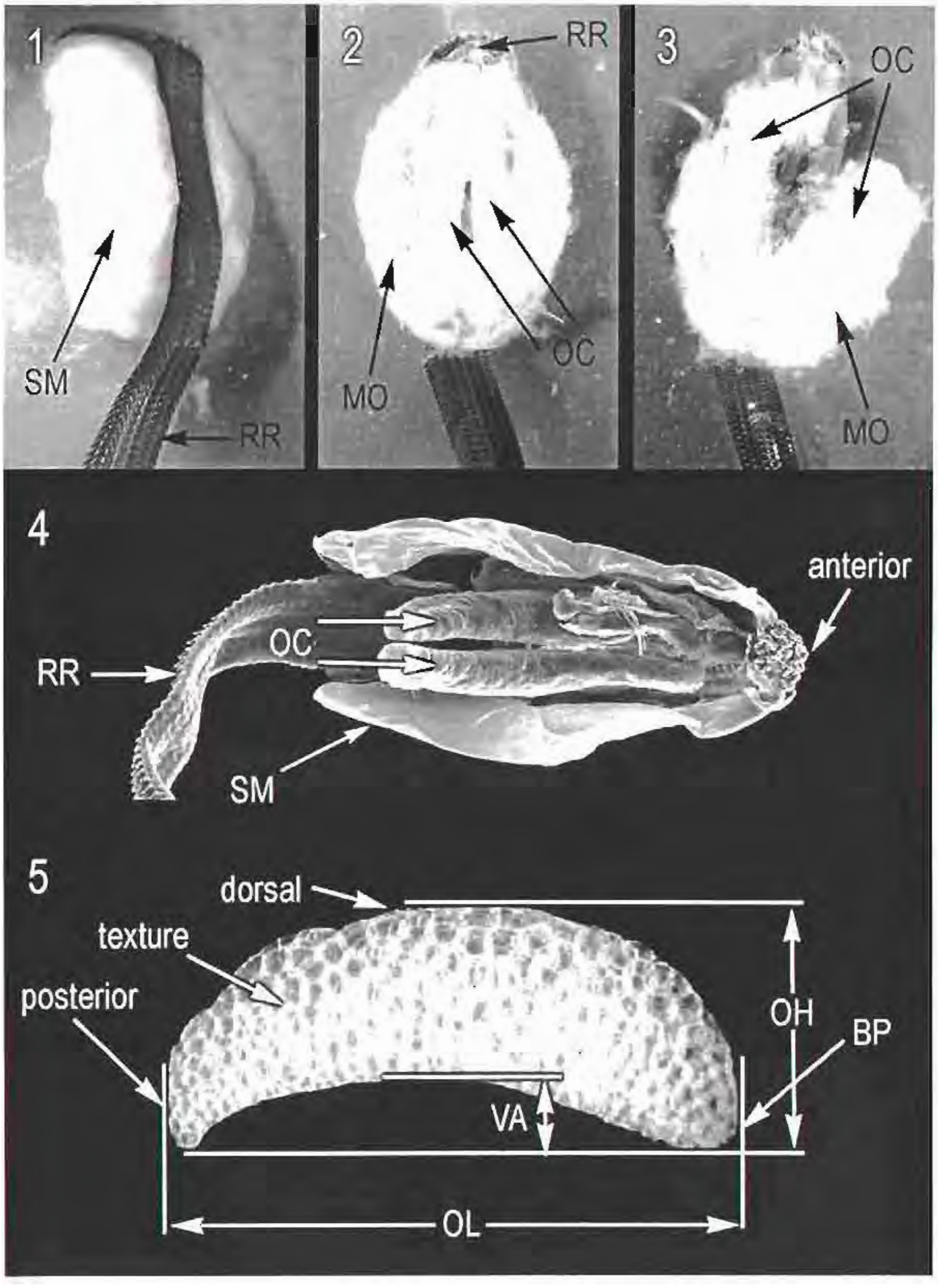
(3.05 mm); **3.155.** *Erosaria obvelata* (Lamarck, 1810) (1.44 mm); **3.156.** *Erosaria* sp. (3.3 mm); **3.157.** *Pustularia mauiensis* (Burgess, 1967) (0.60 mm).

Figures 3.158 and 3.159. Plots of odontophore features. Only three genera with seven or more species sampled are represented by distinct symbols (all others are represented collectively by the symbol X). **3.158.** Odontophore length (mm) versus shell length (mm), showing the direct correlation between shell length and odontophore length; **3.159.** Odontophore length-shell length ratio versus ventral arch-odontophore height ratio. This graph shows that species in the genus *Cribrarula* have a similar OL/SL ratio, but the species of *Erosaria* sampled show a wide variation in OL/SL ratio. See text for discussion.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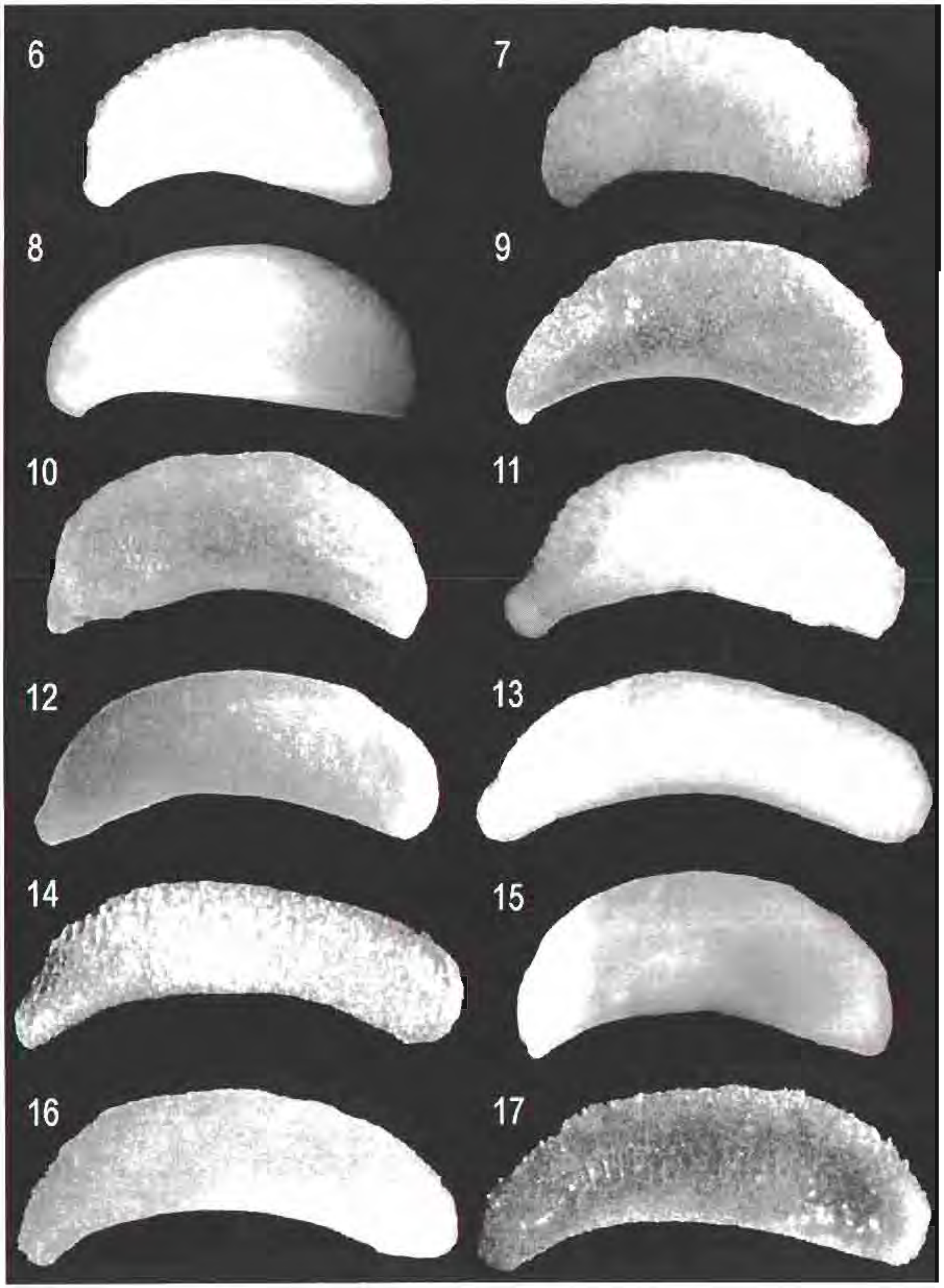
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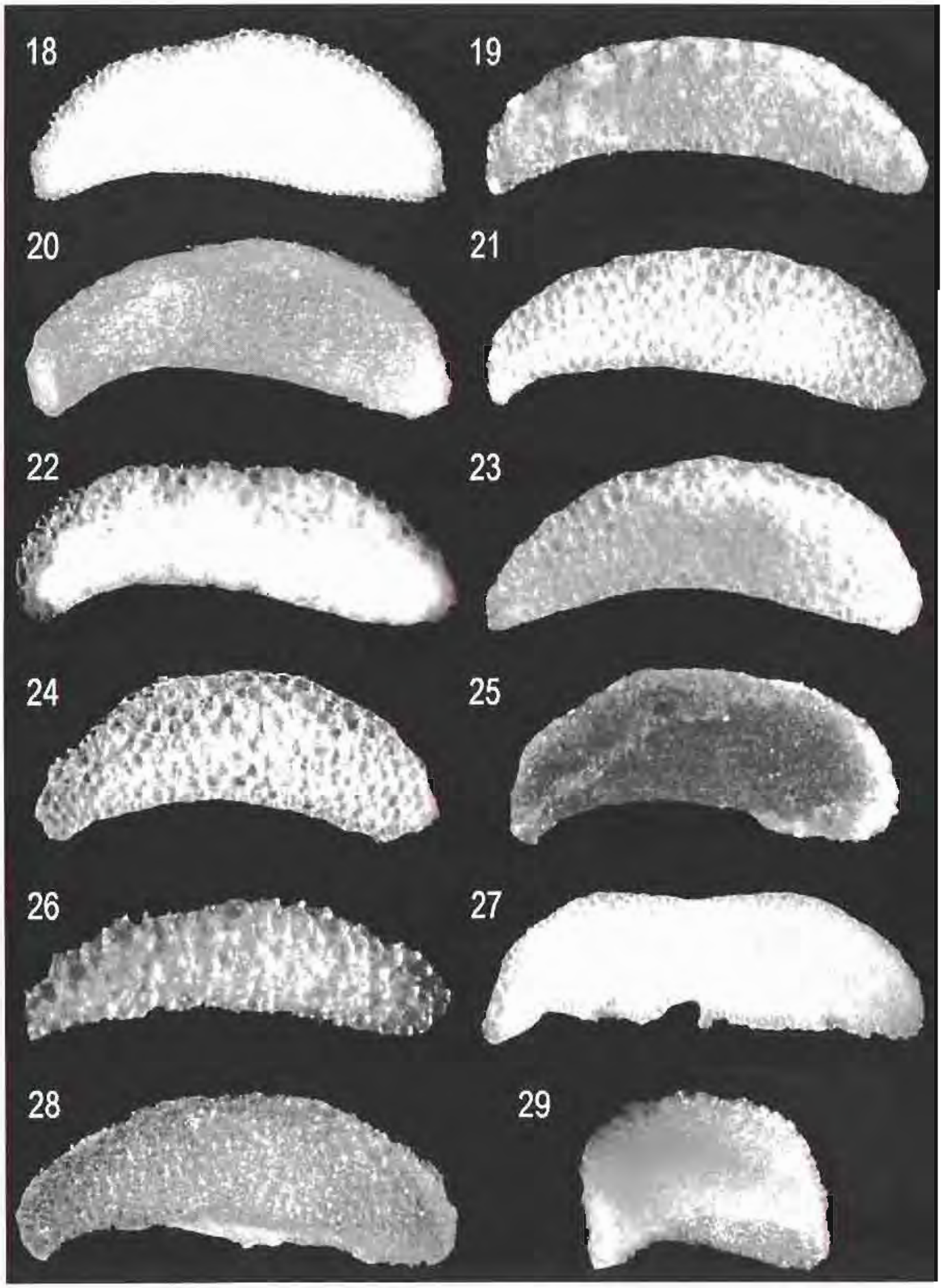
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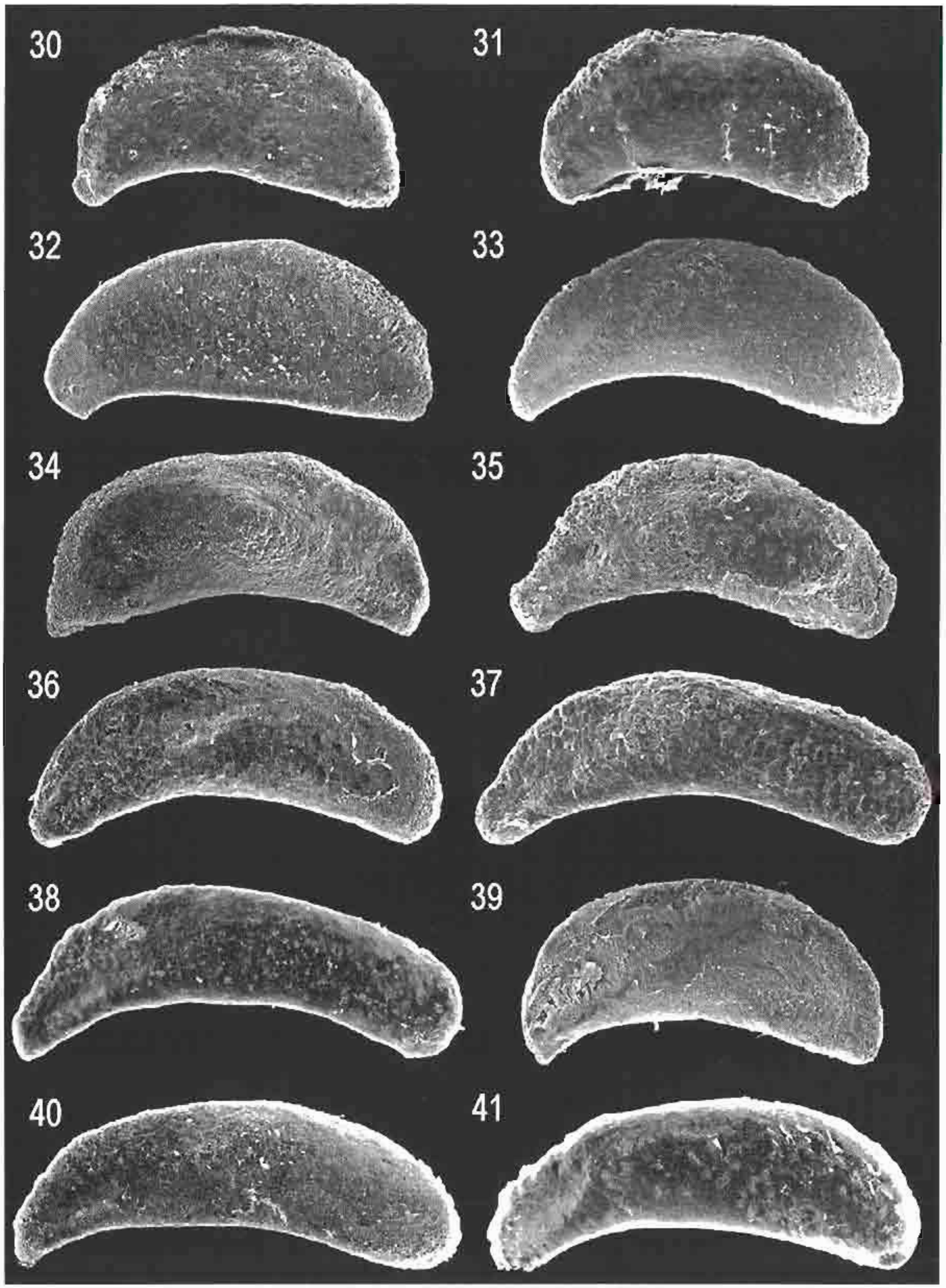
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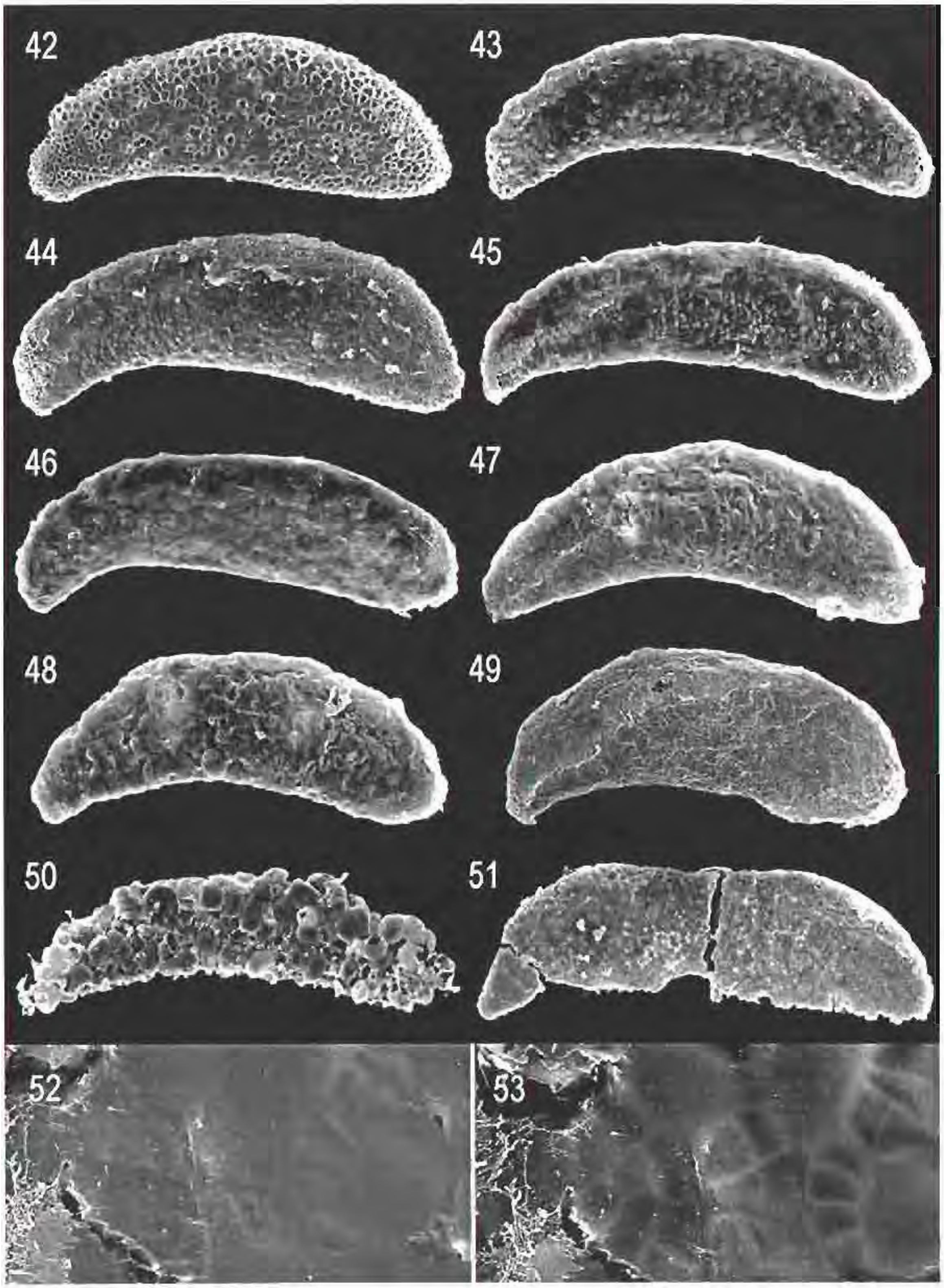
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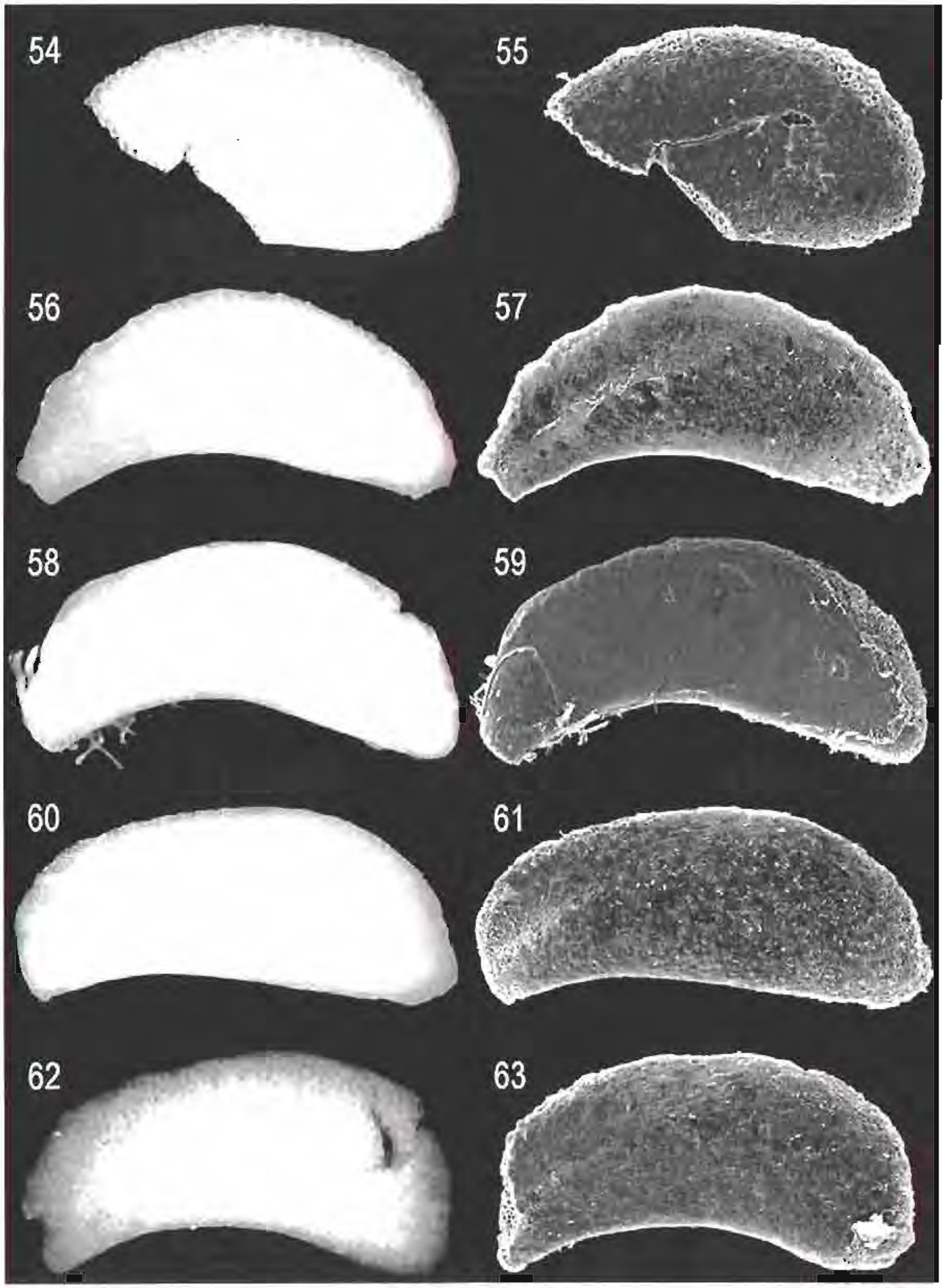
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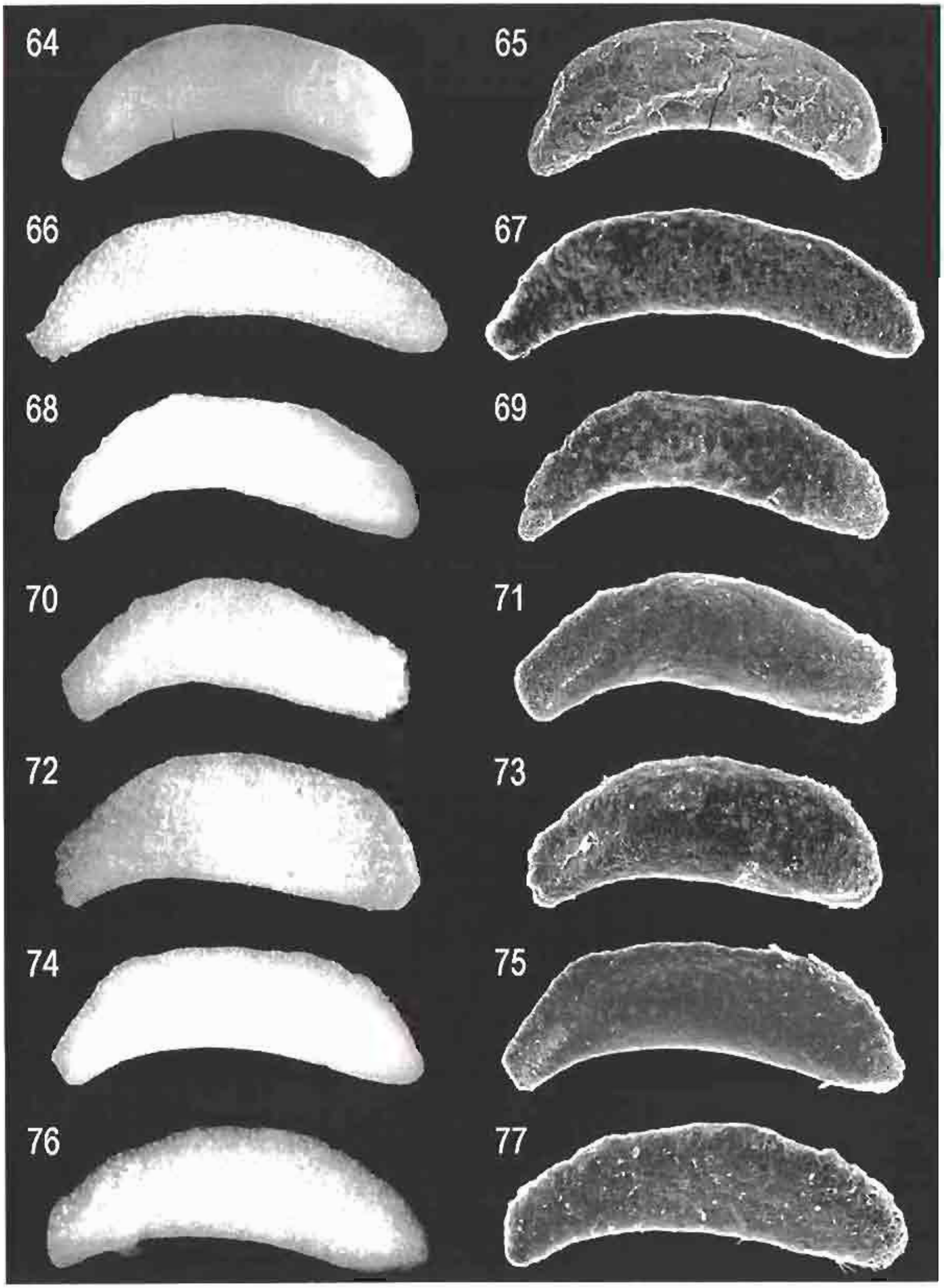
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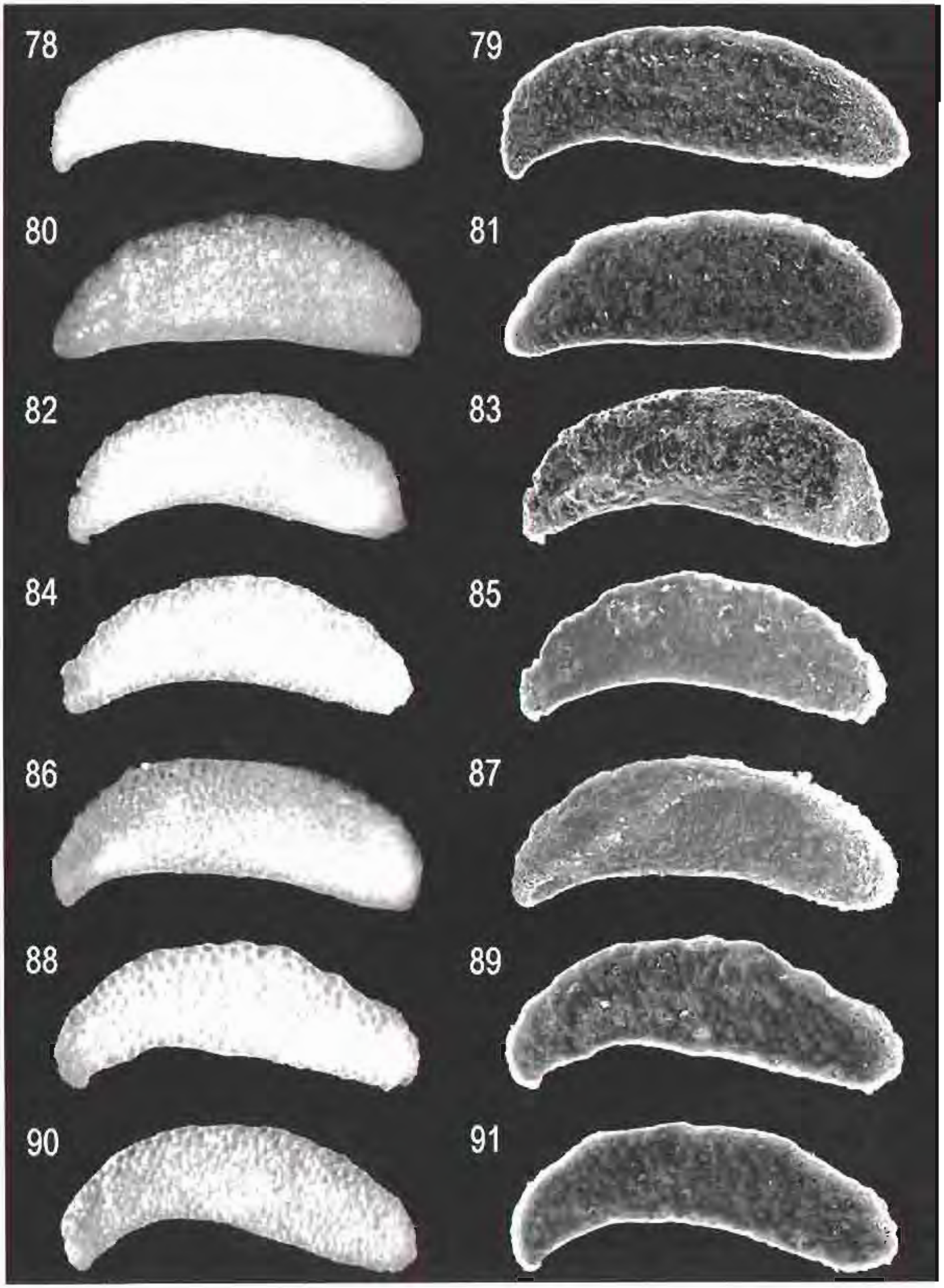
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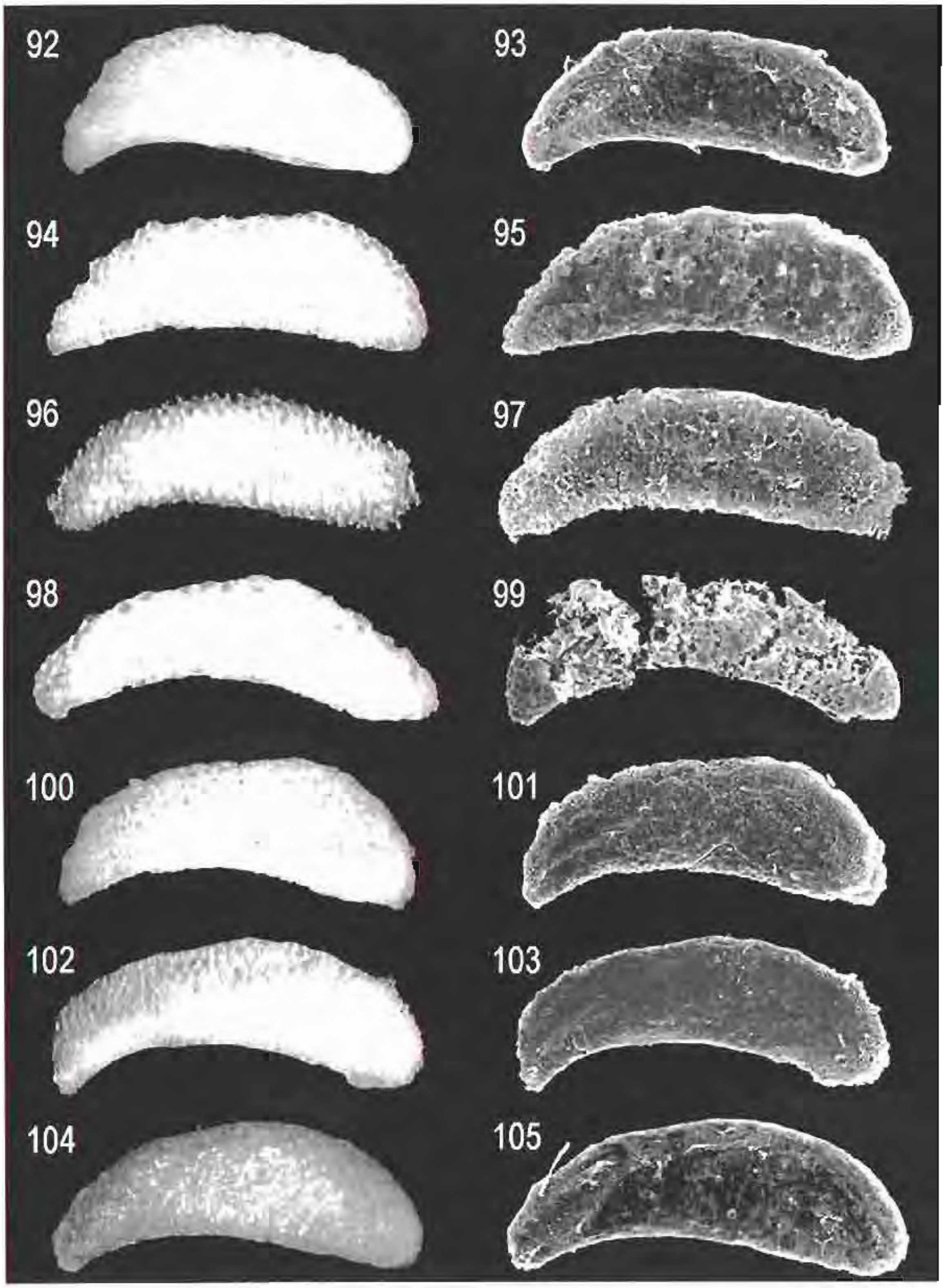
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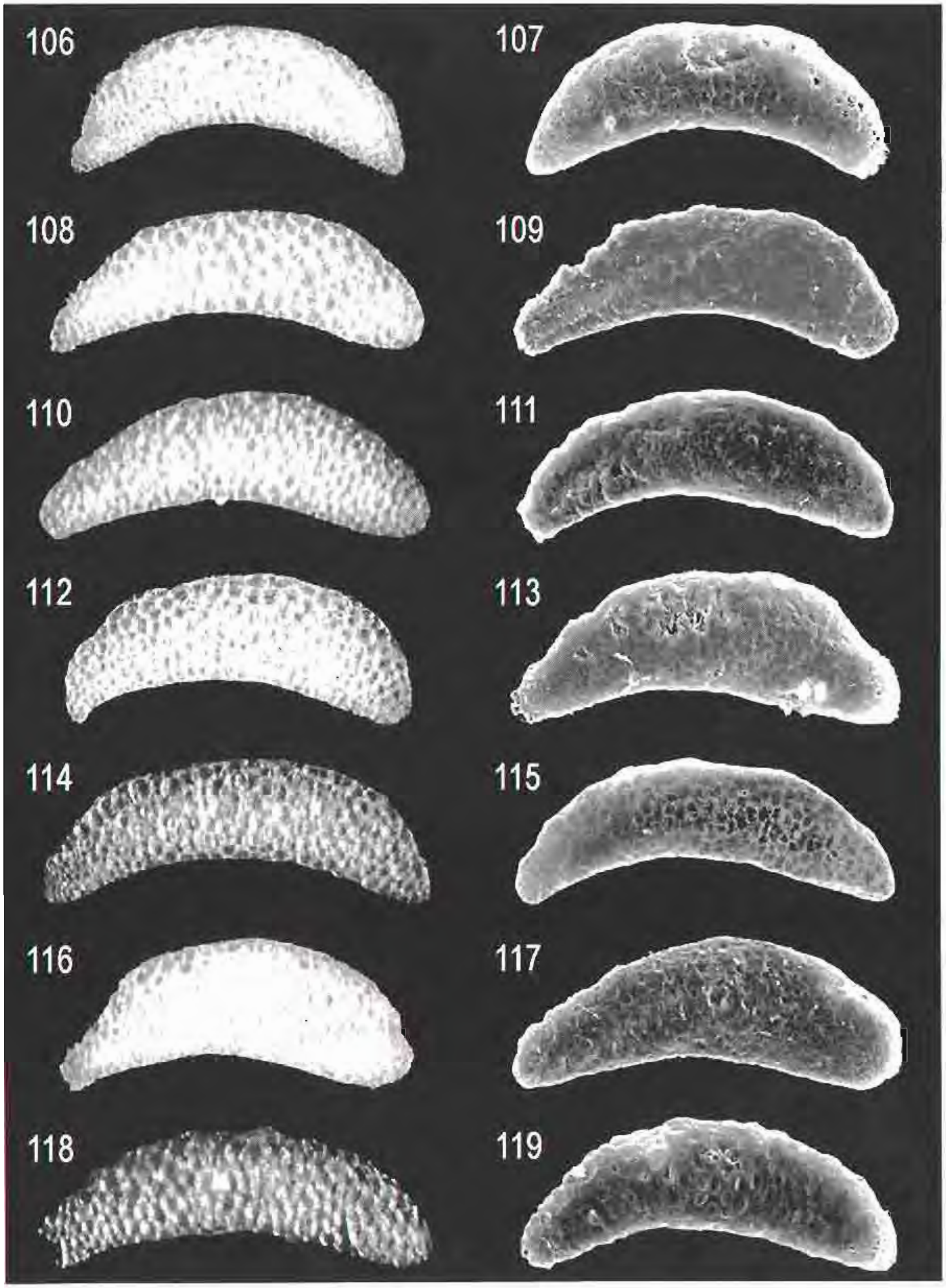
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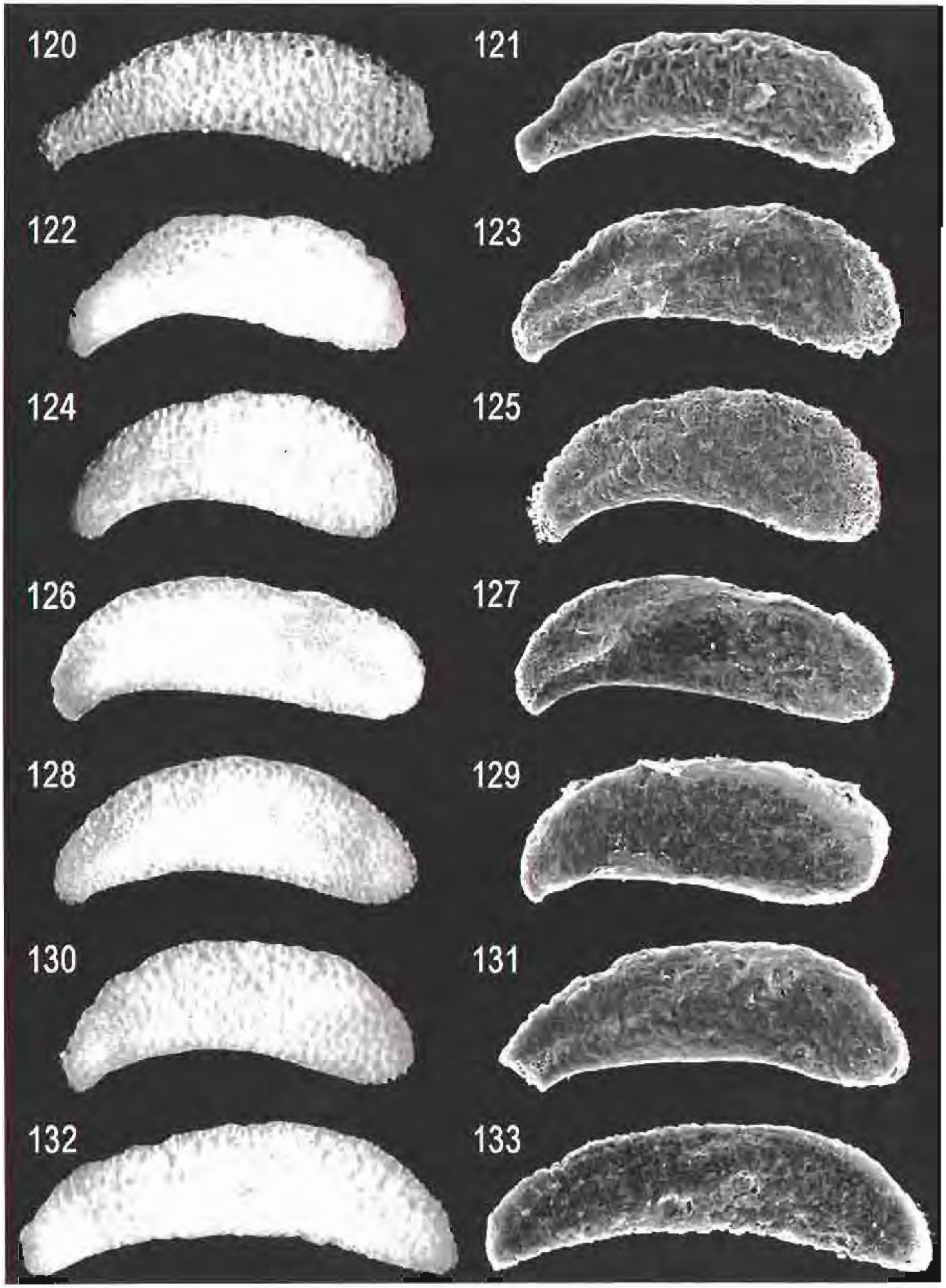
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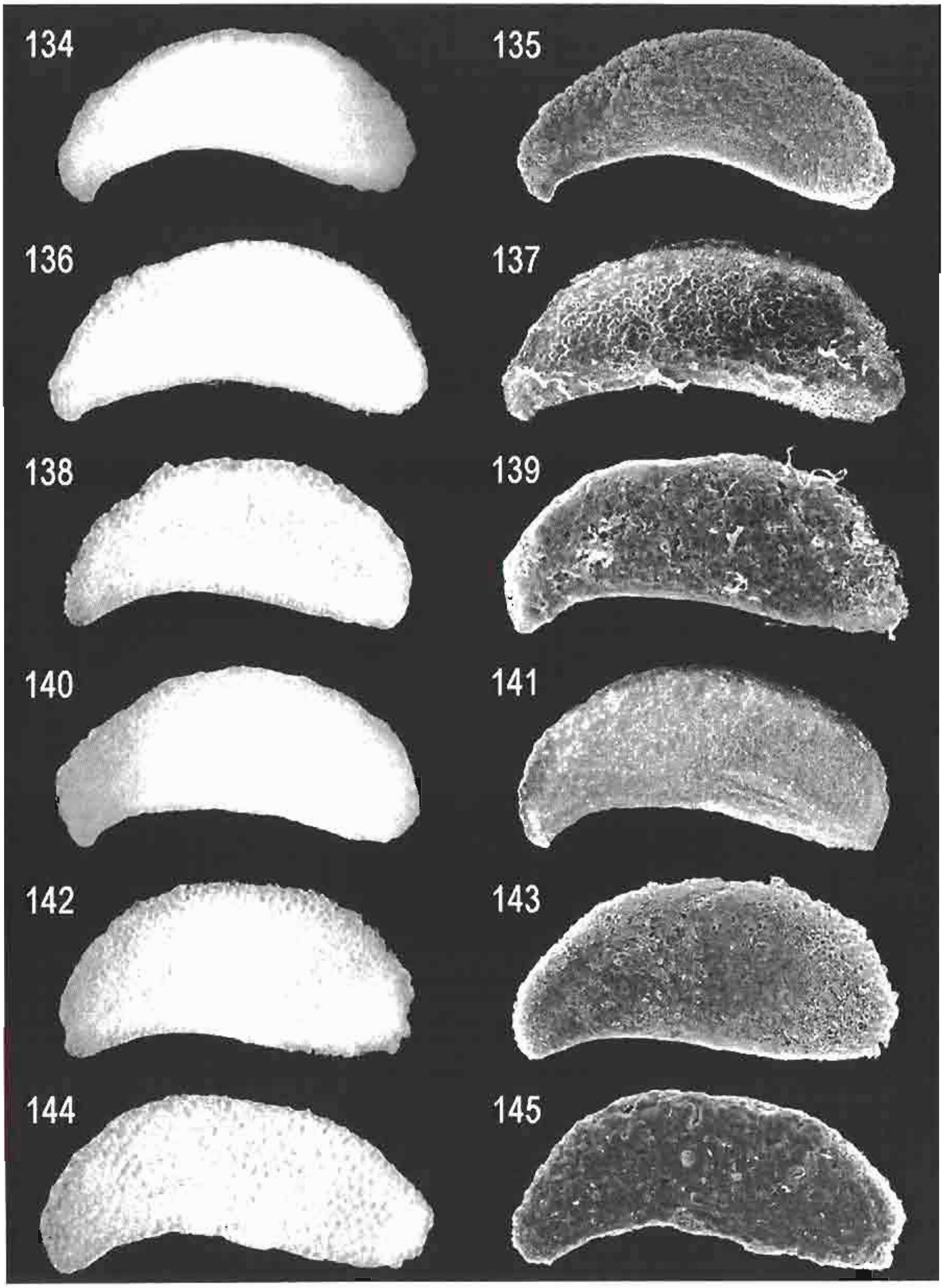
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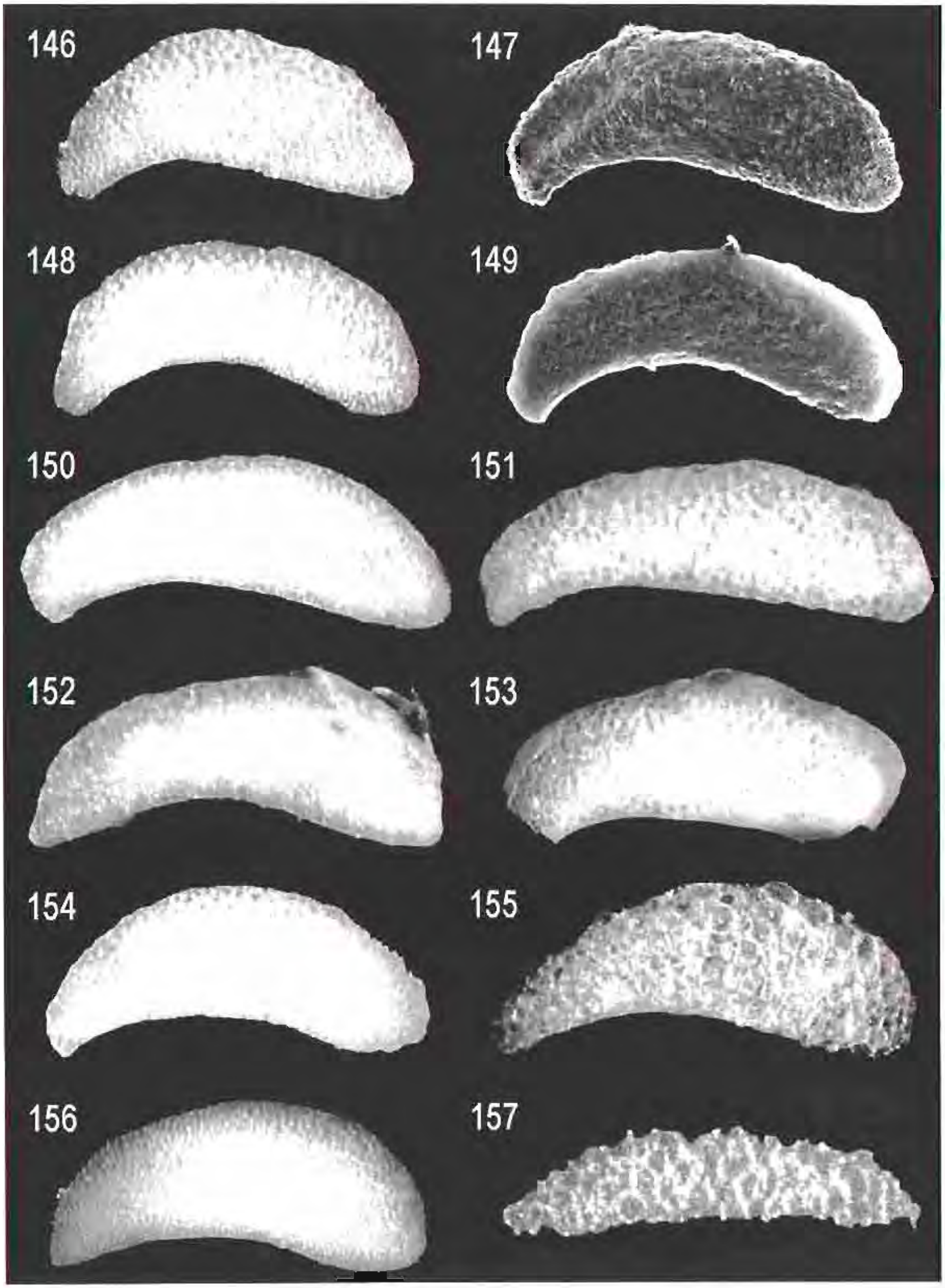
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CHAPTER 4

METHOD FOR MOUNTING RADULAE FOR SEM STUDY USING AN ADHESIVE TAPE DESICCATION CHAMBER [2]

Abstract

A method to mount radulae for low-magnification SEM study for comparative taxonomic purposes is described. The radula is arranged wet over the adhesive side of a piece of adhesive tape. The addition of a few drops of liquid delay desiccation, permits the radula to be arranged. A piece of clear plastic film is added, forming a desiccation chamber. Pinpricks around the radula allow it to desiccate slowly. The desiccation chamber is then cut near the radula, and the radula and its adhesive base are mounted on the SEM stub. The method is simple and produces radulae with little deformation, suitable for SEM.

Keywords: radula, SEM, mounting, method, desiccation

Introduction

The radula is widely studied under the scanning electron microscope (SEM) for taxonomic purposes. Several methods are available by means of which radulae can be prepared and mounted for SEM. Among them, Solem (1972) and Bradner and Kay (1995) suggest mounting the radula directly on the SEM stub using a thin layer of

[2] Manuscript currently in review (*American Malacological Bulletin*)

adhesive (double-sided tape or contact cement). There are problems with this approach, however: it is difficult to reposition the radula once it touches the adhesive, and the radular ribbon may curl and distort during desiccation, changing position or breaking. During the study of the *Cribrarula cribraria* (Linnaeus, 1758) species complex (Cypraeidae) (Moretzsohn, in review B) [Chapter 6], a new method to mount radulae for SEM study was developed as a simpler alternative to other methods. The purpose of this paper is to describe this method, which allows ample time to manipulate the radula, minimizes deformation due to desiccation, and produces radulae suitable for SEM study at low magnification, typical in comparative taxonomic work. It is assumed that the reader is familiar with radular extraction and cleaning methods. Some cleaning and mounting methods were described or discussed by: Radwin (1969), Bleakney (1982), Bradner and Kay (1995), Holznagel (1998) and Hickman (1999).

The method

Mounting on adhesive tape strip

Prepare a strip of adhesive tape with both ends looped backwards (adhesive side up) and attached to a glass slide (or cardboard piece; see Table 4.1 for materials and equipment). Lay the radula flat with teeth up and radular ribbon down on the adhesive side of the adhesive tape (Fig. 4.1), with a drop or two of alcohol. Arrange the radular ribbon as desired. For comparative taxonomic study, Hickman (1977) suggests arranging the radula flat and straight (Fig. 4.7), so it can be easily compared to radulae mounted on glass slides for optical microscopy. Add more liquid with a Pasteur pipette as needed to delay desiccation as the radula is arranged on the adhesive tape. If the alcohol evaporates too fast, use a solution with lower percentage alcohol (e.g. 25%). In my experience, it is best to work when the radula is wet but not excessively wet, or the radula may curl (Fig. 4.3). When the alcohol starts to evaporate, the adhesive tape becomes sticky and the radula can be attached to the tape. It can be re-arranged if more alcohol is added.

Table 4.1. Materials needed

Ethanol solutions (70%, 25%)
Dissecting microscope
Adhesive tape ("Scotch tape" TM)
Clear flexible plastic film (polyethylene or similar)
Glass slides or pieces of cardboard
2 fine point needles (e.g. insect pins)
Pasteur pipette
Scissors
Fine pair of tweezers
Double-sided tape or nail polish
SEM aluminum stubs
Airtight container with desiccant

Desiccation chamber and stub mounting

Cover the radula with non-adhesive clear plastic film (e.g. polyethylene or acetate); press it against the adhesive tape forming a desiccation chamber with a wet radula inside. Use an insect pin to prick a few small holes around the radula, about 5-10 mm away from it (Fig. 4.2). The alcohol in the desiccation chamber evaporates slowly, depending on temperature, humidity outside the chamber, and size of holes. The clear film allows monitoring of radular desiccation. The radula should be dry enough to be mounted on an aluminum stub for SEM after 48 hours at room temperature. Allow longer desiccation time if the radula still looks wet or there is condensation in the plastic chamber. Extra pinpricks may be necessary if desiccation is slow.

Finally, prepare a clean aluminum SEM stub (Solem, 1972), coating it with nail polish, double-sided adhesive tape, or other adhesive to bond the desiccation chamber to the stub. Cut the adhesive tape chamber close to the radula; using a pair of fine tweezers, remove the non-adhesive cover film, and place the adhesive base with the radula on the SEM stub (Figs. 4.4 and 4.5). Next, press the sides of the adhesive base close to the radula against the stub to ensure good bonding. Be sure the radula and its tape base are oriented so that the radula is uppermost. Use of colored adhesive tape may prevent misalignment. Place the SEM stub in an airtight container with fresh desiccant (silica gel or similar) immediately, preventing settlement of dust particles (Hickman, 1999), and ensuring complete desiccation before sputter-coating the specimen with gold-palladium (or equivalent) for SEM observation.

Discussion

Radulae obtained from fresh or rehydrated dried tissue are flexible and have a tendency to curl, especially when the radula desiccates. It may be difficult to prevent curling if the radula is mounted directly onto an SEM stub. Too much adhesive prevents the radula from being manipulated. It is easier to manipulate a wet radula attached to a strip of adhesive tape than to mount a radula directly onto a stub. The addition of a drop or two of alcohol permits the radula to be moved about while it is still being positioned on the adhesive tape, and more liquid can be added as needed.

Percentage of alcohol, temperature and humidity outside the chamber play an important role in radular desiccation in the desiccation chamber. If desiccation is too fast, or uneven, the teeth or radular ribbon may distort or break. A low percentage alcohol (e.g. 25% ethanol) and the desiccation chamber described here slow desiccation and prevent breakage in the radular ribbon. A graded alcohol series can also be useful to reduce water content, but the more steps involved in handling the radula can be more challenging with fragile or very small radulae than in the simpler method described here.

The desiccation chamber with clear film allows monitoring of desiccation and maintains the radula flat until it dries. This is easier on the radula and more gentle than an alternative method using an unweighted glass cover slip over the radula, or with a rubber band to maintain the glass slip in place (Bradner and Kay, 1995), which can crack teeth in large radulae. In addition, the desiccation chamber slows desiccation, as compared to the glass cover slip method, and reduces artifacts caused by fast desiccation.

This method was employed successfully to mount Cypraeidae radulae ranging from 6 mm to 30 mm in length with little deformation caused by desiccation. The radula of many other mollusks may be smaller than those mentioned above. Only experimentation will show if the method is applicable to radulae from other taxonomic groups, or of different sizes. The method may have to be adapted to work with radulae of micromollusks, for example, but because there are fewer steps involved with this method, it may be preferred over methods that require more steps (such as an alcohol series).

Age of specimen and type of preservation (alcohol-preserved versus dried tissue) do not seem to negatively affect the quality of the radulae recovered (Moretzsohn and de

Couet, in prep.), although fresh specimens can be more easily dissected than those preserved in alcohol. Specimens collected more than 120 years ago and stored dried produced good-quality radulae (Moretzsohn, personal observation).

Small radulae were mounted whole (Figs. 4.4 and 4.7) on standard aluminum stubs (12.5 mm diameter); comparable portions of larger radulae were cut and mounted onto stubs. It is possible to mount several specimens side by side on the stubs (Fig. 4.4) saving some time at the SEM by reducing the time needed to change stubs. However, if the specimens are from different museum collections and the radulae must be returned to the museums upon study, it may be sensible to mount the radulae separately.

Figure Captions

Figure 4.1. Diagram of a wet radula arranged on the adhesive surface of adhesive tape. The radula can be positioned as wanted with insect pins or tweezers prior to covering the radula with clear plastic film (Fig. 4.2).

Figure 4.2. Diagram of a desiccation chamber made with adhesive tape and clear non-adhesive polyethylene film for slow desiccation of radulae for SEM. Ethanol evaporates slowly through pinpricks made around the radula (arrows).

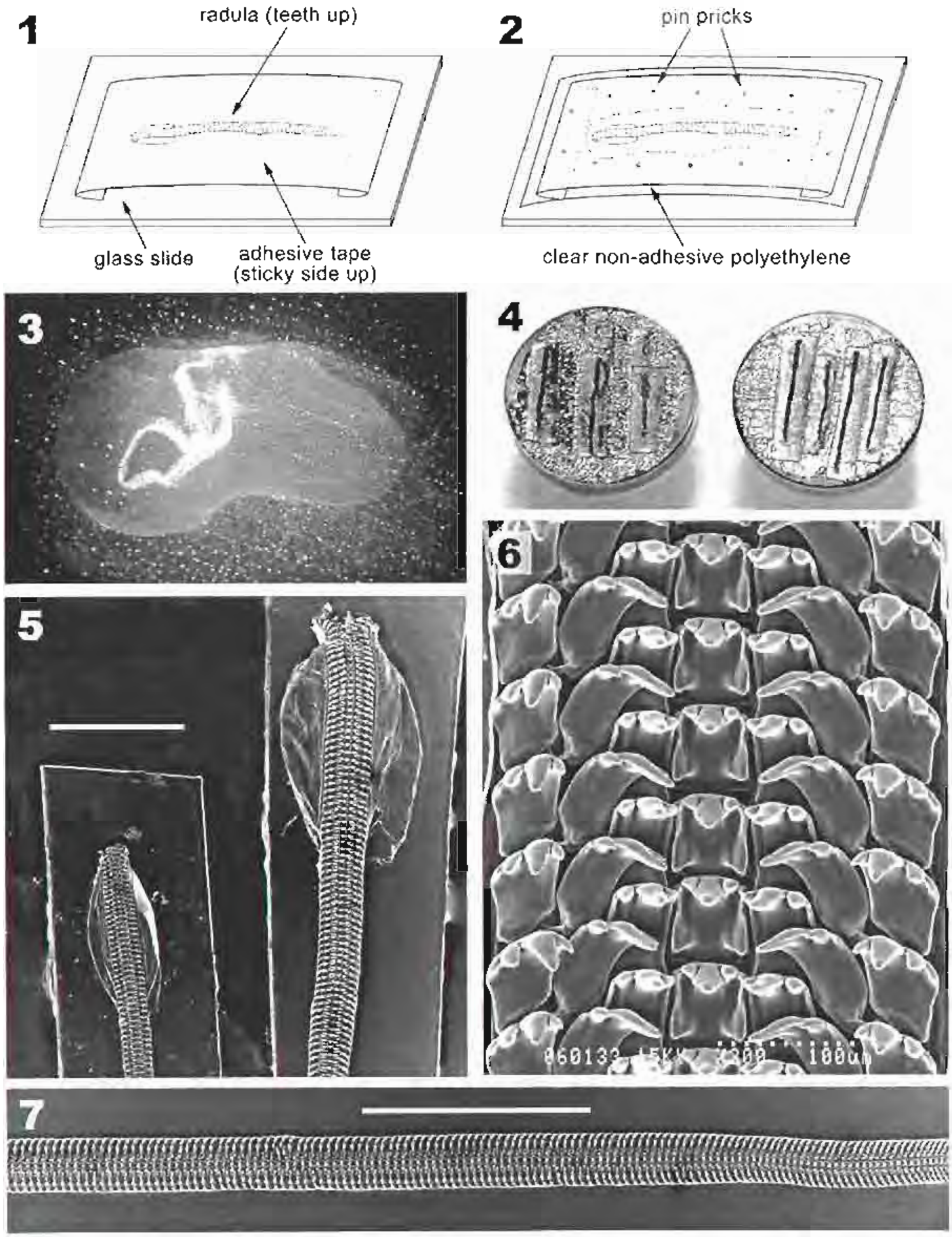
Figure 4.3. Curling radula with excessive ethanol prior to being positioned in the desiccation chamber. Note the beads of adhesive on the surface of adhesive tape (field is about 3 cm wide).

Figure 4.4. Small radulae of cowries in the *Cribrarula cribraria* complex mounted on SEM stubs and coated with gold-palladium for SEM observation.

Figure 4.5. Scanning electron micrograph showing parts of two radulae of *C. gaskoinii* (Reeve, 1846) prepared as described in text. Note the plastic bases cut close to the radulae and mounted on SEM stubs. Bar = 1500 μm.

Figure 4.6. Scanning electron micrograph of the radula of *C. gaskoinii* desiccated as described in the text, showing no significant distortion of the radula and individual teeth.

Figure 4.7. Portion of the radula of *C. cribraria* mounted straight for a comparative study with glass-mounted radulae. Bar = 1500 μm.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radula (teeth up)
glass slide
adhesive tape
(sticky side up)
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pin pricks
clear non-adhesive polyethylene
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CHAPTER 5

A NEW SPECIES OF *CRIBRARULA* (GASTROPODA: CYPRAEIDAE) FROM NEW SOUTH WALES, AUSTRALIA [3]

Abstract

A new species in the *Cribrarula cribraria* complex (Cypraeidae) is described from New South Wales, Australia, on the basis of a multivariate analysis of shell characters, the radula and odontophore cartilage. *Cribrarula gravida* **sp. nov.**, can be easily separated from its congeners by its large, inflated shell, with rostrate extremities, large elliptical off-white dorsal spots against a light brown dorsal coat, and columellar teeth thicker than in shells of most species of *Cribrarula*. This is the twelfth known species in *Cribrarula*, and the third from Australian waters.

Keywords: Cypraeidae, *Cribrarula gravida* sp. nov., new species description, *C. cribraria* complex, Australia, radula, odontophore

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Introduction

Species in the genus *Cribrarula* Strand, 1929 are attributed to the *Cribrarula cribraria* Linnaeus, 1758 species complex (Gastropoda: Cypraeidae), and have shells with characteristic white dorsal spots on a brown background and orange-red mantles. In the past ten years six new taxa have been proposed in *Cribrarula*: *gaspardi* Biraghi and Nicolay, 1993 and *oceanica* Raybaudi, 1993, apparently two names for the same new subspecies of *C. cribraria* from the Marshall Islands (*gaspardi* has priority); *C. taitae* (Burgess, 1993) from American Samoa; *C. cribraria ganteri* Lorenz, 1997 from Sri Lanka; *C. pellisserpentis* Lorenz, 1999 from Madagascar, and *C. garciai* Lorenz and Raines, 2001 from Easter Island.

For a systematic review of the genus *Cribrarula* Strand, 1929 (Moretzsohn, in review B), several major museums were visited in the USA and Australia, and hundreds of specimens borrowed for multivariate morphometric, radular and molecular analyses. The complete results from these analyses are beyond the scope of the present article and will be presented elsewhere (Moretzsohn, in review B) [Chapter 6].

Among the specimens studied at the Australian Museum, Sydney (AMS), one remarkable specimen from New South Wales clearly suggested that there is at least another yet undescribed species in the complex. This specimen is much larger than any Eastern Australian specimens of *C. cribraria* (and larger than most specimens from most places), and is segregated from others by multivariate morphometric analyses; its radula and odontophores differed from those of other taxa in the complex, thus providing support for a new species description. Additionally, rather complete collection data show that this specimen was collected outside the usual range of its closest taxon, *C. cribraria*, a widespread species which in Eastern Australia occurs more frequently in Queensland than in New South Wales (Schilder, 1965b; Wilson, 1993; Lorenz and Hubert, 2000). Thus, despite the fact that only one specimen is currently known, it merits description as a new species.

Systematics

Cypraeidae Gray, 1847

Cribrarula Strand, 1929 - (Type species: *Cypraea cribraria* Linnaeus, 1758)

Cribrarula gravida Moretzsohn new species

(Figs. 5.1 to 5.6, 5.22)

Type material: Holotype (Figs. 5.1 to 5.6, 5.22) deposited in the Australian Museum, Sydney, AMS C. 91000 (length 35.15 mm, width 22.10 mm, height 18.25 mm, 20 columellar and 21 labral teeth, umbilicus (spire region) diameter 6.20 mm; see Table 5.1 for additional measurements and comparison with other material). The radula of the holotype was prepared and mounted on two SEM stubs and deposited at the AMS (AMS C. 91000). Two samples of genomic DNA obtained from the holotype's dried tissue were deposited in the tissue collection of the Australian Museum's Evolutionary Biology Unit (EBU # 11517 and 11518). Additionally, a cast of the holotype made from a protective coat of clear nail polish (Fig. 5.28) (used to protect the shell during tissue digestion with a protease) was also deposited with the holotype (AMS C. 91000).

Type locality: Fish Rock, south side, 2 km SE of Smoky Cape, New South Wales, Australia, 30° 56.4'S, 153° 5.9'E (Fig. 5.27), collected at 18 m depth outside a cave.

Diagnosis: Large inflated pyriform shell, rostrate extremities, with large elliptical dorsal spots, no marginal spots, columellar teeth thicker than in other congeneric species, flared dorsal anterior extremity.

Description: Shell (Figs. 5.1 to 5.6): The shell of the holotype is large for the genus (35.15 mm in length), pyriform in dorsal profile, with produced extremities (Fig. 5.1) and thick marginal calluses. The base and labrum are convex (Figs. 5.4 to 5.6), and the shell is considerably inflated dorso-ventrally (shell width/length ratio is 62.9%, and height/width ratio 82.6%). The aperture is slightly constricted at the center (minimum width 2.10 mm, maximum width 2.70 mm), and curved to the left. Labral teeth (21) are thick, extending about 64% of the labrum width (Fig. 5.3). Columellar teeth (20) are thicker than those on shells of most congeneric species, not extending far onto the base, but reaching deeply into the aperture, and forming distinctly ribbed fossula and peristome. Both the fossula and peristome are sloped, concave, and wide. The terminal ridge is long, thick, and nearly parallel to the anterior extremity of the labrum's. The gap between the terminal ridge and anterior columellar teeth is similar in width to neighboring intertooth spaces. The base, labral and columellar margins and extremities are white. The white marginal calluses obliterate the dorsal pattern up to about half of the shell height on each side (Figs. 5.2, 5.4). There are no marginal spots (Figs 5.2, 5.4) (common on the shells of most species of *Cribrarula,* but rare in shells of *C. cribraria*). The labrum is thick, keeled and forms a marginal sulcus near the extremities (Fig. 5.1). The anterior region of the labrum is declivous towards the aperture (Fig. 5.6), and the labral margin is upturned at the center (Figs. 5.5, 5.6). Both the labral and columellar marginal calluses are irregular, forming slightly crenulated margins (Fig. 5.3). The dorsum is distinctly convex, its highest point about 23.4 mm from the anterior extremity (67% of the shell length). The dorsum is light brown, densely peppered with 88 off-white elliptical spots of variable size (ranging in maximum diameter from 2.80 to 3.50 mm) (Fig. 5.1). The dorsal spots are not very distinct, and there are no dark rings around the dorsal spots. The dorsal line is not well defined, but there are patches with overlaid "double exposure" (*sensu* Savazzi, 1998) pigmented layers along a region corresponding to the dorsal line (Figs 5.1, 5.2). There are also smaller patches of overlaid pigmented layers on other parts of the dorsum. The dorsal line region forms an angle of about 40° with the base of the shell (dorsal line angle) when seen from the anterior canal (Fig. 5.6). The dorsal coat produced by both lobes of the mantle is similar in color, but the dorsal spots produced by the right mantle lobe are slightly smaller than those produced by the left lobe (Fig. 5.2 vs. Fig. 5.1). The umbilicus (spire region) is wide (c. 6.2 mm in diameter) and slightly umbilicated (Fig. 5.5). The extremities are rostrate, and both anterior and posterior canals have thick margins (Figs. 5.5, 5.6). The dorsal part of the anterior canal is flared up (Figs. 5.2, 5.4).

Animal: The animal was dried inside the shell, with part of the mantle showing inside the aperture. The mantle bore apparently simple papillae: short, finger-like in the dry state, similar to those of other species of *Cribrarula.*

Radula (Fig. 5.22): The radula of *C. gravida* sp. nov. is a typical radula of *Cribrarula* (the 'Cicercula' pattern of Bradner and Kay, 1996:125-147). The central tooth has two rounded basal denticles (left arrow in Fig. 5.22). The outer marginal teeth have a small projection (right arrow in Fig. 5.22) near the outer margin that was not seen in radulae of other species of *Cribrarula*. The average size of the central tooth of *C. gravida* sp. nov. was 108.4 x 93.55 μm (n= 18), and central tooth L/W ratio was 1.19 (n= 14) in *C. gravida* sp. nov. The radular ribbon had an average width of 595 μm, with an average 11.4 rows of teeth per mm of radula (n= 4).

Odontophore cartilage: The pair of odontophore cartilages conforms to that of congeneric species: falciform elongated, with a spongy texture, and cream in color, except that it is larger, about double of the size of the odontophores of other species in *Cribrarula* (estimated at about four mm long).

Schilders' formula: 35.63.19.18. The figures represent the following values for the holotype of *C. gravida* sp. nov.: 1) shell length in mm (rounded up or down to closest integer); 2) shell width-length ratio as percent; 3) number of labral teeth; and 4) number of columellar teeth (both tooth counts are "reduced" (Schilder and

Schilder 1938-1939: 123-124), representing the equivalent number of teeth in a hypothetical shell of 25 mm in length. The transformation is the following:

Number of reduced teeth = 7 + (absolute tooth count – 7)$\sqrt{(25/\text{shell length})}$

New formula: 35.2/ 62.9/ 6.2/ 2.0/ 0. The figures represent the values for the holotype of *C. gravida* sp. nov.: 1) shell length in mm; 2) shell width-length ratio as percent; 3) umbilicus (spire region) diameter in mm; 4) relative columella teeth thickness; and 5) labral spot size (Moretzsohn, in review B) [4].

Etymology: The epithet *gravida* is a noun in apposition, derived from the Portuguese, meaning pregnant, alluding to the inflated shell of the holotype. I dedicate this species to my wife, Heather, who was pregnant with our daughter Olivia when I first became convinced that this was an undescribed species.

Comparative Analysis

Materials and methods

List of material examined – See Appendix 5.1.

Cowrie specimens with dried tissue were borrowed from several museums. Tissues were digested *in situ* with a protease, yielding the radula, odontophores and DNA (Moretzsohn and de Couet, in prep.). Radulae were mounted on aluminum stubs and studied under SEM (Moretzsohn, in review C) [Chapter 4].

[4] Note that a revised, slightly different formula appears in Chapter 6

A multivariate principal component analysis (PCA) of shell characters was performed with the statistics package Minitab (v. 12.1). A suite of 67 shell characters and 1247 shells representing all taxa in the *Cribrarula* complex from different locales in the Indo-Pacific were used in an initial analysis (see Moretzsohn, in review B for character list and details on the morphometric analyses [Appendix 6.1 [5]]). The absolute scores for the first three principal components (PC1, PC2 and PC3) for each character (variable) were added, the sum ranked, and the characters that contributed the least variation were removed from further analyses. Also removed from further analyses were specimens from other locales. This iterative procedure of pruning characters and specimens continued until the number of characters was reduced to the eight apparently most influential characters, and only specimens from Eastern Australia were included.

Abbreviations used throughout the text: AMNH - American Museum of Natural History, New York, NY; AMS - Australian Museum, Sydney, Australia; AMS C. – catalog number of specimens at AMS; ANSP - Academy of Natural Sciences, Philadelphia, PA; bp – DNA base pairs; BPBM - Bernice Pauahi Bishop Museum, Honolulu, HI; CAS - California Academy of Sciences, San Francisco, CA; CM - Carnegie Museum of Natural History, Pittsburgh, PA; CMB - private collection of the late C.M. “Pat” Burgess, Honolulu, HI (now at BPBM); COI – cytochrome oxidase I gene; DMNH - Delaware Museum of Natural History, Wilmington, DE; FMNH - Field Museum of Natural History, Chicago, IL; HBR - private collection of Hugh Bradner, Scripps Institution, La Jolla, CA; LACM – Natural History Museum of Los Angeles

[5] Note that the list of conchological characters in Appendix 6.1 was reduced to 61 characters

County, Los Angeles, CA; L/W – length-width ratio; mtDNA – mitochondrial DNA; NSW – New South Wales, Australia; PCA – principal component analysis; PC1, PC2, PC3 – principal component 1, 2 and 3; PCR – polymerase chain reaction; SEM – scanning electron microscope; sp. nov. – *species nova* (new species); USNM - US National Museum, Smithsonian Institution, Washington, DC.

Shell character terminology follows Schilder and Schilder (1938-1939) and Lorenz and Hubert (2000).

Results

Even when a large number of specimens and characters (e.g. 60 characters and 200 shells representing all species) were used in PCA analyses of shell characters, the holotype of *Cribrarula gravida* sp. nov. showed its distinctiveness (not illustrated here, but available upon request). The initial analyses showed a cloud of data points with some recognizable groups (e.g. *C. fallax*) and *C. gravida* separated from other specimens, but with too many points to see the groups clearly. Iterative analyses with fewer specimens and characters helped to focus the attention on specimens most similar to the holotype of *C. gravida* sp. nov. Specimens from East Africa, then Western Australia, Hawaii, etc., were sequentially removed from the analysis, resulting in increasingly clearer groupings.

The final PCA analysis, with 36 specimens from Eastern Australia and using eight shell characters (Fig. 5.26), showed the holotype of *C. gravida* sp. nov. is separated from the others on both PC1 and PC2; the holotype of *C. cribraria melwardi* Iredale, 1930 (described as *Nivigera melwardi* Iredale, 1930) (Figs. 5.8 to 5.13) was among the specimens closest to the holotype of *C. gravida* sp. nov. on PC1, while an elongated shell of *C. c. cribraria* was the closest one to *C. gravida* on PC2. Shells of *melwardi* and *cribraria* are not separable from each other by either PC1 or PC2 in this analysis.

Discussion

Cribrarula gravida sp. nov. is conchologically distinct from all other currently known taxa in *Cribrarula*. No apparent intermediate specimens were found connecting the holotype of *C. gravida* sp. nov. conchologically to specimens of other species. In some of the morphometric analyses (not shown, but available upon request), large specimens of *C. cribraria*, *C. esontropia*, *C. fallax*, and *C. gaskoini* [6] sometimes appeared close to the holotype of *C. gravida* sp. nov., probably because of the effect of shell size (judging by variable scores) had in the analyses. However, even with the exclusion of size-related characters, the holotype of *C. gravida* sp. nov. remained distinctive (albeit less then when size-related characters were used). Other characters that contributed to the distinctiveness of *C. gravida* sp. nov. were: umbilicus diameter, thickness of the anterior canal, relative size of columellar marginal callus, shell height-width ratio, and the number of columellar teeth.

The holotype of *C. gravida* sp. nov. shares some shell features with representatives of other species of *Cribrarula* (Table 5.1), but a combination of characters can easily separate the former from the latter. For example, the absence of

[6] The original spelling of the epithet is *gaskoinii* (with –ii), although most recent authors spell it with a single –i. Since the publication of this paper, I adopted the original spelling, and elsewhere in this dissertation it is spelt with –ii (see note in Chapter 6, under discussion of *gaskoinii*).

marginal spots on the holotype of *C. gravida* separates it from specimens of *C. esontropia* and *C. gaskoini*. Some shells of *C. cribraria exmouthensis* and *C. fallax* may be large, pyriform and inflated, but these taxa occur in Western Australia.

Some specimens of *C. cribraria cribraria* may have large shells, but these specimens are usually found in Melanesia or the Central Pacific, not in Eastern Australia, even though Schilder and Schilder (1967) found that the average shell size (length) is slightly larger, but not statistically significant, than the average from other locales. Among the specimens examined in this study, the largest shell from Eastern Australia was 27.2 mm (USNM 773542), from Queensland, but that specimen looks more like a typical *C. cribraria cribraria*, with a non-inflated, non rostrate shell, with fine columellar teeth, and short labral teeth of medium thickness. The average shell length for the specimens studied from Eastern Australia was 21.50 mm (St. Dev. 2.33, N= 51), thus significantly smaller than the holotype of *C. gravida* ($p = 0.0000$, 1-tailed P).

Shell inflation is not always directly related to shell size: small specimens in the *cribraria* complex may be inflated (e.g. shells of *C. gaskoini* (Reeve, 1846) as small as 20 mm (Fig. 5.21), and large ones may not be inflated (e.g. shells of *C. cribraria* as large as 36 mm (Fig. 5.14).

The dorsal spots on the holotype of *C. gravida* sp. nov. are not so distinct as in shells of *C. cribraria* (Linnaeus, 1758) (Figs 5.14 to 5.20), and there are no dark rings around the spots as in shells of *C. astaryi* Schilder, 1971 and *C. garciai* Lorenz and Raines 2001. The dorsal margin of the anterior canal is flared up in *C. gravida*, different from shells of *C. cribraria melwardi* (Iredale, 1930) (Figs. 5.9, 5.11). The labral margin is upturned at the center (Figs. 5.5, 5.6), similar to shells of *C. cumingii* (Sowerby, 1832). Both the labral and columellar marginal calluses are irregular, forming slightly crenulated margins (Fig. 5.3), similar to shells of *C. fallax* (Smith, 1881). See Table 5.1 for more comparisons with congeneric species.

Lorenz and Hubert (2000) map the distribution of *C. cribraria cribraria* as Queensland and *C. cribraria melwardi* as far south as New South Wales, although the text (Lorenz and Hubert, 2000: 178) cites only Queensland (*melwardi*), and does not specify specimens in New South Wales. Wilson (1993) notes southern Queensland as the southern limit of distribution of *C. cribraria*. The southernmost record in eastern Australia of *C. cribraria melwardi* that was examined in this study was a lot of 8 specimens from Fairfax Is., Bunker Group, Great Barrier Reef, 023°51'S, 152°22'E (AMS. C. 363556), about 800 km north of Smoky Cape, New South Wales, the type locality of *C. gravida* sp. nov. (Fig. 5.27).

Schilder and Schilder (1971) and Lorenz and Hubert (2000), among the "splitters," recognize subspecies in the Cypraeidae, and therefore note two subspecies of *C. cribraria* in Eastern Australia, *cribraria* and *melwardi*. Burgess (1985) and Wilson (1993), among the "lumpers," do not recognize subspecies, and lump all populations of *C. cribraria* into a single species. Moretzsohn (in review B) reviewed the taxa in the genus *Cribrarula*, and found that some populations of *C. cribraria* can be separated from others. *C. cribraria melwardi*, is perhaps the most distinct of the subspecies recognized in *C. cribraria*, not only in coloration (i.e. albino or partially albino shells), but also in shell characters such as the marginal calluses (Moretzsohn, in review B) [Chapter 6]. The PCA analysis shown in Fig 5.26 does not separate shells of *C. cribraria cribraria* and *C. cribraria melwardi*, but they can be separated if other characters are used.

Although only one specimen was discovered, it is so different from shells of other species of *Cribrarula* in a several shell characters (Table 5.1), it discriminated in multivariate analyses (using more characters and shells from other locations, not shown here, but available upon request), and its radula and odontophore are larger and show some differences from those of congeneric species, that it merits description as a new species. Several valid cowrie species have been described based on a single or few specimens (e.g. *Lyncina leucodon* (Broderip, 1828) (Burgess, 1985: 96)) and later confirmed by the discovery of additional specimens. Moreover, *C. gravida* sp. nov. is described here after a large number of specimens (over 1200) were studied in the *cribraria* complex, and it proved to be morphologically and geographically distinct from all other specimens studied.

DNA was obtained from dried tissues by digesting the whole body *in situ* inside the shell (Moretzsohn and de Couet, in prep.). Unfortunately, the specimen was fixed in formalin (I. Loch, pers. comm., 2000), which cross-links with DNA, inhibiting its amplification by PCR. Several attempts were made to amplify a 313 bp fragment of mtDNA COI using cowrie-specific primers (courtesy of C. Meyer, pers. comm., 1999) that work with other DNA samples from museum specimens with dried tissue, but no amplification was obtained. The DNA is now deposited in the tissue collection at the Australian Museum's Evolutionary Biology Unit (EBU # 11517 and 11518), and samples can be obtained from the Museum for further attempts to amplify the DNA. Sequencing of *C. gravida* DNA would contribute to better understanding of its phylogenetic relationships.

The radula was recovered and studied under SEM. The radula is similar to that of other *Cribrarula* spp. (Bradner and Kay, 1996; Moretzsohn, in review B), except that it is larger than the radula of its congeners (Figs. 5.23 to 5.25), and the central tooth is larger than, and has different proportions from, the central tooth in *C. cribraria.* The average size of the central tooth of *C. gravida* sp. nov. was 108.4 x 93.55 µm (n= 18), compared to 68.5 x 54.4 µm (n= 9) (Bradner and Kay, 1996: 125) in other species in *Cribrarula.* Central tooth L/W ratio was 1.19 (n= 14, St. Dev. 0.06) compared to 1.23 (n = 9) for other species in *Cribrarula* (Bradner and Kay, 1996) (p = 0.078, t-test). Additionally, there are at least two differences from the radula of *C. cribraria*: 1) the central tooth in *C. gravida* sp. nov. has two rounded basal denticles (left arrow in Fig. 5.22), while in *C. cribraria* the basal denticles are pointed (Figs. 5.23 to 5.25); and 2) the outer marginal teeth have a small projection (right arrow in Fig. 5.22) near the outer margin that was not seen in radulae of other species of *Cribrarula*. These differences are comparable to interspecific differences in other species of *Cribrarula* (Bradner and Kay, 1996; Moretzsohn, in review B) [Chapter 6].

Odontophore cartilages are a promising new character set for molluscan taxonomy (Moretzsohn, in review A) [Chapter 3]. Examination of the odontophore of *C. gravida* sp. nov. showed it to be almost double the size (c. 4 mm long) of that in other congeneric species (odontophores range between 0.8 and 1.8 mm in length in species in

Cribrarula) (Moretzsohn, in review B). Other features of the odontophore such as texture, shape and color were similar to those of congeneric species.

Part of the dried mantle could be seen inside the aperture prior to digestion of the tissues and it bore short, finger-like papillae similar to specimens with dried tissue in other species of *Cribrarula.* The presence of dorsal spots on the shells of congeneric species suggests that in *C. gravida* sp. nov., the dorsal spots correspond to the papillae of the mantle as in *C. cribraria* (Moretzsohn, 2002a), and that the dorsal spot pattern represents the "thick paint" type of dorsal spot of Savazzi (1998) [Chapter 2].

Conclusion

The specimen discussed and illustrated here clearly belongs to a species distinct from others in *Cribrarula*, based on shell characters, radula and odontophore, and therefore it is described here as *Cribrarula gravida* Moretzsohn **new species**. The holotype is deposited at the Australian Museum, Sydney, and it bears the number AMS C. 91000.

Table 5.1. Comparison of shell characters, showing average figures or most common conditions.

	gravida* *sp. nov.	***crib. cribraria***	***crib. exmouthensis***	***crib. melwardi***	***esontropia***	***fallax***	***gaskoini***
Shell shape	Pyriform, inflated	Ovate, not inflated	Pyriform-rhomboidal	Ovate callous	Oval to rhomboidal	Pyriform, somewhat inflated	Ovate callous
Shell length (Ave/range)	35.2	22.5/ 11-45	23.0/ 14-42	21.7/ 15-26	23.2/ 12-32	31.3/ 20-36	17.3/ 10-30
Marginal calluses	Callused	Some shells callused	Some shells very callused	Very callused	Very callused	Somewhat callused	Some shells very callused
Marginal spots (Color/ Ave. No.)	No spots	No spots	No spots	No spots	Light brown/ 20	No spots	Brown/ 27
Columellar teeth (Ave./ thickness)	20, medium	18.2, fine	15.7, medium-fine	16.1, medium-fine	17.2, fine-medium	23.6, fine	17.5, fine
Labral teeth (Ave/ thickness.)	21, thick	17.2, medium	16.2, medium	16.3, medium	16.1, medium-thick	21.9, medium	17.7, fine-medium
Dorsal coat color	Light brown	Orange brown to brown	Brown to dark brown	White to light brown	Light to medium brown	Light to dark yellow	Orange brown
Shell extremities	Rostrate	Slightly rostrate	Slightly rostrate	Blunt	Slightly rostrate	Rostrate	Slightly rostrate

Table 5.1 (Continued) Comparison of shell characters.

	***gravida* sp. nov.**	***crib. cribraria***	***crib. exmouthensis***	***crib. melwardi***	***esontropia***	***fallax***	***gaskoini***
Fossula	Sloped, concave	Steep, concave	Abrupt, flat	Steep, concave	Steep, flat	Sloped, concave	Steep, concave
Umbilicus diameter (Ave in mm)	6.2/ slightly umbilicated	2.8/ umbilicated	3.3/ umbilicated	3.4/ umbilicated	3.2/ umbilicated	4.6/ umbilicated	2.7/ umbilicated
Dorsal flare (anterior extremity)	Flared	Flared	Most shells flared	Convex in most shells	Some shells flared	Not flared	Flared
No. Dorsal Spots (DS) (Ave./range)	88	50/ 25-120	42/ 35-77	28/ 0-90	70/ 45-190	50/ 35-75	65/ 45-170
DS shape/ min.-max. diameter	Elliptical/ 2.8-3.5	Round/ 1.2-2.2	Elliptical/ 1.1-2.3	Round-irregular/ 0.7-1.2	Round-elliptical/ 1.0-2.1	Elliptical/ 1.3-2.4	Round/ 0.6-1.1
DS density/ sharpness	High /not sharp	Medium/ sharp	High/not sharp	Medium /not sharp	High/sharp	Low-medium/not sharp	Medium to high/sharp
Schilders formula	35.63.19.18	22.58.18.19	23.61.17.16	22.63.17.17	23.62.16.18	31.59.20.22	17.64.20.20
New formula	35.2/ 62.9/ 6.2/ 2.0/ 0	22.5/ 58.2/ 3.3/ 1.3/ 0.1	23.0/ 60.6/ 3.3/ 1.7/ 0	21.7/ 63.2/ 3.4/ 1.8/ 0	23.2/ 62.0/ 3.2/ 1.3/ 2.1	31.3/ 59.4/ 4.5/ 1.0/ 0	17.3/ 63.2/ 2.6/ 1.1/ 1.3

Appendix 5.1. Materials examined and illustrated

Specimens from Eastern Australia used in the PCA analysis (Fig. 5.26):

Type material: Holotype of *Cribrarula gravida* **sp. nov.**, Type Locality: Fish Rock, S. side, 2 km SE of Smoky Cape, New South Wales, Australia outside cave, 18 m, 030°56.4'S, 153°5.9'E, V. Taylor!, Nov. 1972 (AMS-C 91000, 1 specimen).

Other materials – *Cribrarula cribraria cribraria*, Queensland, D. Pisor! (HBR R-141, 1 specimen); *C. crib. cribraria*, Queensland, GBR, Whitsunday Ids., Hayman Is., 020°3.6'S, 148°53.5'E, FA McNeill!, Dec.1932 (AMS-C 81677, 1 specimen); *C. crib. cribraria,* Queensland, Albany Passage, Cape York Peninsula, 16-22 m, 010°45'S, 142°37'E, Mel Ward!, Sep. 1928 (AMS-C 58655, 1 specimen); *C. crib. cribraria,* Queensland, Keppel Is., Coral Sea, ex WE Old Jr. coll., C. Coucom!, 1964 (AMNH 292280, 3 specimens); *C. crib. cribraria*, Queensland, Great Barrier Reef, ex WM Ingram # 262. Blue dot on label, ex WM Ingram (DMNH 43219, 2 specimens); *Cribrarula cribraria melwardi*: Holotype of *Nivigera melwardi* Iredale, 1930 (= *Cribrarula cribraria melwardi* Iredale, 1930), Type Locality: North West Island, Capricorn Group, Queensland, (*Memoirs of the Queensland Museum* 10: 84, pl. 9, figs. 12, 13) (AMS-C 57743, 1 albinistic specimen); *C. crib. melwardi,* Queensland, GBR, Bunker Group, Fairfax Is., 023°51'S, 152°22'E, J. Booth!, 1968 (AMS-C 363556, 8 specimens, ranging from completely albinistic to fully pigmented shells); *C. crib. melwardi,* Queensland, GBR, Capricorn Group, North West Is., 023°18'S, 151°42'E, coll

T. Iredale, M. Ward and GP Whitley!, May 1931 (AMS-C 81687, 2 specimens); *C. crib. melwardi*, Queensland, Swinger Reef, on sand, J.E. du Pont!, 25 Oct. 1968 (DMNH 31496, 1 specimen); *C. crib. melwardi*, Queensland, GBR, North West Is., under rocks, collected in extreme low tides, ex Kienle coll., Jun. 1976 (DMNH 196951, 1 albinistic specimen); *C. crib. melwardi*, Queensland, GBR, Capricorn Is. Group, ex Kienle coll. (DMNH 196194, 1 albinistic specimen); *C. crib. melwardi*, Queensland, NW Is., ex R. Summers coll., A. Nash!, Feb.1958 (AMNH 292268, 4 specimens); *C. crib. melwardi*, Queensland, Yeppon, Keppel Is, Coral Sea, C. Coucom!, 1964 (AMNH 292281, 1 specimen); *C. crib. melwardi*, Queensland, Northwest Is., R. Summers!, 1958 (BPBM 246796, 1 albinistic specimen); *C. crib. melwardi*, Queensland, Tryon Is., ex Glenn Goodfriend coll., under dead coral at low tide, V. Harris!, 17 Mar. 1969 (AMNH 260790, 1 albinistic specimen); *C. crib. melwardi*, Queensland, Tryon Is., Coral Sea, ex R. Summers coll., A. Nash!, Oct. 1959 (AMNH 292269, 3 specimens); *C. crib. melwardi*, Queensland, Keppel Bay, North Keppel Is., 023°04'S, 150°54'E, TA Garrard!, pre-1970 (AMS-C 363560, 1 specimen).

Specimens the shells and radulae of which were illustrated here (not mentioned above): *C. crib. cribraria*, Philippines, Cebu Is., Olonga Is., ex Eugenia Wright coll., under coral rocks in shallow water (USNM 773378, 1 out of 4 specimens); *Cribrarula gaskoini*, Oahu, Hawaii, D. Woodman!, pre-1996 (CMB 8-37, 1 out of 7 specimens); *C. crib. cribraria*, Fiji, Mamanuca Group, ex E. Wright coll., W. Cernohorsky!, 20 Jul. 1966 (USNM 773496, 5 specimens); *C. crib. cribraria*, New Caledonia, Noumea, 0-7 ft, rocks, some coral and weeds, near radio station, Baie Ouemo, 022°15' 24"S, 166°25' 44"E, G Kline and M. and V. Orr!, Dec. 1960-Jan. 1961 (ANSP 271247, 1 melanistic specimen out of 2 specimens).

Figure captions:

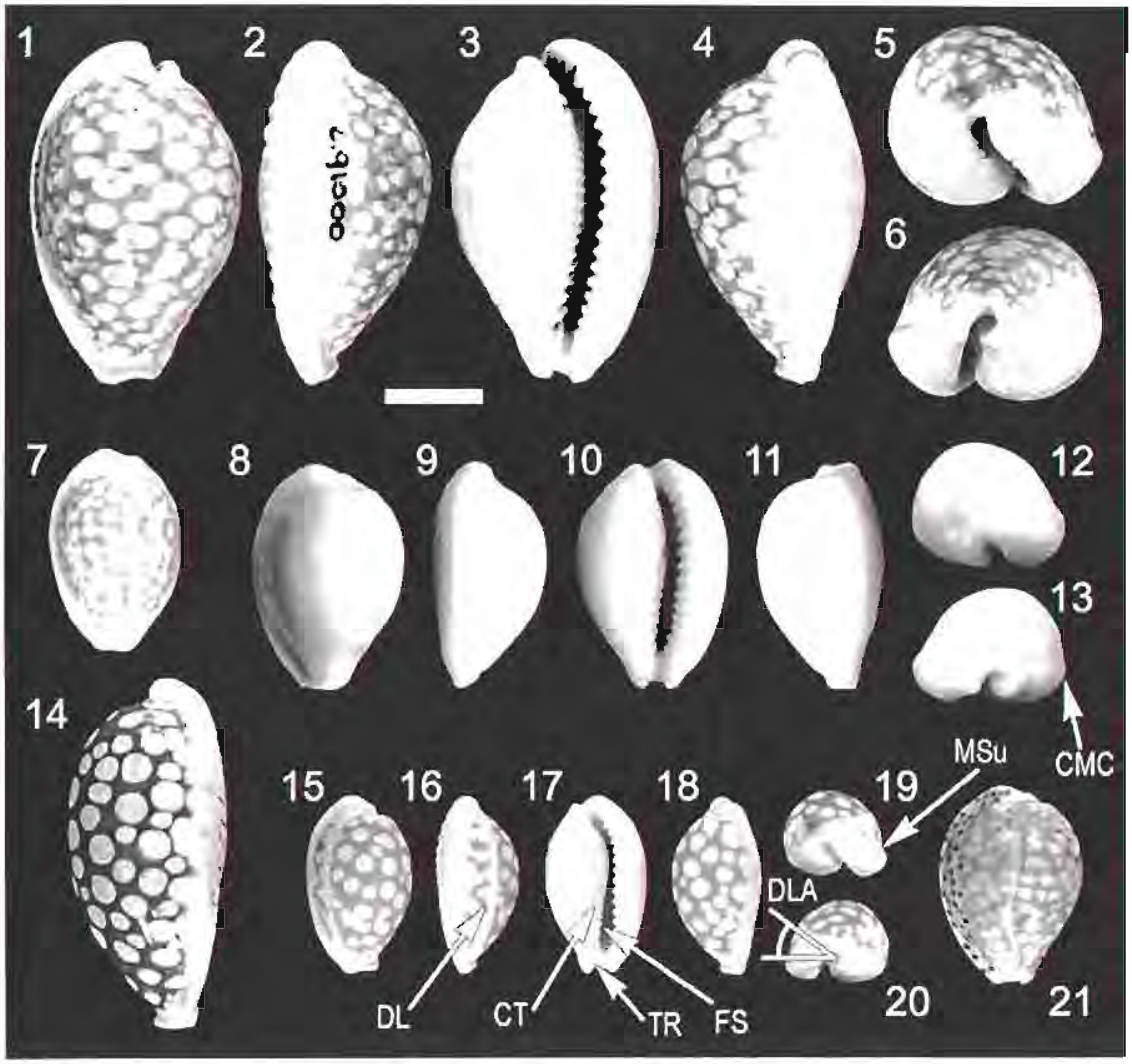
Figures 5.1 to 5.6. Holotype of *Cribrarula gravida* **sp. nov.** from NSW, Australia (AMS C. 91000); **5.1.** dorsal view, with posterior extremity up; **5.2.** labral side view; **5.3.** ventral view; **5.4.** columellar side view; **5.5.** view of the anterior extremity, and **5.6.** view of the posterior extremity; **5.7.** pigmented shell of *C. cribraria melwardi* from Queensland, Australia (AMS C. 363556); **5.8 to 5.13.** holotype of *C. cribraria melwardi*, from Queensland (AMS C. 57743); **5.14.** large shell of *C. cribraria* (usually identified as "*zadela*") from Cebu, Philippines (USNM 773378); **5.15 to 5.20.** typical shell of *C. cribraria cribraria* from Queensland (AMS C. 81677); and **5.21.** inflated shell of *C. gaskoini* from Hawaii (CMB 8-37). Scale bar is 10 mm. Arrows in the figures (5.13, 5.16 to 5.20) show the following characters: CMC= columellar marginal callus; CT= columellar teeth; DL= dorsal line; DLA= dorsal line angle; FS= fossula; Msu= marginal sulcus; and TR= terminal ridge.

Figures 5.22 to 5.25. Scanning electron micrographs of radulae: **5.22.** *Cribrarula gravida* **sp. nov., holotype** (AMS C. 91000), New South Wales, Australia - arrows point to two differences from other radulae shown here (see discussion); **5.23.** *C. cribraria melwardi* (DMNH 31496), Swinger Reef, Queensland, Australia; **5.24.** *C. cribraria cribraria* (USNM 773496), Mamanuca Group, Fiji; and **5.25.** *C. cribraria cribraria* (melanic) (ANSP 271247), Baie Ouemo, New Caledonia.

Figure 5.26. Plot of first two components of a PCA analysis (PC1 and PC2), representing 66.5% of the variation, using 36 shells from Eastern Australia and eight shell characters (shell length (L); columellar teeth count (CT); umbilicus diameter; CT/L; shell height/width ratio (H/W), CT thickness; anterior terminal thickness; columellar marginal callus). The shells of a few specimens are illustrated (the shell of *C. gravida* sp. nov., blue triangle, top left, is 35.15 mm long). Specimens identified as *C. cribraria melwardi* are represented in the figure by red circles, those of *C. cribraria cribraria* by black diamonds. The albino shell is the holotype of *melwardi* (Iredale, 1930) (shown in Figs. 5.9 to 5.13).

Figure 5.27. Map of Eastern Australia showing the type locality of *Cribrarula gravida* sp. nov., Smoky Cape, NSW, 030°56.4'S, 153°5.9'E (✪), as well as locality records of *C. cribraria cribraria* and *C. cribraria melwardi* (▲) used in the multivariate analysis (Fig. 5.26) of shell characters to compare with the new species.

Figure 5.28. Holotype of *C. gravida* sp. nov. and its cast made of clear nail polish, used to protect the glossy exterior surface of the shell against the slightly etching buffer used during *in situ* digestion of the dried tissue in the shell (Moretzsohn and de Couet, in prep.). After the digestion is complete, the polish coat is peeled away, and if done carefully, a perfect cast of the shell can be obtained. Note that the polish removed the China ink used to write the catalog number on the shell labrum. The cast was returned to the Australian Museum, and now is part of the lot AMS C. 91000.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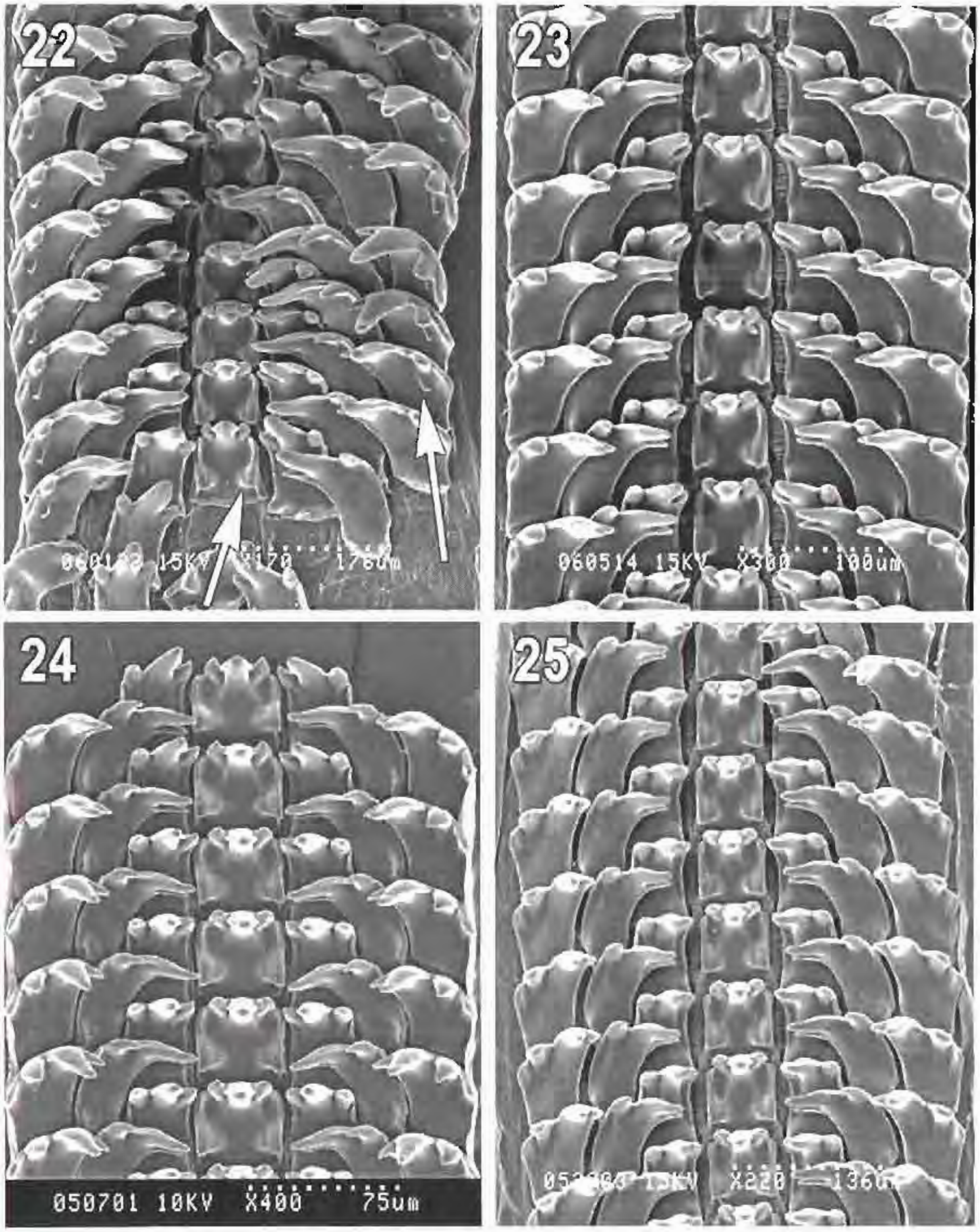
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060514 15KV X300 100um
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050701 10KV X400 75um
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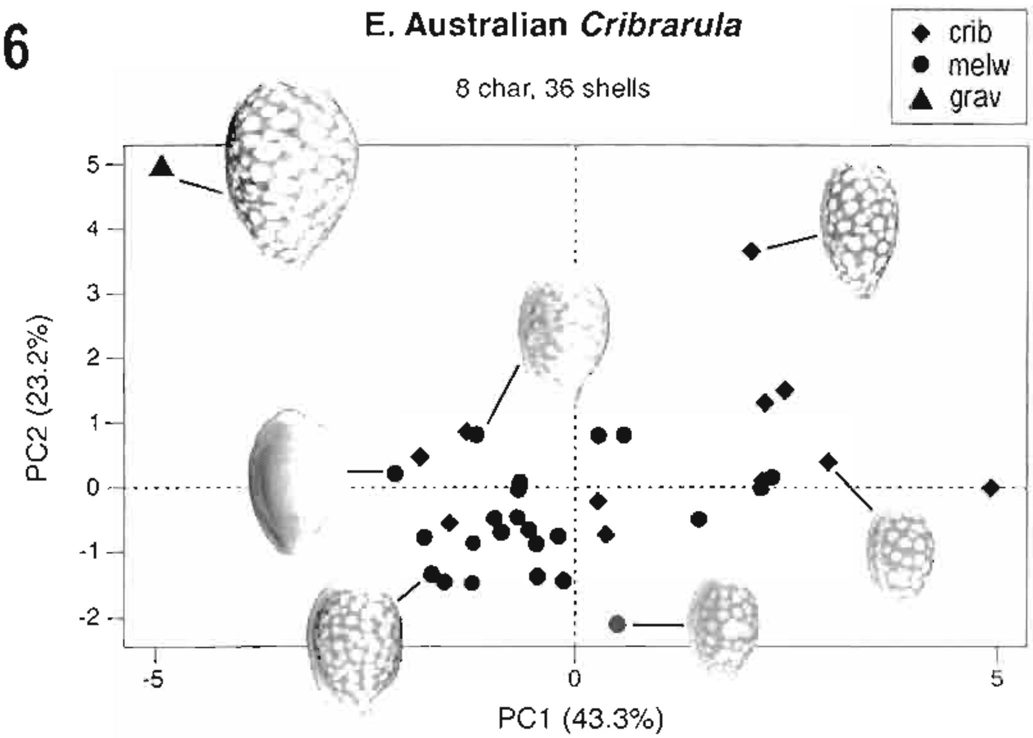
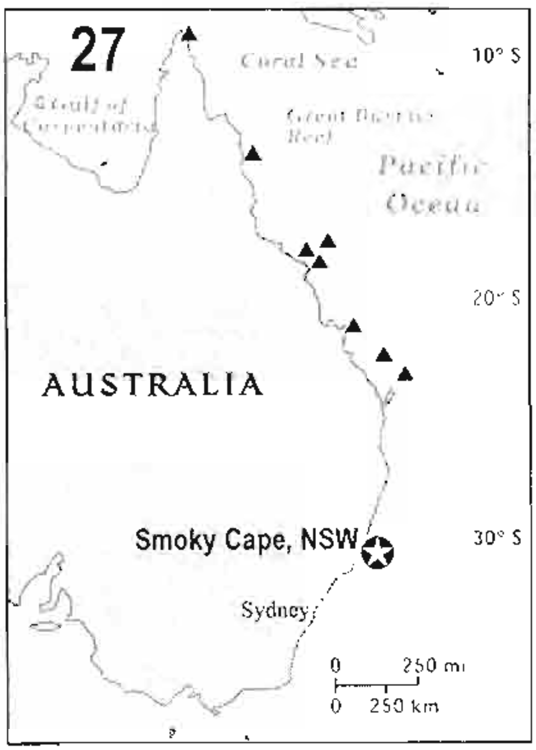
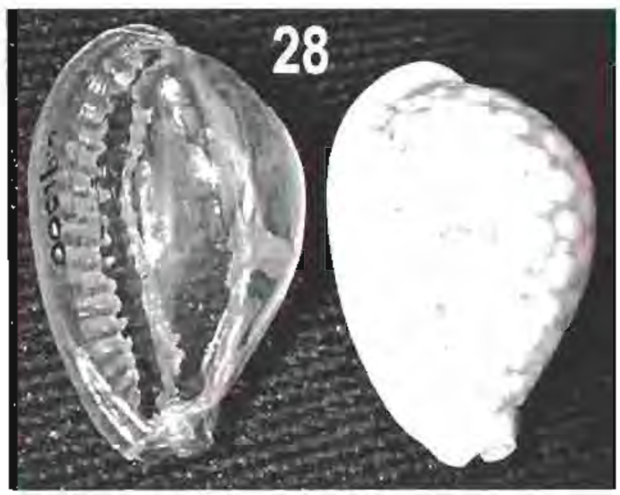


E. Australian *Cribrarula*
8 char, 36 shells
crib
melw
grav
PC2 (23.2%)
PC1 (43.3%)
5
4
3
2
1
0
-1
-2
-5
0
5



27
Coral Sea
Great Barrier Reef
Pacific Ocean
10° S
20° S
30° S
AUSTRALIA
Smoky Cape, NSW
Sydney
0 250 mi
0 250 km



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CHAPTER 6

A REVIEW OF THE INDO-PACIFIC GENUS *Cribrarula* STRAND, 1929 (GASTROPODA: CYPRAEOIDEA: CYPRAEIDAE) [7]

Abstract

The genus *Cribrarula* Strand, 1929 (Gastropoda: Cypraeidae) is reviewed. The following twelve species are recognized in the genus, based on radular and odontophoral characters and multivariate analyses of shell characters: *cribraria* (Linnaeus, 1758), ranging from E. Africa to the Central Pacific; *cumingii* (Sowerby II, 1832) from Polynesia; *esontropia* (Duclos, 1833) from Mauritius; *gaskoinii* (Reeve, 1846) from the Hawaiian Is.; *cribellum* (Gaskoin, 1849) from Mauritius; *fallax* (Smith, 1881) from S.W. Australia; *catholicorum* (Schilder and Schilder, 1938) from Melanesia; *astaryi* Schilder, 1971 from N.W. Polynesia; *taitae* (Burgess, 1993) from Melanesia; *pellisserpentis* Lorenz, 1999 from Madagascar; *garciai* Lorenz and Raines, 2001 from Easter Island, and *gravida* Moretzsohn, 2002 from New South Wales, Australia. Also recognized are five subspecies of *cribraria*, in addition to *cribraria cribraria*: *comma* Perry, 1811 from East Africa; *exmouthensis* Melvill, 1888 from Western Australia; *melwardi* Iredale, 1930 from Queensland, Australia; *gaspardi* Biraghi and Nicolay, 1993 from Kwajalein, and *ganteri* Lorenz, 1999 from Sri Lanka. Shells, radulae and odontophore cartilages of each taxon are illustrated, shell morphometrics presented, and a key for the identification of the taxa of *Cribrarula* is provided.

[7] Manuscript currently in review, submitted to *Zootaxa*.

Key words: Cypraeidae, *Cribrarula cribraria* complex, review, taxonomy, synonymy, multivariate analysis, shell characters, radula, odontophore, identification key.

Introduction

Twelve species are currently recognized in the genus *Cribrarula* Strand, 1929 (Cypraeidae), type species *cribraria* (Linnaeus, 1758), also known as the *cribraria* complex. The shells of species in this complex are readily distinguished from those of other cowries by a brown dorsal coat on a white background, with well-defined white dorsal spots. These gastropods have carmine- to crimson-colored mantles, and are often found on or near similarly colored sponges (Figs. 6.1-6.3) (Johnson, 1982; Hayes, 1983). The nominal species, *cribraria* (Linnaeus, 1758), ranges widely across the Indo-Pacific, and an additional eleven species have narrow ranges within the Indo-Pacific, some restricted to a few islands (Fig. 6.4). The fossil record suggests that this complex represents a relatively recent radiation: the oldest known fossil dates from the Pleistocene of Fiji (Ladd, 1977; Bradner and Kay, 1996; Moretzsohn, unpublished) and Indonesia (Kay, 1990, 1996); on the other hand, molecular data suggest the *Cribrarula* clade may have split from the *Talostolida* clade about 14 Ma (Miocene) (Meyer, 1998).

Jousseaume (1884a) proposed the genus *Cribraria* by tautonymy to accommodate *Cypraea cribraria* and a group of species then recognized as allied: *cumingii* Sowerby II, 1832; *esontropia* Duclos, 1833; *gaskoinii* Reeve, 1846; *cribellum* Gaskoin, 1849.

Strand (1929) proposed the genus *Cribrarula* as a replacement for *Cribraria* Jousseaume, 1884, a junior homonym of *Cribraria* Schrader ex Gmelin, 1792

(Myxomycetes – slime molds). Because Myxomycetes have been classified as animals (but now classified in the kingdom Protista in the five-kingdom system) (Botany Dept., California State University, 2003), the International Code of Zoological Nomenclature (ICZN Code), Article 2.2 (ICZN, 1999: 3-4) applies: "any available name of a taxon that has at any time been classified as animal continues to compete in homonymy in zoological nomenclature even though the taxon is later not classified as animal." Therefore, *Cribrarula* Strand, 1929 is the accepted (valid) genus group name for the *cribraria* complex (Schilder and Schilder, 1967, 1971).

Generic classification in the Cypraeidae is disputed (e.g. Steadman and Cotton, 1946; Allan, 1956; Kay 1957b, 1960b; Schilder and Schilder, 1971; and Bradner and Kay, 1996) and causes problems with secondary homonymy (e.g. *Annepona mariae* Schilder, 1927 versus *Cypraea mantellum* Walls and Burgess, 1980), depending on whether *Cypraea sensu lato* or several genera are recognized in the family. This problem potentially affects only one taxon in the genus *Cribrarula*: the recently proposed *magnifica* Lorenz, 2002 (as a subspecies of *exmouthensis*; not recognized in this review, until further data are available). Lorenz (2002: 132, footnote) points out that the taxon is available for *Cribrarula*; but if the genus *Cypraea sensu lato* is used, *Bernaya magnifica* Schilder, 1931, a fossil species, and *Palmadusta magnifica* Coen, 1949 (a synonym of *P. diluculum* Reeve, 1845) have priority. The important point is that for a given system of classification only one name is valid (Rosenberg, 1997).

In this study, I follow the generic arrangement of Lorenz and Hubert (2000), and use *Cribrarula* Strand, 1929 as the most inclusive group for the species in the *cribraria* complex (Table 6.1). Species level identifications follow Burgess (1985), and, in part, Lorenz and Hubert (2000).

Phylogenies of the Cypraeidae

Few phylogenies of the Cypraeidae have been proposed to date, and most are based on shell characters without explicit and/or rigorous methods (but see below). The Schilders (e.g., Schilder and Schilder, 1938-1939, 1971) suggested a number of generic arrangements based primarily on shell and anatomical characters. The Schilders' arrangements and generic placement varied widely in the nearly 300 papers on cowries of which they were the authors over nearly 50 years (1922 to 1971). Unfortunately, their methods were not explicitly stated, and coding of characters is not always clear, preventing re-analysis with modern methods. However, most of the Schilders' work (e.g. Schilder, 1936) predates that of Willi Hennig, who, in 1950, laid the foundations of modern cladistics. Hennig's work remained largely unknown outside of Germany until the English translation of his work, *Phylogenetic Systematics* appeared in 1966 (Amorim, 1997). There is no apparent indication that the Schilders were aware of Hennig's methods.

Lorenz and Hubert (2000) on the basis of shell and mantle pattern similarities suggest that *Cribrarula* is derived from the *Erronea* group, with a close relationship to *Blasicrura*, but although their systematic arrangement supposedly follows a phylogenetic framework, neither method nor result in the form of cladograms is presented.

In the most explicit phylogeny of the family Cypraeidae, Meyer (1998) suggests that *Cribrarula* is monophyletic, and the sister group to the *Talostolida teres* (Gmelin, 1791) group ("*teres* complex") of *Blasicrura*, with well-supported branches on a number of most parsimonious trees based on 1106 bp (base pairs) of mitochondrial DNA (cytochrome oxidase I [COI] and 16S rRNA). He had access to fresh or preserved samples for most species in the Cypraeidae (168 species of some 215 species), and provides a useful picture of the relationships of the different clades. Meyer has continued to add more taxa and data to his analysis [the Cowrie Genetic Database Project (http://www.flmnh.ufl.edu/cowries/)], and a family-wide phylogeny based on molecular data will soon be published (Meyer, in press).

A phylogenetic hypothesis for the *Cribrarula cribraria* complex based on shell characters, anatomical data (radula and odontophore), and molecular (mtDNA COI) is being prepared, but is beyond the scope of this systematic review, and will be presented elsewhere (Moretzsohn, in prep.).

Depositories (acronyms as in Cummings et al, 2000)

AMNH – American Museum of Natural History, New York, NY, USA

AMS – The Australian Museum, Sydney, Australia

ANSP – Academy of Natural Sciences of Philadelphia, Philadelphia, PA, USA

BMNH – The Natural History Museum, London, United Kingdom

BPBM – Bishop Museum, Honolulu, HI, USA

CAS – California Academy of Sciences, San Francisco, CA, USA

CM – Carnegie Museum of Natural History, Pittsburgh, PA, USA

CMB – private collection of the late C.M. "Pat" Burgess, Honolulu, HI (now at BPBM), USA

DAN – private collection of Don Anderson, Honolulu, HI, USA

DMNH – Delaware Museum of Natural History, Wilmington, DE, USA

EAK – private collection of E. Alison Kay, Univ. Hawaii, Honolulu, HI, USA

FM – private collection of F. Moretzsohn, Univ. Hawaii, Honolulu, HI, USA

FMNH – Field Museum of Natural History, Chicago, IL, USA

HBR – private collection of Hugh Bradner, Scripps Institution, La Jolla, CA, USA

LACM – The Natural History Museum of Los Angeles County, Los Angeles, CA, USA

MNHN – Muséum National d'Histoire Naturelle, Paris, France

TAK – private collection of Chris Takahashi, shell collector and dealer, Honolulu, HI, USA

USNM –National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

WAM – The Western Australian Museum, Perth, WA, Australia.

Materials and methods

A total of 1298 specimens representing all taxa in the *Cribrarula cribraria* complex was studied in eight museums; additional specimens were borrowed from an additional five museums and from five private collections. Specimens with dried tissue inside the shell were selected for DNA extraction and to recover the radula and odontophore cartilage (Moretzsohn and de Couet, in preparation). Odontophore cartilages were prepared and studied as described in Moretzsohn (in review A) [Chapter 3], using the terminology in that paper. Radulae were prepared and mounted on SEM stubs (Moretzsohn, in review C) [Chapter 4] for comparative taxonomic study.

Shell character terminology was adapted from Schilder and Schilder (1938-1939), Burgess (1985) and Lorenz and Hubert (2000), and terminology regarding shell coloration and dorsal spots adapted from Savazzi (1998). Columellar and labral tooth (apertural teeth) counts were made using a 0.5 mm diameter metal needle placed in a mechanical pencil, the needle gently moved across the teeth, and the "clicks" counted. The count was repeated until two consecutive counts were identical. The anterior and posterior terminal ridges were counted as teeth if they were raised as a tooth but not if they were sunken (i.e., did not produce a "click").

Huber (1998) and Ruedas et al. (2000) emphasize the importance of voucher specimens so that other researchers can re-examine the specimens used in a study. Most (93.8 %) of the specimens examined in this study were museum specimens, and the collection name and catalog (lot) numbers are listed in the Appendix 6.4. Of the remaining 6.2 % (81 specimens) not deposited in museums, 65 specimens were in the author's collection, and the others in a few private collections. Representative specimens from the author's collection will be deposited in BPBM and ANSP.

Locality data were used to produce distributional maps (following Winston, 1999 and Geiger, 2000). Named localities and those with geocoordinates were located in atlases and online gazetteers and plotted manually to the nearest approximation possible as solid circles in Adobe Photoshop. Distribution ranges from the literature are shown on maps as bold lines, while records with questionable identity or locality are represented by a triangle. Type locality, when known, was represented by a white star in a solid black circle. Records with too broad (e.g. "Pacific Ocean"), incomplete or obviously erroneous locality data (e.g. "Australia" for a Mauritius endemic) were not represented on maps nor used for morphometric analyses.

Most of the shells studied were digitally photographed in either two views (dorsal and ventral) or six views (dorsal, ventral, columellar, labral, anterior and posterior) for comparisons. Initial photographs were made with a Konica Q-Mini digital camera (640 x 480 pixels, or 0.3 megapixels (MP)). The low-resolution photos are pixilated but still useful for specimen recognition and measurements. Later, a Nikon Coolpix 950 (2 MP) and a Casio QV-3000EX (3.3 MP) were used. Some shells were "photographed" using a flatbed scanner (Moretzsohn, 1998, in press).

Shell formulae

The Schilders' "formula" (Schilder and Schilder, 1938-1939: 123-124) was in vogue at least into the 1960s (e.g. Cernohorsky, 1964a; Griffiths, 1964), but its use has become increasingly less noticeable in the recent literature (Heiman, 2000) (with the exception of recent papers by Felix Lorenz, e.g. Lorenz and Raines, 2001; Lorenz, 2002). The formula consists of four numbers, which describe cowrie shell sizes in a condensed format: 1) average shell length (L) in mm; 2) average shell width/length ratio (W/L) (in %); 3) number of labral teeth (LT), and 4) number of columellar teeth (CT). The latter two numbers are transformed ("reduced" fide Schilder) to a hypothetical shell length of 25 mm to make possible comparison of shells of different sizes. The reduced number teeth is calculated as:

$$X = 7 + (\text{absolute number} - 7)\sqrt{(25/\text{shell length})}.$$

Lorenz (2002: 3-4) introduced a modification of the Schilders' formula by adding shell height/length ratio to the formula. I propose a different adaptation of the Schilder's formula, which I call the "New Cowrie Formula" to represent the five most useful cowrie shell measurements, based on the multivariate analyses of shell characters mentioned above. Part of the new formula is the same as that of the Schilders' (minus LT), with two extra figures:

New cowrie formula: L/ W:L/ CT/ SD/ LSS

Where:

L = shell length (in mm);

W:L = shell width-length ratio (expressed as percent);

CT = transformed number of columellar teeth (as in the Schilders' formula);

SD = spire diameter (in mm);

LSS = labral (marginal) spot size: (0) none; (1) small; (2) medium; and (3) large.

The figures in the new cowrie formula are separated by a slash "/" to avoid confusion with a decimal period (in contrast to the Schilders' formula). *Cribrarula cumingii*, for example, could be represented by: 12.9/ 56.7/ 32/ 1.9/ 1.6.

Advantages of the new formula include: 1) a more complete shell description than provided by the Schilders' formula; 2) the figures can be used directly in a PCA analysis (Fig. 6.6); 3) the measurements represented in the formula can be obtained from photographs, allowing the inclusion of material illustrated in the literature or posted on the Internet; and 4) a more balanced representation of shell characters -- the Schilders' formula puts too much weight on apertural teeth (two out of four characters), emphasizing specimens, such as those of *Cribrarula cumingii,* that have a large number of teeth (Fig. 6.7). The disadvantage is that other researchers have not yet used it, so results cannot be compared directly with the literature.

The Schilders' formulae based on the data collected by E.A. Kay (unpublished), and on specimens examined in this study are compared with the figures from the literature (Schilder and Schilder, 1938-1939; Schilder, 1967) (Table 6.2). Table 6.3 compares the Schilders' formula to the new formula (the figures of which are the basis for Figs. 6.6 and 6.7). All formulae presented in this study are based on the specimens examined, unless noted otherwise.

Systematics

This review is restricted to the taxa in the *Cribrarula cribraria* species complex. Although some researchers dismiss the subspecies concept as biologically meaningless (e.g. Wilson, 1993), several infraspecific taxa are discussed here because at some point they were considered at the species level, or because they were considered to represent geographical subspecies with consistent differences from other populations. Some may satisfy the 75% rule of thumb for subspecies (Amadon, 1949; Mayr, 1969), meaning that 75% or more specimens from a population can be recognized and differentiated from other populations in some features (e.g. most specimens of *Cribrarula cribraria melwardi* Iredale, 1930 are easily recognizable as distinct from other populations of *cribraria*). Additionally, as Randall (1998: 263) remarks: "I maintain that the use of subspecies is preferred when the differences of the 2 populations is slight and the systematist is faced with difficulty in deciding whether to regard them as 2 species or not. If he calls them 1 species without the trinomial, we have lost information on their distribution. If he calls them 2 species, we have also lost information on the close relationship of the 2 populations." The problem of the trinomen also applies to populations of *cribraria* described as subspecies. Although not available under the ICZN code (ICZN, 1999: 3, Art. 10.2), some infrasubspecific taxa are listed here for reference only. Lorenz (2002) recently elevated a subspecies (*exmouthensis*) to the species-level, and then described three new subspecies of the newly elevated species, thus making available a name (*rottnestensis*) that was proposed earlier as a form (see discussion under *exmouthensis* below). Had Lorenz (2002) not elevated *exmouthensis* to the species-level, his newly proposed taxon would have been of infrasubspecific rank, and not available under the ICZN rules. A list of the names (including infrasubspecific rank) in *Cribrarula* is presented in the Appendix 6.2, with notation of those in this review recognized as valid; a dichotomous key is presented in Appendix 6.3.

Genus ***Cribrarula*** Strand, 1929

Cribraria Jousseaume, 1884a by tautonym, invalid (junior homonym of *Cribraria* in Myxomycetes). Type species (by original designation): *Cypraea cribraria* Linnaeus, 1758.

Criraria criraria [sic] Jousseaume, 1884b: 414 (*lapsus calami*).

Cribrarula Strand, E. 1929: 8. Replacement name for *Cribraria* Jousseaume, 1884. Type species: *Cypraea cribraria* Linnaeus, 1758.

Nivigena Iredale, 1930: 84, synonym. Type species (by monotypy): *Nivigena melwardi* Iredale 1930 (= *Cribrarula cribraria melwardi* (Iredale 1930)).

Nivigera [sic] Iredale, 1930. Moretzsohn, 2002b: 9, 15 (typo, should be *Nivigena*).

Diagnosis – Shells with characteristic white or cream dorsal spots (or lacunae) against a caramel to orange-brown (sometimes brown) dorsal coat; base, sides and shell extremities white or off-white. Shells of most species have small to large brown (to black) marginal spots. Shell oval to pyriform, small to medium in size, fossula and peristome usually denticulate, columellar teeth fine to medium.

1.a. *Cribrarula cribraria cribraria* (Linnaeus, 1758) (Figs. 6.8-6.19, 6.219-6.223, 6.229, 6.242, and 6.286-6.288).

Cypraea cribraria Linnaeus, 1758, ed. 10, No. 310, p. 723. Linnaeus, 1767, ed. 12, No. 353, p. 1178. Type locality: not provided by Linnaeus; subsequent designation by Iredale, 1935 as Ceylon (Sri Lanka) (Schilder, 1965a).

Cypraea cribraria Linnaeus, 1758 – Lister, 1685 (reprinted in 1770): pl. 695, fig. 42 (figure of a characteristic, non-marginally spotted shell). Argenville, 1742: pl. 12, fig. 7 (figure of a marginally spotted shell). Regenfuss, 1758: pl. 12, fig. 74 (shell with marginal spotting). Linnaeus, 1764: 577. Martini, 1769-1777: 403, pl. 31, fig. 336. Born, 1780: 186. Bruguière, 1791: pl. 355, fig. 5. Gmelin, 1791: 3414. Lamarck, 1810: 94. Dillwyn, 1817: 458. Mawe, 1823: pl. 21, fig. 5. Gray, 1824: 382. Wood, 1828: pl. 17, fig. 42. Deshayes, 1832: 828. Quoy and Gaimard, 1832: 41, pl. 48, fig. 12 (shell and animal). Sowerby, 1836: fig. 63. Deshayes in Lamarck, 1844: 519. Kiener, 1843-1844: 26, pl. 29, fig. 1. Reeve, 1845-1846: fig. 81. Man, 1877: 38. Sowerby II, 1870: 33, figs. 161, 163-164 (including a labrally spotted shell – fig. 161). Weinkauff, 1881: 115, pl. 34, figs. 5-8 (as *esontropia* non Duclos, 1833), figs.10-11 (as *cribraria*). Brazier, 1882: 29. Roberts in Tryon, 1885: 190, pl. 17, figs. 71-72. Melvill, 1888: 229-231, 248. Dautzenberg, 1902: 360. Hidalgo, 1906-1907: 137, 194, 322-325. Gillett and McNeil, 1959: 66. Griffiths, 1961: 14-15. Cernohorsky, 1964b: 199, pl. 24, fig. 28. Cernohorsky, 1967: 103, pl. 20, fig. 114. Cate, 1969: 129, pl. 25, fig. 56. Burgess, 1970: 189-190, pl. 13, fig. G. Donohue, 1977: 160. Walls, 1979: 201, 2 unnumbered figs. Roth, 1980: 18. Foin, 1982: 48-51. Burgess, 1985: 238, 3 unnumbered figs. Wilson, 1993: 178, pl. 35, figs. 19a-d.

Cypraea ocellata Bolten, 1798 non Linnaeus, 1758 (*fide* Hidalgo, 1906-1907: 138).

Cypraea maculata Anonymous, 1810 – *Encyclopaedia Metropolitana*, 1810, London, Atlas, pl. 14.

Cribraria cribraria (Linnaeus, 1758) – Jousseaume, 1884a: 94. Allan, 1956: 63, pl. 7, figs. 3-4 (*cribraria* from Sri Lanka), pl. 12, figs. 5-8 (*melwardi*).

Criraria criraria [sic] Jousseaume, 1884b: 414 (*lapsus calami*).

Cypraea (*Luponia*) *cribraria* monstr. *rostrata* Dautzenberg, 1902: 361.

Cribraria (Cribraria) cribraria cribraria (Linnaeus, 1758) – Schilder and Schilder, 1938-1939: 171-172. Schilder and Schilder, 1952: 171-172. Cate, 1967: 17.

Cribraria cribraria zadela Iredale, 1939: 310 – Allan, 1956: 63. Burgess, 1985: 238.

Cribraria (*Cribraria*) *cribraria orientalis* Schilder and Schilder, 1940: 43 – Schilder and Schilder, 1952: 171-172. Schilder and Schilder, 1952: 171-172. Cate, 1966: 263-264, pl. 45, fig. 72. Cate, 1967: 17-18, 41. Burgess, 1985: 238.

Cribraria cribraria northi Steadman and Cotton, 1943: 318 – Steadman and Cotton, 1946: pl. 11, figs. 7-9. Burgess, 1985: 238 (as a junior synonym of *cribraria*).

Cypraea (*Cribraria*) *cribraria* Linnaeus, 1758 – Dodge, 1953: 95-96. Ladd, 1977: 25, pl. 6, figs. 2-4 (fossil shell of *Cypraea cribraria* from the Pliocene of Fiji).

Cypraea melwardi (Iredale, 1930) – Griffiths, 1961: 14-15. Burgess, 1970: 190.

Cribraria cribraria (Linnaeus, 1758) – Cernohorsky, 1967: 103, pl. 20, fig. 114.

Cribrarula cribraria cribraria (Linnaeus, 1758) – Schilder and Schilder, 1971: 56. Lorenz and Hubert, 1993, 2000: 176, pl. 69: figs. 12-15, 20, 23, 24; pl. 109: figs. 15-18 (melanistic shells from New Caledonia). Moretzsohn, 2002b: 1, 2, 4, 6, 9-12, 15, figs. 14-20 (shells), figs. 24-25 (SEM of radulae), fig. 26 (graph and shells).

Cribrarula cribraria (Linnaeus, 1758) – Cate, 1969: 129, pl. 25, fig. 57. Bradner and Kay, 1996: 11, 125, fig. 201 (radula). Meyer, 1998: 35, 47, 51, 85, 122, 129, 175 (phylogeny).

Cypraea comma Perry, 1811 – Burgess, 1985: 238.

Cypraea fallax Smith, 1881 – Burgess, 1985: 238.

Nivigena melwardi Iredale, 1930 – Burgess, 1985: 238 (as a synonym of *cribraria*). Wilson, 1993: 178 (as an aberrant white form of *cribraria*; treated as a synonym).

Cribrarula cribraria cribraria (Linnaeus, 1758) – Lorenz and Hubert, 1993, 2000: 176-177, pl. 69, figs. 12-15, 20, 23-24 (*cribraria cribraria*), pl. 109, figs. 15-18 (melanistic forms from New Caledonia). Lorenz, 2002: 135-137, map 33 (with shell figure), 260 (species No. 58a, 4 unnumbered figures).

Cribrarula cribraria cribraria "*zadela*" (Iredale, 1939) – Lorenz and Hubert, 1993, 2000: 176, pl. 69, figs. 1-3 ("*zadela*").

Cribrarula cribraria cribraria "*gaspardi*" Biraghi and Nicolay, 1993 – Lorenz and Hubert, 1993, 2000: 176, pl. 69, figs. 21-22.

Cribrarula cribraria cribraria "*ganteri*" Lorenz, 1997 – Lorenz and Hubert, 2000: 176, 483 (fig. A1), plate 127, figs. 3-4.

Cribrarula cribraria ganteri Lorenz, 1997 – Lorenz 2002: 140 (map 33 with shell fig.), 260, species No. 58f, unnumbered fig.

Cribrarula cribraria zadela (Iredale, 1939) – Lorenz 2002: 135-138, 140, map 33 (with shell figure), pl. 35 (figs. 14-15), 260 (species No. 58b, 3 unnumbered figures)

Cribrarula cribraria northi (Steadman and Cotton, 1943) – Lorenz 2002: 136, 140 (map 33 with shell figure).

Description – Shell (Figs. 6.9-6.20): The shells of *Cribrarula cribraria cribraria* are the most variable in the genus, ranging in shape from pyriform to cylindrical, with shell length from just about 10 mm to more than 45 mm (Table 6.4). The dorsal coat varies from orange to dark brown, with well defined white round dorsal spots and, rarely, a few faint marginal spots. Extremities are finely marginated. Columellar teeth range from fine to medium, while labral teeth are generally coarser, extending to about mid labrum.

Animal: "Sole and dorsum of foot pale orange. Mantle bright red, with faint pustules over entire area; mantle area in between flecked with crescent-shaped black lines. Papillae numerous, short, simple, orange tipped with white; some papillae are pure white, and have a cluster of white patches at the base. Tentacles red; siphon red and not fringed" (Cernohorsky, 1964b: 199). The red mantle and verrucose finger-like papillae (including some white papillae) are shown in animals from Kwajalein (Figs. 6.2 and 6.3), as well as the similarly colored sponge where these animals are often found. The dorsal pattern of the shell can be seen through the mantle in these specimens.

Radula (Figs. 6.219-6.223): As in other characters, the radula of the nominotypical subspecies is also variable, for example in size, central tooth proportions, etc., but still similar to those of other congeneric taxa. The taenioglossan radula of species of *Cribrarula* was assigned to the "cicercula" pattern by Bradner and Kay (1996: 125), and characterized by a five-cusp central tooth which bears a pair of mid-shaft denticles that in most congeneric taxa is pointed and sharp (personal observation). The central tooth in *Cribrarula* is relatively small (mean dimensions 97 x 70 μm, N = 9), for example, compared to cowries in the "isabella" pattern. The teeth are crowded, with the marginals and laterals overlapping, and the laterals approximately the same size as the central tooth (Bradner and Kay, 1996).

Odontophore (Figs. 6.229, 6.242): Also varied in size and somewhat in shape within *cribraria cribraria*, but all 46 odontophores (of *Cribrarula cribraria* subspecies) examined showed the characteristic spongy texture of other congeneric taxa (Moretzsohn, in review A). The pair of curved, long odontophore cartilages, with a slightly broader anterior end (bending plane) than the posterior end, was white in most specimens; a few had a faint yellowish tint. Table 6.6 shows odontophore measurements as described in Moretzsohn (in review A) [Chapter 3].

Distribution: Western Indian Ocean to Australia, and the Central Pacific (Fig. 6.20). Several populations show distinctive characteristics and have been named as subspecies, some of which may be recognized in the future as valid species.

Discussion: This subspecies can be common in certain localities, such as the Philippines, but is never abundant. It is also the most widely distributed, and most variable subspecies in the complex. In this study, any specimen that did not fit the characteristics of the different subspecies was identified as *cribraria cribraria*. Therefore, a more conservative approach is used here than that adopted by the

Schilders (e.g. Schilder and Schilder, 1938-1939) and Lorenz (in Lorenz and Hubert, 1993, 2000; Lorenz, 2002) who recognize and name many infraspecific taxa. The result is a wider distribution of the nominotypical subspecies than that recognized by Lorenz and Hubert (2000) (bold line in Fig. 6.20), who call all specimens of *cribraria* from East Africa *cribraria comma*. Lorenz and Hubert (2000)'s approach avoids overlap of the distribution of subspecies in East Africa (but not in other regions, e.g. in Eastern Australia). The problem of sympatric (at least partially) subspecies presents a biological difficulty, and is one of the reasons why many researchers dismiss the subspecies concept. However, subspecies are used in this study because most specimens can be readily identified as belonging to one or another subspecies (thus satisfying the "75% rule for subspecies" for at least some features) (Amadon, 1949, Mayr, 1969)) on the basis of shell characters.

Some specimens from New Caledonia are distinctly melanistic and/or rostrate, but the degree of melanism and rostration varies. In a localized population, only some shells are melanistic or rostrate, or both. Most specimens in the same population are neither melanistic nor rostrate. This phenomenon has been recorded for 38 species of Cypraeidae (Chatenay, 1977), and apparently is more common in the southwest shore of New Caledonia than elsewhere. The more extreme specimens are highly prized by shell collectors, and are now becoming rare. Several specimens of *cribraria* (usually identified by shell collectors as form "niger") with either melanism or rostration were examined in museum collections.

Lorenz (2002) adopts *cribraria zadela* (Iredale, 1939) for specimens from northern Queensland, Australia, which are closer conchologically to the typical *cribraria cribraria* than to *melwardi*. The name *zadela* is used among shell collectors for large specimens of *cribraria cribraria* (such as the 40.8 mm long specimen illustrated in Figs. 6.15-6.20, from Cebu, Philippines). The holotype of *zadela* (AMS-C 60554, from Queensland, Australia, illustrated here, Figs. 6.254-6.257) is 22.7 mm long, not significantly different from the average length of shells of *cribraria cribraria* from Queensland (21.50 mm, St. Dev. 2.33, N = 51), therefore *zadela* is regarded here as a junior synonym of *cribraria cribraria*.

Schilder's formula: 22.58.18.19. New formula: 22.5/ 58.2/ 19/ 3.3/ 0.1.

Etymology: Name derived from "*cribrum,*" Latin for sieve, referring to the white dorsal spots, and perforated appearance of the shell (Dodge, 1953).

Types: Three syntypes (Figs. 6.286 to 6.288) of *Cypraea cribraria* Linnaeus, 1758, in the Linnaean Collection (BMNH, no catalog number), no locality data. Label remarks (Fig. 6.286): "Hanley [1855] has isolated three unmarked shells which he said were found in the Linnaean marked box" (Dance, S. P., 1963, specimen label). Holotype of *Cribrarula cribraria zadela* Iredale 1939 (junior synonym of *cribraria cribraria* Linnaeus, 1758), Australia, Queensland, Whitsunday Group, Hamilton Is. (AMS-C 60554, 1 specimen) (Figs. 6.254-6.257).

Material examined: Japan, Okinawa, Bolo Point, Nakagami-gun, L.T. Withington!, Mar. 1961 (USNM 670743, 9 specimens); Philippines, Cebu Is., Olonga Is., ex Eugenia Wright coll., under coral rocks in shallow water (USNM 773378, 4 specimens); Thailand, Phuket Is., sand lagoon and coral reefs, airport beach, R.T. Abbott and F.N. Crider!, Int. Indian Ocean Expedition, 08°05' 45"N, 098°18' 00"E, 22 Feb. 1963 (ANSP 286678, 1 specimen); Guam, USO Beach, collected at glass breakwater at night, 8-10 ft., G. Paulay!, 24 Nov. 1995 (FM 8, 1 specimen); New Caledonia, Noumea, 0-7 ft, rocks, some coral and weeds, near radio station, Baie Ouemo, 022°15' 24"S, 166°25' 44"E, G. Kline and M. and V. Orr!, Dec. 1960-Jan. 1961 (ANSP 271247, 2 specimens); Japan, Okinawa, Bolo Point, -0.3 m tide, Halpern Malacological Fund, ex Cate coll., B. Kelly!, 6 Mar. 1966 (AMNH 292279, 2 specimens); Fiji, Mamanuca Group, ex E. Wright coll., W. Cernohorsky!, 20 Jul. 1966 (USNM 773496, 5 specimens); and 359 additional specimens (Appendix 6.4).

1.b. *Cribrarula cribraria comma* (Perry, 1811) (Figs. 6.21-6.32, 6.227, 6.234, and 6.247).

Cypraea comma Perry, 1811: pl. 21, f. 5. Type locality: not given by Perry; Zanzibar, by subsequent designation (Schilder, 1930).

Cribraria (Cribraria) cribraria comma (Perry, 1811) – Schilder and Schilder, 1938-1939: 172. Schilder and Schilder, 1952: 171.

Cribraria cribraria comma (Perry, 1811) – Allan, 1956: 64.

Cypraea (*Cribraria*) *comma* Perry, 1811 – Dodge, 1953: 96.

Cypraea cribraria Linnaeus, 1758 – Hidalgo, 1906-1907: 137. Burgess, 1970: 189, pl. 13, fig. H.

Cribrarula cribraria (Linnaeus, 1758) – Schilder and Schilder, 1971: 56.

Cribrarula cribraria comma (Perry, 1811) – Lorenz and Hubert, 1993, 2000: 177, pl. 69: Figs. 6.11, pl. 108: fig 26-27 (teratological shells). Lorenz, 2002: 126, 129, maps 32-33 (with shell figure), pl. 32 (figs. 1-5), 260 (species No. 58d, one unnumbered figure).

Cribrarula cribraria abaliena Lorenz, 1989: 14-15 (originally described as a subspecies) – Lorenz, 2002: 126, 129, 140, map 33 (with photo of shell), 261 (species No. 58g, 2 unnumbered figures).

Cribrarula cribraria comma "*abaliena*" Lorenz, 1989 – Lorenz and Hubert, 2000: 177, pl. 69: figs. 16-19.

Description – Shell (Figs. 6.22-6.33): Most shells of *comma* can be distinguished from the nominotypical subspecies by a dark brown dorsal coating and, sometimes, with not too sharply defined dorsal spots (Fig. 6.22). The shells of *comma* resemble those of shallow-water *exmouthensis* (*australiensis sensu* Lorenz, 2002) (and *esontropia francescoi* but the former lacks dorsal banding (Lorenz, 2002: 260)), in particular the dark dorsal coating and the not too distinct dorsal spots. The shell is ovate-pyriform, ranging from 16 to 25 mm in length. Marginal spotting is present in some shells, but is rare in shells of most populations of *cribraria* (except *cribraria ganteri*).

Radula (Figs. 6.227, 6.258): Similar to the radulae of other subspecies of *cribraria* (Figs. 6.219-6.226), except that the central tooth is more "squarish" (slightly wider) than in some radulae of *cribraria* subspecies, and most similar to the specimen of *cribraria cribraria* from Fiji illustrated in Fig. 6.223. The radula of a specimen tentatively identified as "*abaliena*" (Fig. 6.258) is similar to that of *comma* (Fig. 6.219), although the central tooth is slightly narrower than in *comma*.

Odontophore (Figs. 6.234, 6.247, and 6.259): Similar to the odontophore of *cribraria cribraria*, but more slender and longer than the latter (Table 6.6), with a lower odontophore thickness at center/odontophore length (OT/OL) ratio. The specimen identified as "*abaliena*" and illustrated in Fig. 6.259 is very much like the specimen of *comma* in Figs. 6.234 and 6.247, and it contributes to the decision of regarding "*abaliena*" as a synonym of *comma* (see remarks below).

Distribution: Western Indian Ocean (Fig. 6.33).

Remarks: *Cribrarula cribraria abaliena* Lorenz, 1989 was described to represent small specimens of *comma*, but Lorenz and Hubert (2000: 177) state that recent findings of very variable shells of *cribraria comma* have raised questions in their minds about the status of *abaliena*, and they call it a form of *comma*. Lorenz (2002: 129) says the status of *abaliena* is still unclear, but then lists the taxon again at the subspecies level. I examined seven shells of *comma* that fit the description of *abaliena*, but small shell size and lighter dorsal color are about the only differences from shells of *comma.* One specimen (HBR, no catalog number, from Madagascar) yielded a radula and odontophore (Figs. 6.258 and 6.259), both similar to those of *comma* (Figs. 6.227 and 6.234). Therefore, in this review, *abaliena* is considered a junior synonym of *comma*.

Discussion: Lorenz and Hubert (2000) consider all *cribraria* from the African coast as *cribraria comma*, but occasional shells are similar to the nominotypical subspecies; those are here identified as *cribraria cribraria.* PCA analyses of morphometric shell characters suggest that most specimens of *comma* are separable from those identified as *cribraria cribraria* according to the criteria adopted above (Fig. 6.278).

Schilder's formula: 20.62.17.17. New formula: 19.6/ 62.0/ 17/ 3.0/ 0.1.

Etymology: Perry's specimen had incomplete dorsal spots resembling a comma (Hidalgo 1906-1907).

Material examined: Mauritius, E.E. Hand coll., 020°18'S, 057°36'E, E.E. Hand! (FMNH 63255, 2 specimens); S. Africa, Cape Province, 035°00'S, 020°00'E, C. Kauffman! (DMNH 155472, 2 specimens); Mozambique, Port Amelia, F.M. Borges! (AMNH 292286, 1 specimen); Madagascar, Tulear (Toliara), 23°12'S, 43°39'E, Maurice Jay! (HBR, no catalog number, 1 specimen); and an additional 68 specimens (Appendix 6.4).

1.c. *Cribrarula cribraria exmouthensis* (Melvill, 1888) (Figs. 6.34-6.45, 6.226, 6.231, 6.244 and 6.299-6.300).

Cypraea cribraria var. *exmouthensis* Melvill, 1888: 229-230 (original description). Type locality and etymology: Exmouth Gulf, N.W. Australia, by tautonymy (Melvill, 1888) (Figs. 6.299-6.300).

Cribraria (Cribraria) cribraria exmouthensis (Melvill, 1888) – Schilder and Schilder, 1938-1939:172.

Cribraria (*Cribraria*) *cribraria fallax* (Smith, 1881) – Schilder and Schilder, 1952: 171-172. Cate, 1964: 21, 28.

Cribraria cribraria fallax (Smith, 1881) – Allan, 1956: 64 (as the Northwest Australian population of *cribraria*).

Cribraria cribraria exmouthensis (Melvill, 1888) – Allan, 1956: 64.

Cypraea fallax Smith, 1881 – Dodge, 1953: 96.

Cypraea cribraria Linnaeus, 1758 – Burgess, 1970: 189, pl. 13, fig. I (as *Cypraea fallax*).

Cribrarula cribraria (Linnaeus, 1758) – Schilder and Schilder, 1971: 56.

Cypraea cribraria fallax Smith, 1881 – Wilson and Gillett, 1971: 52.

Cribrarula cribraria occidentalis Raybaudi Massilia, 1987: 43 – Lorenz, 2002: 130, 131 (*nomen dubium*), 137.

Cribrarula cribraria occidentalis f. *rottnestensis* Raybaudi Massilia, 1987: 43 – Lorenz, 2002: 134 (elevated to subspecies and re-described as *Cribrarula exmouthensis rottnestensis* Lorenz, 2002).

Cypraea cribraria Linnaeus, 1758 – Wilson, 1993: 178, figs. (does not recognize subspecies).

Cribrarula cribraria exmouthensis (Melvill, 1888) – Lorenz and Hubert, 1993, 2000: 178, pl. 69, figs. 29-30 (as *cribraria exmouthensis "rottnestensis"*), figs. 33-37. Lorenz, 2002: 130. Moretzsohn, 2002b: 6, 9.

Cribrarula exmouthensis (Melvill, 1888) – Meyer, 1998: 47, 51, 85, 122, 175 (phylogeny). Lorenz, 2002: 234, unnumbered figure of the holotype (elevated to the species-level – see discussion below).

Cribrarula exmouthensis exmouthensis (Melvill, 1888) – Lorenz, 2002: 133, 136-139, map 34 (with shell figure), pl. 36 (figs. 5-9), 260, 264 (species No. 79a, 3 unnumbered figures).

Cribrarula exmouthensis abrolhensis Lorenz 2002: 133-134, 137-139, map 34 (with shell figure), pl. 37 (figs. 1-4), 264 (species No. 79c, 4 unnumbered figures).

Cribrarula exmouthensis magnifica Lorenz, 2002: 132, 136-139, map 34 (with shell figure), pl. 36 (figs. 1-4), 264 (species No. 79b, 3 unnumbered figures).

Cribrarula exmouthensis rottnestensis Lorenz, 2002: 134-135, 137-139, map 34 (with shell figure), pl. 37 (figs. 5-10), 264 (species No. 79d, 3 unnumbered figures).

Cribrarula cribraria australiensis Lorenz, 2002: 131 (proposed as a replacement name for *Cribraria cribraria exmouthensis* sensu Lorenz and Hubert 2000), 132, 136-139, map. 33 (with shell figure), pl. 35 (figs. 1-8), 260 (species No. 58c, 3 unnumbered figures).

Description – Shell (Figs. 6.35-6.46): This subspecies is better known as "*fallax*". The shells are variable: dark dorsal color, sometimes chocolate, indistinct dorsal spots, which can be yellow in deep-water specimens. Shell shape pyriform to rhomboidal, usually from 20 to 31 mm in length. See Table 6.4 for a comparison with other subspecies of *cribraria.*

Radula (Fig. 6.226): Similar to those of other *cribraria* subspecies, except that the marginal teeth have a small projection near the outer margin that resembles the projection seen in *catholicorum* (Fig. 6.217), and *gravida* (Fig. 6.216), although the projection in the latter is sharp.

Odontophore (Figs. 6.231 and 6.244): Similar to those of other *cribraria* subspecies, except that in light microscopy the odontophore has a faint yellow tint, and the ventral arch/odontophore height (VA/OH) ratio is the lowest among the odontophores studied in the genus, meaning that the ventral margin is not so arched as in other congeneric taxa (Table 6.6).

Distribution: Northwestern Australia to Albany, SW Australia (Fig. 6.46).

Discussion: There is both debate and confusion involving the names *exmouthensis* and *fallax.* Wilson (1993: 178) reviews the history of the usage of the names used by different authors to refer to the shells from Western Australia (WA) (recognized here as *exmouthensis* Melvill). The Schilders and most recent authors have incorrectly used *fallax* Smith for the WA *cribraria*, but *fallax* applies to a different species that is restricted to the Albany region, in Southwestern Australia (see discussion under *fallax*). Wilson (1993) then says it is appropriate to reinstate *exmouthensis* Melvill, 1888 as the valid name for the northern WA population (even though Wilson does not recognize subspecies). Melvill's *exmouthensis* is not a *nomem dubium* as some authors assume, because there is a holotype at the British Museum (well illustrated by Raybaudi Massilia, 1986: fig. 3; a recent enquiry at BMNH revealed a syntype (illustrated in Figs. 6.299-6.300), perhaps the same specimen illustrated by Raybaudi Massilia, 1986) and a specified type locality (Exmouth Gulf) (Wilson, 1993). Lorenz and Hubert (2000) consider the holotype of *exmouthensis* conspecific with the northwestern Australian population of *cribraria* (but see below).

Lorenz (2002) further complicates the taxonomy of the group by ascribing all specimens previously identified as *exmouthensis* (*sensu* Lorenz and Hubert, 1993, 2000) to a new subspecies of *cribraria, australiensis* Lorenz 2002, then elevating *exmouthensis* to the species level, and splitting it into four subspecies by describing three new subspecies (*abrolhensis*, *magnifica* and *rottnestensis*). Lorenz (2002) adequately describes and illustrates several specimens of each new taxon, but provides narrow distribution ranges for each new taxon that conveniently are not overlapping. I re-examined specimens from Western Australia borrowed from the Western Australian Museum, and I had difficulty identifying some of the specimens according to Lorenz (2002)'s new descriptions, either because the specimens seemed to be intergrades between the new taxa, or because of range extensions. These range extensions would cause some of the new taxa to partially overlap in some places, in addition to the wide overlap with *cribraria australiensis* Lorenz, 2002 (formerly known as *cribraria exmouthensis*).

I ran multivariate analyses of shell characters identifying specimens I examined from the West Indian Ocean both according to Lorenz and Hubert (2000) (Fig. 6.276) and to Lorenz's (2002) new taxa (Fig. 6.277). Most points representing *australiensis*, *exmouthensis exmouthensis* (*sensu* Lorenz, 2002) and *abrolhensis* overlapped and could not be separated using the shell characters included in the analysis (Fig. 6.277). On the other hand, when the specimens were identified *sensu* Lorenz and Hubert (2000), one large grouping, *exmouthensis*, was easily recognized and separated for the most part from the other taxa (Fig. 6.276). Other analyses (not shown) using larger sets of characters produced similarly overlapping points (although fewer specimens were included in the analyses because of missing characters – see more under morphometrics). Points representing the new taxon *rottnestensis* in figure 277 were the most distinct among Lorenz's new taxa from Western Australia. However, until more data become available (such as radular, odontophoral, anatomy, photos of living animals, Meyer's molecular data, etc.), I prefer to be more conservative and provisionally do not accept Lorenz (2002)'s new taxa as valid.

Schilders' formula: 23.61.17.16. New formula: 23.0/ 60.6/ 16/ 3.3/ 0.

Etymology: Named after its type locality, Exmouth Gulf, in Western Australia (Lorenz and Hubert, 1993).

Type: Syntype of *Cypraea cribraria exmouthensis* Melvill, 1888, from Exmouth Gulf, West Australia (Leg. & Pres. T.H. Haynes) (BMNH 1887.5.10.7) (Figs. 6.299-6.300).

Material examined: Western Australia, Broome, ex Kienle coll. (DMNH 196958, 1 specimen); Australia, Exmouth Gulf, ex Kienle coll. (DMNH 196197, 2 specimens); and additional 68 specimens (Appendix 6.4).

1.d. *Cribrarula cribraria melwardi* (Iredale, 1930) (Figs. 6.47-6.58, 6.225, 6.233, and 6.246).

Nivigena melwardi Iredale, 1930: 84. Type locality: North West Island, Capricorn Group, Great Barrier Reef, Australia (Iredale, 1930).

Nivigena melwardi Iredale, 1930 – Allan, 1956: 65-66, pl. 12, figs. 3-4 (as *melwardi*), figs. 5-8 (as *cribraria*). Gillett and McNeil, 1959: 66, pl. 55-56 (figures of shells ranging from white to pigmented, and photo of live animal of *melwardi*).

Cribraria (Cribraria) cribraria melwardi (Iredale, 1930) – Schilder and Schilder, 1938-1939: 172.

Cypraea (*Cribraria*) *melwardi* (Iredale, 1930) – Dodge, 1953: 96.

Cypraea cribraria Linnaeus, 1758 – Cernohorsky, 1964b: 199. Burgess, 1970: 189, pl. 13, fig. J. Walls, 1979: 25 (photo of live albino animal, identified as *Nivigena melwardi*).

Cribrarula cribraria (Linnaeus, 1758) – Schilder and Schilder, 1971: 56.

Cypraea melwardi Iredale, 1930 – Wilson and Gillett, 1971: 52, figs. 10, 10a (one pigmented and one albinistic shell), and fig. 31 (two live specimens). Wilson, 1993: 178.

Cribrarula cribraria melwardi (Iredale, 1930) – Lorenz and Hubert, 1993, 2000: 178, pl. 69: figs. 25-28 (shells ranging from white to pigmented). Lorenz, 2002: 135, 138, map 33 (with shell figure), pl. 35 (figs. 9-13), 261 (species No. 58h, 2 unnumbered figures). Moretzsohn, 2002b: 6, 9-11, 15, figs. 7-13 (shells, including that of holotype of *melwardi*), 23 (SEM of radula), 26 (graph and shells), and 27 (map).

Description – Shell (Figs. 6.48-6.59): Oval with blunt extremities, marginally callous, slightly dorso-ventrally depressed. Shells may have normal dorsal spotting, but albino specimens are not uncommon. Most specimens, however, have partially albino shells (meaning that part of the dorsal coating is missing). When present, dorsal spots on average are the smallest among shells of other subspecies of *cribraria*. There are no marginal spots, and the dorsal color, when present, is usually light brown.

Radula (Fig. 6.225): Similar to the radula of other subspecies of *cribraria*, with the basal denticles on the central tooth not so sharp as in *cribraria cribraria*.

Odontophore (Figs. 6.233 and 6.246): Overall similarity with odontophores of congeneric species, but with a faint yellow cast in light microscopy, and a more slender and curved shape than other *cribraria* subspecies. The SEM micrograph shown in Fig.

6.246 reveals a texture under the cuticle different from those in all other odontophores examined in the genus, perhaps an artifact of the preparation, or a thinner cuticle that allowed the electrons to penetrate deeper into the odontophore to reveal the underlying structure. All odontophores examined in the genus *Cribrarula* were observed under the same SEM conditions (25 kV, instead of the usual 10 kV, to increase electron penetration through the cuticle (Moretzsohn, in review A)).

Distribution: Queensland, Australia (Fig. 6.59).

Discussion: This species was described from an albino specimen (Figs. 6.47-6.52), and placed in its own genus, *Nivigena* Iredale, 1930 (junior synonym of *Cribrarula* Strand, 1929). As more specimens became available, albino specimens were recognized as occurring almost as frequently as partially albino shells, while normally pigmented shells were less common. Fully pigmented shells of *melwardi* have as many or more dorsal spots as do most shells of other subspecies of *cribraria*. Live specimens, whether or not possessing a completely white shell, have the typical bright red mantle with many simple, dendritic papillae ("verrucose papillae" of Schilder, 1936, or class 4 of Lorenz and Hubert, 1993) (vide Walls, 1979, unnumbered figure on page 25). Ian Loch (pers. comm., 1999) suggests the center of distribution of the albino form is around the Capricorn Group reefs in the Great Barrier Reef, and incidence of partially-albino and normally colored specimens increases with distance from the area. The shells of *melwardi* are never marginally spotted, and when coloration is present, it varies from light brown to brown, with dorsal spots of irregular sizes. Lorenz and Hubert (2000) point out that albino shells of *melwardi* can be confused with white shells of *Notocypraea comptonii casta* (Schilder and Summers, 1963), but the latter are separable from *melwardi* by the lack of a denticulate peristome. Wilson (1993) considers white shells identified as *melwardi* merely aberrations, and treats the name as a synonym of *cribraria.* However, given the high incidence of albinism or partially pigmented shells of *melwardi* among the museum specimens examined (but there could be a sampling bias by collectors), a color polymorphism is more likely than aberrations suggested by Wilson (1993). Additionally, most shells of *melwardi* can be separated from other populations of *cribraria* on the basis of shell characters rather than color (e.g. Fig. 6.274, Table 6.4): blunt extremities, strong marginal calluses, dorsal margin of anterior extremity convex, and the resulting *melwardi* shells comprise perhaps the most distinct population of *cribraria.*

Schilders' formula: 22.63.17.17. New formula: 21.7/ 63.2/ 17/ 3.4/ 0.

Etymology: in honor of Melbourne Ward, malacologist at the Australian Museum, Sydney (Lorenz and Hubert, 2000).

Material examined: Holotype of *Nivigena melwardi* Iredale, 1930 (= *Cribrarula cribraria melwardi* Iredale, 1930), Type Locality: North West Island, Capricorn Group, Queensland, albino shell (AMS-C 57743, 1 specimen); Australia, Queensland, Great Barrier Reef, Bunker Group, Fairfax Is., 023°51'S, 152°22'E, J. Booth!, 1968 (AMS-C 363556, 8 specimens); Australia, Queensland, Swinger Reef, on sand, J. E. du Pont!, 25 Oct. 1968 (DMNH 31496, 1 specimen); and 32 additional specimens (Appendix 6.4).

1.e. *Cribrarula cribraria gaspardi* Biraghi and Nicolay, 1993 (Figs. 6.60-6.65, and 6.224).

Cribrarula cribraria gaspardi Biraghi and Nicolay, 1993: 6.6. Type locality: Kwajalein, Marshall Islands. Lorenz and Hubert, 1993, 2000: 176, pl. 69: 21-22, pl. 110: fig. 11-12. Moretzsohn, 2002b: 1.

Cypraea cribraria Linnaeus, 1758 – Burgess, 1970: 189, pl. 13, fig. K (as *Cypraea cribraria*).

Cribrarula cribraria form *oceanica* Raybaudi, 1993: 22-25 (non Schilder 1930).

Cypraea gaspardi (Biraghi and Nicolay, 1993) – Burgess, 1995: 1, 10, fig. 2.

Cribrarula gaspardi Biraghi and Nicolay, 1993 – Meyer, 1998: 47, 51, 85, 122, 129, 175 (phylogeny).

Cribrarula cribraria cribraria (Linnaeus, 1758) – Lorenz and Hubert, 2000: 176, pl. 69, figs. 21-22 (as *cribraria cribraria*), pl. 110, figs. 11-12 (as *cribraria cribraria* "*gaspardi*").

Cribrarula cribraria gaspardi (Biraghi and Nicolay, 1993) – Lorenz, 2002: 126, 136, map 33 (with shell figure), 260 (species No. 58e, one unnumbered figure).

Description – Shell (Figs. 6.61-6.66): Usually small (11 to 21 mm), with delicate extremities that can be rostrate, large (relative to shell size) dorsal spots and with a pale beige dorsal coating. The protrusion and upward bending of the siphonal canals, and the ovate elongate shell gives it the appearance of a small canoe (Biraghi and Nicolay, 1993). Columellar teeth are very fine, and the labral teeth are medium-fine in thickness. Base convex, and base, sides and extremities are white.

Radula (Fig. 6.224): Similar to the radula of other subspecies of *cribraria*, but with the central tooth slightly narrower.

Odontophore (not illustrated): The single specimen examined with dried tissue yielded the radula and the pair of odontophores overall similar to odontophores of other subspecies of *cribraria.* Although the odontophore of *gaspardi* was photographed in LM, no measurements were attempted because the odontophore was damaged during handling.

Distribution: This subspecies is restricted to the Marshall Is., and most records are from Kwajalein, the type locality (Fig. 6.72). A few shells resembling those of *gaspardi* are also found in the Philippines. Burgess (1995) reports two specimens collected off Pearl Harbor, Honolulu, Oahu, Hawaii, in 1993-1994, and speculates these were brought in as veligers in the ballast water or arrived as adults on the fouling on the hull of ships.

Schilders' formula: 19.57.18.20 (including large shells – see remarks below). New formula: 19.3/ 56.8/ 20/ 2.5/ 0.

Remarks: A notable variation (Figs. 6.66-6.71) (Schilders' formula = 29.54.21.17) found at Truk, Micronesia (DAN collection), has larger and more elongated shells, with extremities more produced than those in shells of *gaspardi* (Schilders' formula = 17.58.18.16), and a flattened base that resembles the shells of *cumingii*.

Etymology: in honor of Alain Gaspard, field collector and shell dealer (Biraghi and Nicolay, 1993).

Material examined: Marshall Is., Kwajalein, West reef, ex Kienle coll., 09°05'N, 167°20'E (DMNH 196199, 1 specimen); Micronesia, Truk, 07°25'N, 151°47'E, fisherman!, Apr. 2000 (DAN no catalog number, 2 specimens); and an additional 8 specimens (Appendix 6.4).

1.f. *Cribrarula cribraria ganteri* Lorenz, 1997 (Figs. 6.73-6.84).

Cribrarula cribraria ganteri Lorenz, 1997: 1-3. Type locality: Sri Lanka (Ceylon), Colombo, beach at Mount Lavinia. Lorenz, 2002: 260 (species No. 58f, one unnumbered figure). Moretzsohn, 2002b: 1.

Cribrarula cribraria cribraria (Linnaeus, 1758) – Lorenz and Hubert, 2000: 176, pl. 127, figs. 3-4 (as *cribraria cribraria* "*ganteri*").

Description – Shell (Figs. 6.74-6.85): This is a recently described subspecies from Sri Lanka that has oval, callous, dorso-ventrally depressed shells with frequent marginal spots. A few shells examined have a distinctly marginal callus, but most specimens resemble those of the nominotypical subspecies, albeit with more frequent marginal spotting (average 3 spots on each columellar and labral margin) (Fig. 6.284). Number of both labral and columellar teeth is higher than in most shells of other subspecies of *cribraria*. Extremities can be blunt. The mean shell length (L = 24.5 mm) was the highest among the subspecies of *cribraria* (Fig. 6.280), although some specimens of *cribraria cribraria* and *exmouthensis* can be larger.

Radula and odontophore: not available for study.

Distribution: Sri Lanka (Fig. 6.85).

Discussion: As the type locality for *cribraria* is Ceylon (Sri Lanka) by subsequent designation (Iredale, 1935) (fide Schilder, 1965a), it is possible that *ganteri* represents the same population as the types (not originally designated as such) used by Linnaeus to describe *Cypraea cribraria* Linnaeus, 1758. Regenfuss (1758: pl. 12, fig. 74) illustrated a shell of *cribraria* with marginal spotting (Hidalgo, 1906-1907) that could be Linnaeus' type. If the types of *cribraria* are similar to *ganteri* Lorenz, 1997, then the latter is a junior synonym of the former, and the population that occurs in Sri Lanka should be considered the nominotypical population, and what is regarded as the "typical" *cribraria cribraria*, without marginal spotting, should be called something else – perhaps one of the synonyms of *cribraria* that were described based on specimens from elsewhere. Provisionally, however, for the sake of stability, the widespread subspecies should be called *cribraria cribraria* Linnaeus, 1758, and the population occurring in Sri Lanka should be recognized as *cribraria ganteri* Lorenz, 1997, unless there is evidence to the contrary.

Remarks: One specimen examined from Sri Lanka had extremely thick marginal calluses (Schilders' formula = 22.88.17.20) (Figs. 6.79-6.84), resulting in a shell that looks dorso-ventrally depressed.

Schilders' formula: 24.60.17.19. New formula: 24.5/ 60.3/ 19/ 3.2/ 0.7.

Etymology: in honor of Dr. Herbert Ganter, who discovered the first specimens (Lorenz, 1997).

Material examined: Sri Lanka, 08°45'N, 082°30'N, C.W. Yarrington! (FMNH 85809, 2 specimens); Sri Lanka, Colombo, Wellaivate Reef, ex Ray Summers coll., label reads: "Obtained from Leo Mendenhall - this and his two specimens differ from any I have seen from Wellaivate reef, Colombo, we were told", L. Mendenhall!, 1969 (AMNH 292276, 1 specimen); and an additional 25 specimens (Appendix 6.4).

2. *Cribrarula cumingii* (Sowerby II, 1832) (Figs. 6.86-6.97, 6.211, 6.238, 6.251, and 6.289-6.292).

Cypraea cumingii Sowerby II, 1832: 8, f. 5. Type locality: not given by Sowerby; subsequent designation by Iredale, 1935: Raiatea, Polynesia (*fide* Schilder, 1965a).

Cypraea cumingii Sowerby II, 1832 – Sowerby II, 1836: fig. 77. Reeve, 1842: pl. 289, fig. 181. Kiener, 1843-1844: 29, pl. 29, fig. 3. Reeve, 1845: fig. 77. Sowerby II, 1870: 34-35, figs. 349-351. Weinkauff, 1881: 114, pl. 34, figs. 9, 12. Roberts in

Tryon, 1885: 191, pl. 17, figs. 78-79. Melvill, 1888: 230. Hidalgo, 1906-1907: 137, 195, 325-326. Burgess, 1970: 181-182, figs. Donohue, 1977: 160. Walls, 1979: 143, 2 unnumbered figs. Foin, 1982: 48-51. Burgess, 1985: 240, 3 unnumbered figs.

Cypraea compta Pease, 1860: 189-190, pl. 51, fig. 1 – Sowerby II, 1870: pl. 31, fig. 351. Roberts in Tryon, 1885: pl. 17, fig. 70. Hidalgo, 1906-1907: 137, 326. Burgess, 1970, pl. 13, figs. B-C. Burgess, 1985: 240.

Cribraria (Cribraria) cumingii cumingii (Sowerby II, 1832) – Schilder and Schilder, 1938: 172-173. Schilder and Schilder, 1952: 175.

Cribraria (Cribraria) cumingii cleopatra Schilder and Schilder, 1938: 172-173 – Schilder and Schilder, 1952: 175.

Cribraria cumingii cumingii (Sowerby II, 1832) – Allan, 1956: 65, pl. 8, figs. 21-22.

Cribraria cumingii cleopatra Schilder and Schilder, 1938 – Allan, 1956: 65.

Cribraria cumingii (Sowerby II, 1832) – Cernohorsky, 1967: 103, pl. 20, fig. 115.

Cribrarula cumingii Schilder and Schilder, 1938 – Schilder and Schilder, 1971: 56. Lorenz and Hubert, 1993, 2000: 180-181, pl. 70, figs. 1-3 (*cumingii cumingii*). Bradner and Kay 1996: 11, 125, fig. 202 (radula). Meyer, 1998: 122, 129, 175 (phylogeny). Moretzsohn, 2002b: 10.

Cypraea cumingii cleopatra Schilder and Schilder, 1938 – Burgess, 1985: 240.

Cribrarula cumingii cleopatra Schilder and Schilder, 1938 – Lorenz and Hubert, 2000: 180-181, pl. 70, Figs. 6.6, 10 (*cum. cumingii* "*cleopatra*").

Cribrarula cumingii compta Pease, 1860 – Lorenz and Hubert, 2000: 180-181, pl. 127, figs. 20-21, pp. 493, fig. A11 (SEM of shells of *cumingii cumingii* and *cumingii compta*). Lorenz, 2002: 126, 261 (species No. 60c, 2 unnumbered figures).

Cribrarula cumingii cumingii Schilder and Schilder, 1938 – Lorenz and Hubert, 2000: 180-181, pl. 127, figs. 20-21, pp. 493, fig. A11 (SEM of shell). Lorenz, 2002: 261 (species No. 60a, 3 unnumbered figures), 287.

Cribrarula cleopatra Schilder and Schilder, 1938 [described as *Cribraria* (*Cribraria*) *cumingii cleopatra*] – Lorenz, 2002: 261 (as a junior synonym of *cumingii cumingii*).

Description – Shells (Figs. 6.86-6.97): Among the smallest in the complex (mean L = 12.9 mm; most are less than 15 mm in shell length), with very fine and numerous teeth, flat labrum inflected towards the inner columella, rostrate extremities, and margins with dark spots. A clear, thin dorsal line is usually present, close to the labral side. Dorsal color is pale yellow to orange-brown. Dark rings around dorsal spots are common.

Radula (Fig. 6.211): It is one of the most distinct, and the smallest radula in the genus, and most similar to that of *astaryi* (Fig. 6.212) and *taitae* (Fig. 6.210). The central tooth is similar to that in *taitae*, with a trapezoidal profile (but not with a wide base as in *astaryi*); marginals wider than in *astaryi* and *taitae*.

Odontophore (Figs. 6.238 and 6.251): Smallest in the genus, more slender and curved than in most congeneric taxa (Table 6.6). Bending plane (anterior end) pointed, similar to that in *astaryi* (Fig. 6.230). Texture and color as typical in the genus.

Distribution: *cumingii* occurs in Polynesia (Fig. 6.98).

Discussion: Schilder and Schilder (1938-1939) introduce the name *cleopatra* as a geographical race of *cumingii*, representing the "giant" specimens varying from 20 to 30 mm (Figs. 6.92-6.97), and comment that no intermediary specimens are known. The Schilders' formula for *Cleopatra* is 22.52.28.32, contrasting to the typical *cumingii* formula 11.54.40.34 (Figs. 6.86-6.91). The two morphs overlap over most of Eastern Polynesia (Schilder and Schilder, 1938-1939). Some authors suggest *cleopatra* represents the female, and typical *cumingii* the male, of the species, but as Schilder and Schilder (1938-1939) point out, *cleopatra* does not seem to occur throughout the known range of *cumingii*. Hidalgo (1906-1907) reports the shell illustrated by Sowerby (1836) as 29 mm in length. Lorenz, who examined the holotype of *cumingii*, measured it at 27 mm in length, implying the larger form, *cleopatra*, is a synonym (Lorenz and Raines (2001). A recent enquiry at the British Museum revealed two syntypes of *cumingii* (Figs. 6.289-6.292), the largest of which is estimated at 27.6 mm (perhaps the same specimen Lorenz calls the holotype?). The smallest syntype is estimated at 13.3 mm. Shell collectors, nevertheless, often refer to the larger form as *cleopatra*. Based on the lack of consistent shell differences (other than size), *cleopatra* is here considered a synonym of *cumingii*. The large *cleopatra*-like shells were included with other shells of *cumingii* in the calculation of the shell formulae, resulting in an average shell length slightly larger than that calculated by Schilder and Schilder (1938-1939) (Table 6.2).

Lorenz and Hubert (2000) treat *astaryi* Schilder, 1971 as a subspecies of *cumingii.* Multivariate analysis of shell characters separates the shells of the two species (Fig. 6.273), and both are considered here as distinct, valid species (see discussion under *astaryi*). The radulae and odontophores are also distinct: in *cumingii* (Fig. 6.211), the marginal teeth are more curved and have longer cusps than in *astaryi* (Fig. 6.212), and the central tooth in *astaryi* has a nearly triangular shape, while in *cumingii* the base of the central tooth is not so wide. The odontophore in *cumingii* (Figs. 6.238, 6.251) is smaller, less curved, and relatively thinner at mid-length than in *astaryi* (Figs. 6.230 and 6.243). Univariate analyses of selected shell characters promptly separate *cumingii* from *astaryi* and its congeners (e.g. Figs. 6.280, 6.282, and 6.283).

Lorenz and Hubert (2000) also recognized *compta* Pease, 1860 as a subspecies of *cumingii*, on the account of differences in the apertural teeth evidenced in SEM micrographs (Lorenz and Hubert, 2000: pp. 493, fig. A11). The holotype of *compta* is illustrated in Figs. 6. 293-6.294. I agree with other authors and consider *compta* a synonym of *cumingii.*

Schilders' formula: 13.57.33.32. New formula: 12.9/ 56.8/ 32/ 1.9/ 1.6.

Etymology: in honor of Hugh Cuming, British collector (1791-1865) (Lorenz and Hubert, 2000).

Types: Two syntypes of *Cypraea cumingii* Sowerby II, 1832, from the Society Islands, deposited in the H. Cumming collection (BMNH, no catalog number) (Figs. 6. 289-6.292). Holotype of *Cypraea compta* Pease, 1860 (junior synonym of *Cypraea cumingii* Sowerby II, 1832), Jarvis Is., near Line Is., 0°23'S, 160°01'W, Garrett! (BMNH 1964276, 1 specimen) (Figs. 6.293-6.294).

Material examined: Society Is., Raiatea, live, under rock in harbor, R. Crammer!, 1973 (USNM 888207, 1 specimen); Society Is., Tahiti, ex Kienle coll. (DMNH 196210, 1 specimen); and 99 additional specimens (Appendix 6.4).

3. *Cribrarula esontropia* (Duclos, 1833) (Figs. 6.99-6.110, 6.214, 6.239, and 6.252).

Cypraea esontropia Duclos, 1833: 5, pl. 26 (original description). Type locality: original designation by Duclos as the Pacific Ocean erroneous; Schilder (1932) designated Mauritius in correction.

Cypraea esontropia Duclos, 1833 – Deshayes in Lamarck, 1844: 559. Reeve, 1845, fig. 80. Kiener, 1843-1844: 27, pl. 29, fig. 2. Sowerby II, 1870: 33, figs. 169-171. Weinkauff, 1881: 113, pl. 37, figs. 6-7. Roberts in Tryon, 1885: 190, pl. 17, figs. 76-77. Melvill, 1888: 220. Hidalgo, 1906-1907: 138, 344-345. Burgess, 1970: 187-188, pl. 13, fig. E. Donohue, 1977: 160. Walls, 1979: 204, 2 unnumbered figs. Foin, 1982: 48-51. Burgess, 1985: 241, 3 unnumbered figs. Drivas and Jay, 1988: 5, pl. 1, top row.

Cypraea peasei var. *monstrosa* Smith, 1878: 733, t. 46, fig. 13-14.

Cypraea cribraria var. *translucida* Melvill, 1888: 229.

Cypraea esontropia var. *pellucida* Taylor, 1916: 122 (*fide* Schilder and Schilder, 1971: 142).

Cribraria (Cribraria) esontropia (Duclos, 1833) – Schilder and Schilder, 1938-1939: 172. Schilder and Schilder, 1952: 173.

Cribraria esontropia (Duclos, 1833) – Allan, 1956: 64, pl. 8, figs. 19-20.

Cypraea (*Cribraria*) *esontropia* Duclos, 1833 – Dodge, 1953: 95-96.

Cribrarula esontropia (Duclos, 1833) – Schilder and Schilder, 1971: 56. Bradner and Kay, 1996: 12, 125, figs. 203-205 (radulae). Meyer, 1998: 122 (phylogeny). Lorenz, 2002: 126. Moretzsohn, 2002b: 6, 9.

Cribrarula esontropia esontropia (Duclos, 1833) – Lorenz and Hubert, 1993, 2000: 179-180, pl. 70, figs. 21-23, 27-28. Lorenz, 2002: 128-129, map 32 (with shell figure), pl. 33 (figs. 1-3), 263 (species No. 78a, 2 unnumbered figures), 280.

Cribrarula esontropia francescoi Lorenz, 2002: 127-129, map 32 (with shell figure), pl. 34 (figs. 1-7), 264 (species No. 78c, 3 unnumbered figures).

Description – Shell (Figs. 6.99-6.110): Usually oval, but sometimes cylindrical or callous, and with coarse teeth. Dorsal spots are usually large, but can also be densely packed and variable in size. Both margins are spotted, the spots on the columellar side reaching the base. Three or four dorsal bands can be seen on most shells. Some shells of *esontropia* most closely resemble those of *gaskoini*, but the dorsal spots are larger, and marginal spotting less numerous than in shells of *gaskoini*.

Radula (Fig. 6.214): Typical radula of *Cribrarula*, most closely resembles that of *cribellum*, but larger. The rather narrow and high central tooth in both species differs from that of the other congeneric species, and the basal denticles are smaller and less projected as in other species of *Cribrarula*.

Odontophore (Figs. 6.239 and 6.252): The only orange odontophore examined in the genus -- all others are white or off-white, like the majority of the odontophores in 80 species of cowries examined (a few cowries in other genera have yellow or red odontophores) (Moretzsohn, in review A). The odontophore of *esontropia* is similar to that of *cribellum* (Figs. 6.240 and 6.253), but larger and slightly less curved (Table 6.6).

Distribution: This species occurs sympatrically with *cribellum* in the Mascarenes Islands, off East Africa, and also from Tanzania to South Africa (Fig. 6.111).

Discussion: Lorenz and Hubert (1993, 2000), and Lorenz (2002), contrary to the opinion of most authors (e.g. Schilder and Schilder, 1938-1939; Walls, 1979; Burgess, 1985) consider *cribellum* a subspecies of *esontropia.* Morphometric analysis of shell characters (Figs. 6.267 and 6.278) separates most specimens identified as *esontropia* and *cribellum*, with little overlap. Univariate analysis of shell characters separates the shells of *esontropia* and *cribellum* (e.g. Figs. 6.280, 6.282, 6.284, and 6.285) with some overlap. It is possible that both taxa represent the shells of the two sexes in a sexually dimorphic species like *gaskoini*. Currently data are not available to test this hypothesis of sexual dimorphism in *esontropia-cribellum*. If the two taxa are indeed one species, then *esontropia* Duclos, 1833 has priority over *cribellum* Gaskoin, 1849. Lorenz (2002: 128) cites a personal communication by Meyer (2001) that genetic analysis has not solved the status of *esontropia-cribellum*.

Lorenz (2002) described a new subspecies of *esontropia*, *francescoi* Lorenz, 2002, on the basis of shell characters and molecular evidence (Meyer, in press). Lorenz (2002: 229, pl. 33) illustrates the shells of two specimens of *pellisserpentis*; the slender specimen (No. 4 on plate 33) looks like an intermediary between *pellisserpentis* and *esontropia*, especially the newly described *esontropia francescoi*, which is sympatric with *pellisserpentis* in southern Madagascar. For this reason, I do not recognize *esontropia francescoi* as a new subspecies until more evidence is available.

Schilders' formula: 23.62.16.18. New formula: 23.2/ 62.0/ 18/ 3.2/ 2.1.

Etymology: the keeled cowry, referring to the sharp edge formed by the columellar teeth (Lorenz and Hubert, 2000).

Material examined: Mauritius, ex J.C. Cox, ex F. Button coll., 20°11'S, 57°32'E (FMNH 85773, 2 specimens); Mauritius, ex J.C. Cox coll., 20°11'S, 57°32'E, pre-1912 (AMS-C 84792, 1 specimen); Mauritius, 20°11'S, 57°32'E, ex N. Buckland, pre-1972 (AMS C. 364815, 1 specimen); and an additional 58 specimens (Appendix 6.4).

4. ***Cribrarula gaskoinii*** (Reeve, 1846) (Figs. 6.112-6.123, 6.213, 6.218, 6.235, 6.237, 6.248, 6.250, and 6.295-6.296).

Cypraea gaskoinii Reeve, 1846: 23, fig. 122. Type locality: not given by Reeve; Hawaii by subsequent designation (Vayssière, 1910).

Cypraea gaskoinii Reeve, 1846 – Sowerby II, 1870: 34, figs. 352-353 (small, non-inflated shell; large shell as *Cypraea peasei*).

Cypraea gaskoini Reeve, 1846 – Garrett, 1879: 113. Weinkauff, 1881: 113, pl. 34, figs. 2-3. Roberts in Tryon, 1885: 191, pl. 17, figs. 73-74. Melvill, 1888: 230. Hidalgo, 1906-1907: 138, 200, 366. Ostergaard, 1928 (Pleistocene fossils). Ingram, 1947: 1, 3, 8-9, fig. 2c. Dodge, 1953: 96 (footnote). Demond, 1954: 89 (key to Hawaiian cowries). Burgess, 1970: 188-189, pl. 13, fig. F. Donohue, 1977: 160. Taylor, 1975: 247, pl. 33, figs. d, e (veliger shells). Thorsson, 1978: 3. Takahashi, 1985: 5. Thorsson, 1988: 13. Walls, 1979: 242, 2 unnumbered figs. Kay, 1979: 193, fig. (frontispiece). Foin, 1982: 48-51. Hayes, 1983. Burgess, 1985: 239, 3 unnumbered figs. Burch and Burch, 1992: 12, fig. (live specimen of *gaskoini*).

Cypraea (*Cypraea*) *peasei* Sowerby II, 1870: 33, figs.167-168 (large inflated shell, described as a new species) – Ostergaard, 1928. Ingram, 1937: 80.

Cypraea fischeri Vayssière, 1910: 302, 307, t. 13, fig. 1-3 – Burgess, 1985: 239.

Cribraria fischeri (Vayssière, 1910) – Schilder, 1930: 58.

Cribraria gaskoini (Reeve, 1846) – Schilder, 1933: 4, 7, Table 6.1.

Cribraria esontropia Duclos, 1833 – Schilder, 1933: 4, 7, Table 6.1.

Cribraria (Cribraria) gaskoini (Reeve, 1846) – Schilder and Schilder, 1938-1939: 172. Schilder and Schilder, 1952: 174-175.

Cribraria gaskoini (Reeve, 1846) – Allan, 1956: 64-65, pl. 8, figs. 45-46. Cate, 1965: 56, pl. 7, figs. 21a, b. Cernohorsky, 1967: 103, pl. 20, fig. 117 (figs. 116 and 116a were identified as *fischeri* from Fiji, later described as *Cypraea taitae* Burgess, 1993).

Cribrarula gaskoini gaskoini (Reeve, 1846) – Schilder and Schilder, 1971: 56.

Cribrarula gaskoini fischeri (Vayssière, 1910) – Schilder and Schilder, 1971: 56.

Cypraea fiscneri [sic] Joyssiere [sic] (typos, should read *fischeri* Vayssiere) – Johnson 1976: 6.

Cypraea peasei Sowerby II, 1870 – Burgess, 1985: 239.

Cypraea cribraria var. *translucida* Melvill, 1888 – Burgess, 1985: 239.

Cribrarula gaskoinii [sic] (Reeve, 1846) – Lorenz and Hubert, 1993, 2000: 182, pl. 70: figs. 13-14, 19, 24-26. Meyer, 1998: 47,51, 85, 122, 129, 175 (phylogeny). Lorenz, 2002: 267 (species No. 91).

Cribrarula gaskoini (Reeve, 1846) – Bradner and Kay, 1996: 12, 125, fig. 207 (radula). Moretzsohn, 2002b: 6, 9, 15, fig. 21 (shell).

Cribrarula fischeri (Vayssière, 1910) – Lorenz, 2002: 126 (as a junior synonym of *esontropia*), 267 (as shell dealer jargon for small *gaskoini*; Lorenz points out that the holotype of *fischeri* is a slightly distorted *esontropia*, but see discussion below).

Description – Shell (Figs. 6.112-6.123, 6.260-6.265): color bright orange-brown coat when specimens are freshly collected, but the color seems to fade faster than in other species in the complex, becoming pale orange in old museum specimens. The shells have a large number of brown marginal spots (as many as 70 or more on the labral and columellar margins) (Fig. 6.284), as well as numerous dorsal spots (Fig. 6.285). The shells of *gaskoinii* are morphologically variable, with a bimodal distribution in shell size and shape, one peak representing small and elongate-oval shells (peak around 14 mm), the other peak larger (peak around 19 mm) and more globose, ovate shells. The latter are easily separated from shells of other species, but small specimens can and have been confused with *taitae*.

Radula (Figs. 6.213 and 6.218): Typical *Cribrarula* radula, similar to that of *cribraria*: central tooth wide with triangular, pointed basal denticles. There is a sexual dimorphism in the radula: not only are the female larger, but the central tooth is wider than in males.

Odontophore (Figs. 6.235, 6.237, 6.248, and 6.250): Overall similarity to those of congeneric species. Sexual dimorphism is also expressed in odontophore size and shape. The odontophore of the female (Figs. 6.235 and 6.248) is higher and less curved than in the male (Figs. 6.237 and 6.250) (Table 6.6), and both the bending plane and posterior end are more pointed in the male's odontophore.

Distribution: This species is considered endemic to the Hawaiian Island chain recorded as far north as Midway (Fig. 6.124) (Kay, 1979, Burgess, 1985), and apparently most abundant on Oahu (but this observation could be due to a sampling effort bias). There are a few records from the Marshall Islands (e.g. Johnson, 1976, as *Cypraea fischeri*).

Discussion: Ingram (1947: 8-9) noticed the dimorphic shells. Dissections of specimens of *gaskoini*, and the observed bimodal distribution in shell size and shape, strongly suggest sexual dimorphism: males have small, more elongated shells (Schilders' formula = 14.62.20.20), and females large and inflated shells (Schilders' formula = 23.65.20.19). Sexual dimorphism is also indicated in the radulae and odontophore cartilage (see above).

The original spelling of the species epithet is *gaskoinii* (with double –ii), and is adopted in this review. However, apparently after the first citation of the species by Sowerby II (1870), most authors adopted the spelling *gaskoini* (with a single -i), until Lorenz and Hubert (1993) resurrected the correct original spelling. ICZN Art. 33.3.1 (ICZN, 1999) states that the original spelling is the correct spelling (but see Art. 32.1).

The type of *Cypraea fischeri* Vayssière, 1910 (Figs. 6.260-6.265), originally in the Dautzenberg collection, Royal Belgian Institute of Natural Sciences, Brussels, Belgium, now in the Museum National d'Histoire Naturelle, Paris, France (MNHN), was examined and regarded by C.M. Burgess (in litt., 1995) and E. A. Kay (pers. comm., 1995) to be conspecific with *gaskoini*. There is some historical confusion regarding the status of this type, however. It was figured by Vayssière (1910: pl. 13, figs. 1-2) in the description of *fischeri*, and labeled "co-type"; Schilder and Schilder (1952: 174) call it a paratype, but the specimen, which was borrowed by Kay from MNHN for Burgess' study, bears a label that states simply "type" (Fig. 6.266). The provenance of the specimen is also disputed. Vayssière (1910) states "Ile Maurice", but Schilder and Schilder (1952) suggest that Vayssière misunderstood Dautzenberg's label "Cote de Haiku, Maui." Schilder and Schilder (1952) add that the small specimen (illustrated here, Figs. 6.260-6.265) is conspecific with the Melanesian *fischeri* (= *taitae* Burgess, 1993), and not with small specimens of the Hawaiian *gaskoini*. Burgess (in litt., 1995), Kay (pers. comm., 1995) and I do not agree with the Schilders conclusion, and therefore, *fischeri* is considered here a junior synonym of *gaskoini*.

Schilder's formula: 17.64.20.20. New formula: 17.3/ 63.2/ 20/ 2.6/ 1.3.

Etymology: in honor of J.S. Gaskoin, British conchologist (1790-1858) (Lorenz and Hubert, 2000).

Types: Syntype of *Cypraea gaskoinii* Reeve, 1846, no locality data (BMNH 1988054) (Figs. 6.295-6.296). Syntype of *Cypraea fischeri* Vayssière, 1910 (= *Cribrarula gaskoinii* (Reeve, 1846)) (MNHN, no catalog number), from Hawaii, Maui, Haiku.

Material examined: Oahu, D. Woodman!, 2000 (FM 912, 3 specimens); Oahu, D. Woodman!, pre-1996 (CMB 8-37, 7 specimens); Oahu, Moanalua, Fantasy Reef, rock and coral, sand between mesas, coral on mesas, 81 ft, W. Thorsson!, 4 May 1984 (BPBM 241414, 6 specimens); and an additional 378 specimens (Appendix 6.4).

5. *Cribrarula cribellum* (Gaskoin, 1849) (Figs. 6.125-6.136, 6.215, 6.240, and 6.253).

Cypraea cribellum Gaskoin, 1849: 22-23. Type locality: erroneous designation of Mediterranean by Gaskoin; corrected to Mauritius by Weinkauff (1881) (Schilder, 1965a).

Cypraea cribellum Gaskoin, 1849 – Sowerby II, 1870: 34, pl. 20, figs. 165-166. Weinkauff, 1881: 112, pl. 34, figs. 1-6. Brazier, 1882: 44. Roberts in Tryon, 1885: 190, pl. 17, figs. 66-67. Melvill, 1888: 230. Hidalgo, 1906-1907: 137, 194, 322. Burgess, 1970: 182, 187, pl. 13, fig. D. Donohue, 1977: 161. Walls, 1979: 242, figs. Burgess, 1985: 243, 2 unnumbered figs. Drivas and Jay, 1988: 5, pl. 1, 2nd row.

Cribraria (Cribraria) cribellum (Gaskoin, 1849) – Schilder and Schilder, 1938-1939: 172. Schilder and Schilder, 1952: 173.

Cribraria cribellum (Gaskoin, 1849) – Allan, 1956: 64 pl. 8, figs. 23-24.

Cribrarula (Cribrarula) cribraria cribellum (Gaskoin, 1849) – Schilder and Schilder, 1971: 56.

Cribrarula esontropia cribellum (Gaskoin, 1849) – Lorenz and Hubert, 1993, 2000: 180, pl. 70, figs. 33-37. Lorenz, 2002: 128, map 32 (with shell figure), pl. 32 (figs. 8-9), 264 (species No. 78b, 2 unnumbered figures).

Cribrarula cribellum (Gaskoin, 1849) – Bradner and Kay, 1996: 11, 125 (error in date: 1949), fig. 200 (radula). Meyer, 1998: 122 (phylogeny).

Description –Shell (Figs. 6.125-6.136): Usually small, cylindrical-elongated, and rather flattened dorso-ventrally. Dentition is similar to that in shells of *esontropia*, with coarse, short teeth, but the two species are distinguished by the large, callous shell, especially with respect to the labral callus, in *esontropia*. Shells of both species show bands on the dorsum, but there are fewer marginal spots in *cribellum* than in *esontropia* (Fig. 6.284, Table 6.5).

Radula (Fig. 6.215): Typical *Cribrarula* radula, most similar to *esontropia* (Fig. 6.214) but smaller. Basal denticles of the central tooth are not pointed and projected as in congeneric species.

Odontophore (Figs. 6.240 and 6.253): Also most similar to that of *esontropia* (Figs. 6.239 and 6.252), but smaller, and slightly more curved than that of *esontropia*. Color white and spongy texture as in other congeneric species (but orange in *esontropia*). SEM micrograph (Fig. 6.253) shows details of the cuticle similar to that of *cumingii* (Fig. 6.251).

Distribution: *Cribrarula cribellum* is one of the two sympatric species restricted to the Mascarene Islands (Mauritius and Réunion) and Madagascar (Fig. 6.137).

Discussion: Most authors consider *cribellum* and *esontropia* separate species, but Lorenz and Hubert (1993, 2000) list *cribellum* as a subspecies of *esontropia*. To their credit, a few shells seem to be intermediate in shape and some other shell characters. Other than that, however, most specimens are easily separable, and in multivariate analyses of shell characters the two species cluster in two groups that overlap only slightly (Figs. 6.267, 6.268, 6.278, and 6.279). The radula and odontophore in *cribellum* (Figs. 6.215, 6.240, and 6.253) are similar in shape but smaller than in *esontropia* (Figs. 6.214, 6.239, and 6.252).

Because these species are sympatric and mainly restricted to the Mascarene Islands, it is possible that shells usually identified as *esontropia* and *cribellum* represent the two sexes in a sexually dimorphic species, as in *gaskoini*. In this case, *esontropia* Duclos, 1833 would have priority over *cribellum* Gaskoin, 1849. However, until evidence of this hypothesized sexual dimorphism is available, I prefer to recognize them as two valid species.

Schilder's formula: 15.57.16.17. New formula: 14.7/ 56.5/ 17/ 2.2/ 1.3.

Etymology: (Latin) fine sieve, in reference to the appearance of fine perforations on the dorsum (Lorenz and Hubert, 2000).

Material examined: Mauritius, Port Louis, dead coral rubble, 020°18'S, 057°36'E, E. Concaud!, 1970 (USNM 866186, 2 specimens); Mauritius, 020°18'S, 057°36'E, ex Kienle coll. (DMNH 196190, 1 specimen); and an additional 48 specimens (Appendix 6.4).

6. *Cribrarula fallax* (Smith, 1881) (Figs. 6.138-6.149, 6.232, 6.245, and 6.297-6.298).

Cypraea fallax Smith, 1881: 441. Type locality: West Australia by original designation; Albany area, S.W. Australia (Lorenz and Hubert, 1993).

Cypraea cribraria Linnaeus, 1758 – Hidalgo, 1906-1907: 137.

Cribraria (Cribraria) fallax (Smith, 1881) – Schilder and Schilder, 1938-1939: 172. [*exmouthensis* Melvill, 1888 was listed incorrectly as a junior synonym of *fallax* Smith, 1881].

Cribraria exmouthensis (Melvill, 1888) – Allan, 1956: 64.

Cribrarula cribraria (Linnaeus, 1758) – Schilder and Schilder, 1971: 56.

Cypraea cribraria fallax Smith, 1881 – Wilson and Gillett, 1971: 52, fig.

Cribraria cribraria haddnightae Trenberth, 1973: pl. 1-2 – Walls, 1979: 197, 3 unnumbered figs.

Cypraea haddnightae (Trenberth, 1973) – Burgess, 1985: 255 (photos of shell appear to be of deep-water *Cribrarula cribraria exmouthensis* form *rottnestensis* Raybaudi Massilia, 1987).

Cribraria haddnightae Trenberth, 1973 – Burgess and Sage, 1992: 3. Lorenz, 2002: 130 (as a junior synonym of *fallax*).

Cribrarula fallax (Smith, 1881) – Lorenz and Hubert, 1993, 2000: 177, 179, pl. 69, figs. 31-32, 37. Bradner and Kay, 1996: 12, 125, fig. 206 (radula). Meyer, 1998: 122 (phylogeny). Lorenz, 2002: 130, 137-139, 264, map. 34 (shell), pl. 37 (Fig. 6.11). Moretzsohn, 2002b: 6, 8-10.

Description – Shell (Figs. 6.138-6.149): Large (usually between 28 and 33 mm in length) and distinct from those of all others in the complex in several characters. The shells are irregularly pyriform, with a gently sloping fossula and peristome, which contrast with a steep columellar region in *cribraria*. Dorsal color is pale yellow, with small, usually not very clear dorsal spots, and no marginal spotting.

Radula: Bradner and Kay (1996: 131, fig. 206) illustrated the radula of *fallax* in SEM. It looks like a typical *Cribrarula* radula but with less crowded teeth. The basal denticles of the central tooth are pointed and triangular.

Odontophore (Figs. 6.232 and 6.245): One of the largest odontophores examined in *Cribrarula*, typical in color and texture, but not in shape: the bending plane is rather round and high, and the anterior end more pointed.

Distribution: This species has a very limited range in Southwestern Australia, in the Albany area (Fig. 6.150).

Discussion: The name *fallax* should be applied to a rather rare cowry that occurs in a very restricted area around Albany, Southwest Australia, but it has been used for specimens from Western Australia (*cribraria exmouthensis*) in error (Lorenz and Hubert, 2000). Lorenz (in Lorenz and Biraghi, 1986) examined the holotype of *fallax* (in the BMNH) (Figs. 6.297-6.298), and concluded that it is conspecific with *haddnightae* Trenberth, 1973 (*fallax* has priority).

When all taxa are included in a PCA analysis of shell characters, points representing shells of *fallax* grouped together with points representing large specimens of *cribraria* (e.g. Figs. 6.267 and 6.268). When only specimens from the East Indian Ocean were included in the analysis, *fallax* was clearly separated from the other taxa (Figs. 6.276 and 6.277). Univariate analyses of size-related shell characters easily separate *fallax* from the other taxa (e.g. Figs. 6.280 and 6.282).

Schilder's formula: 31.59.20.22. New formula: 31.3/ 59.4/ 22/ 6.5/ 0.

Etymology: the fallacious cowry (Lorenz and Hubert, 2000).

Types: Holotype of *Cypraea fallax* Smith, 1881, from West Australia (purchased by G.B. Sowerby) (BMNH 1881.11.8.2) (Figs. 6.297-6.298). Paratype 2 of *Cypraea haddnightae* Trenberth, 1973 (= *Cribrarula fallax* (Smith, 1881)), Western Australia, West of Denmark, Parry's Beach, ex Waverley H. Harmon coll., ex CM Burgess, 35°01'S, 117°09'E, F. Haddrill! (AMNH 268523 Paratype, 1 specimen) (Figs. 6.144-6.149). Holotype of *Cypraea haddnightae* Trenberth, 1973 is in the Western Australian Museum.

Material examined: Western Australia, Parry's beach, Denmark. In tide pool after storm, 35°01'S, 117°09'E, G. F. Herman!, 1978 (AMS-C 313993, 1 specimen); Australia, WA, Ellensbrook, Cowaramup end, 033° 54'S, 114° 59'E, R. Anson!, Dec. 1975 (WAM S14316, 1 specimen); Australia, WA, Southwest WA, Albany, ex E. J. Harrold collection, 035° 00'S, 117° 52'E, pre-1978 (WAM S14319, 2 specimens), and nine additional specimens (Appendix 6.4).

7. *Cribrarula catholicorum* (Schilder and Schilder, 1938) (Fig. 6.151-6.162, 6.217, 6.228, 6.241).

Cribraria (Cribraria) catholicorum Schilder and Schilder, 1938: 114-115 (original description). Type locality: Mope, New Britain, by original designation. Schilder and Schilder, 1952: 173.

Cribraria catholicorum Schilder and Schilder, 1938 – Allan, 1956: 64, pl. 8, figs. 25-26. Cernohorsky, 1967: 102-103, pl. 19, fig. 113.

Cypraea catholicorum (Schilder and Schilder, 1938) – Burgess, 1970: 180, pl. 13, fig. A. Donohue, 1977: 160. Walls, 1979: 229, 2 unnumbered figs. Burgess, 1985: 242, 3 unnumbered figs.

Cribrarula catholicorum (Schilder and Schilder, 1938) – Schilder and Schilder, 1971: 56. Lorenz and Hubert, 1993, 2000: 182, pl. 70: 29-32. Bradner and Kay, 1996: 12, 125, fig. 199 (radula). Meyer, 1998: 122 (phylogeny). Lorenz, 2002: 135, 255.

Description – Shell (Figs. 6.151-6.162): Oval, broad, callous, with blunt extremities, a rather flat base, and convex anterior dorsum (Figs. 6.154 and 6.160) (i.e., without the dorsal flare seen in shells of other species). Margins are spotted with a few faint spots; dorsum has three or four juvenile ("embryonic") bands, with small and dense dorsal spots, variable in size. Dorsal color ranges from caramel to pale yellow. A very distinct, thick and sometimes broken dorsal line is present in most specimens examined.

Radula (Fig. 6.217): Typical *Cribrarula* radula, most similar to that of *gravida* and *exmouthensis* in regard to the small projection on the outer margin of the marginal teeth. The basal denticles of the central tooth are pointed, but with a rather rounded profile, instead of a triangular profile as in *cribraria*.

Odontophore (Figs. 6.228 and 6.241): Typical *Cribrarula* odontophore, white and with spongy texture in LM. The bending plane is rounded, and the posterior end is pointed. The odontophore is close in shape to that in *fallax* (Figs. 6.232 and 6.245), with a long and somewhat straight dorsal posterior margin. High at mid-length; the OH/OL ratio is one of the highest among congeneric species (Table 6.6).

Distribution: This species occurs in Melanesia (Fig. 6.163).

Remarks: There are many paratypes in several museums, but most of them are eroded and faded shells. The species can be common locally; de Couet reports finding many live specimens on red sponges while night diving in the Solomon Islands (de Couet, pers. comm. 2000). Chatenay (1977) reports the occurrence of melanistic and/or rostrate (called form *niger*) specimens of *catholicorum* in New Caledonia, but no such specimen was examined for this study. Also some specimens are reported from Queensland (e.g. Lorenz, 2002), but no specimens from that region were available for study.

Discussion: Shells of *catholicorum* are most similar to those of *gaskoini*, and readily separable from those of other species in the *cribraria* complex: ovate shape and blunt extremities, dorsal bands, light brown dorsal color, convex dorsal margin of anterior canal, and the dorsal line is usually well marked and thick, compared with that of congeneric species. The number of marginal spots easily separates *catholicorum* and *gaskoini*, because there are few marginal spots on the shells of the former (Table 6.5). PCA analysis of shell characters reveals a cohesive group of points that can be distinguished from other groups (e.g. Fig. 6.270), although with some overlap with points representing *gaskoini*. When *gaskoinii* is not included in the analysis, *catholicorum* separates well from the other taxa (Fig. 6.272). Boxplots of the dorsal line angle (DLA) separate *catholicorum* from other taxa: the mean DLA in shells of *catholicorum* is the highest (Fig. 6.280), followed by *pellisserpentis* and *gaskoini*, suggesting that the left lobe of the mantle in those species is approximately double of the length of the right lobe, while in most other species in the genus the left lobe is usually even larger (about three times the length of the right lobe).

Schilder's formula: 15.63.19.20. New formula: 14.9/ 62.7/ 20/ 2.2/ 1.0.

Etymology: in honor of the catholic missionaries in New Britain, who collected most of the shells used by the Schilders to describe the species.

Material examined: Papua New Guinea, New Britain, Mope, paratype of *Cribraria catholicorum* (Schilder and Schilder, 1938), from type locality, ex R. Summers coll., P. J. Schneider!, 1936 (AMNH 186627, 1 specimen); Papua New Guinea, New Britain, Mope, paratype, from type locality, P. J. Schneider!, pre-1938 (AMNH 80580, 1 specimen); Papua New Guinea, New Britain, Mope, paratype from type locality, ex C. and J. Cate coll., pre-1938 (AMNH 203877, 1 specimen); Papua New Guinea, New Britain, Mope, paratype, from type locality, P. J. Schneider!, 1936 (USNM 773691, 1 specimen); Papua New Guinea, New

Britain, Mope, paratype, from type locality, P. J. Schneider! (ANSP 361021, 1 specimen); Solomon Is., Guadalcanal, 09°31'S, 160°11'E, ex Kienle coll. (DMNH 196108, 2 specimens); Tonga, Nuku'alofa, dredged at new harbor, 021°07'S, 175°11'W, H.C. Gray!, 1966 (USNM 773694, 2 specimens); Solomon Is., Guadalcanal, Marau Sound, 09°31'S, 160°11'E, ex E. Wright coll. (USNM 773800, 1 specimen); and an additional 30 specimens (Appendix 6.4).

8. *Cribrarula astaryi* F.A. Schilder, 1971 (Fig. 6.164-175, 212, 230, 243).

Cribrarula fischeri astaryi Schilder, 1971: 297-299 (Note that *fischeri* is a junior synonym of *gaskoini*). Type locality: Marquesas, by original designation.

Cypraea astaryi (Schilder, 1971) – Burgess, 1985: 250, photo of live animal (the shell illustrated is actually the holotype of *Cribrarula taitae* (Burgess 1993)).

Cribrarula cribraria leifaiti Martin and Poppe, 1989 – Martin and Poppe, 1989: 6-7.

Cribrarula leifaiti Martin and Poppe, 1989 – Burgess and Sage, 1992: 3.

Cribrarula astaryi Schilder, 1971 – Bradner and Kay, 1996: 11, 125, fig. 198 (radula). Moretzsohn, 2002b: 10.

Cribrarula cumingii astaryi Schilder, 1971 – Lorenz and Hubert, 1993, pl. 70: 11-12. Lorenz and Hubert, 2000: 181, pl. 70: 11-12. Lorenz, 2002: 261 (species No. 60b, 3 unnumbered figures).

Description –Shell (Figs. 6.164-6.175): Oval to rhomboidal, rostrate, with rather large, dark marginal spots. Teeth fine, but coarser and less numerous than in shells of *cumingii*. Dorsal color dark orange with well defined dorsal spots, usually with a dark ring around each spot.

Radula (Fig. 6.212): It is one of the most distinct radulae in the genus, closest to that of *cumingii* and *taitae*, but with the central tooth trapezoidal with a wide base. The marginal teeth have a rounded outer margin (as seen in the position illustrated in Fig. 6.212).

Odontophore (Figs. 6.230 and 6.243): Typical *Cribrarula* odontophore, white and spongy in texture, but considerably curved, with pointed bending plane and posterior end, resembling the odontophore of *cumingii* but larger and higher (Table 6.6).

Distribution: Northwestern Polynesia (Marquesas) (Fig. 6.176).

Discussion: Lorenz and Hubert (2000) consider *astaryi* a subspecies of *cumingii*, and suggest that the holotype of *compta* Pease 1860 (judged from an illustration in Roberts' monograph (1885)) is similar to the shell later described as *astaryi*. However, that type specimen (BMNH 1964276) (Figs. 6.293-6.294) was examined in this study, and it appears to represent a small specimen of *cumingii*. *Cribrarula compta* thus is here regarded as a synonym of *cumingii*. The paratype of *astaryi* (USNM 862332) (Figs. 6.164-6.169) was also examined: it is not conspecific with *cumingii*, and *astaryi* is therefore regarded as a distinct and valid species. Multivariate analyses of shell characters support the opinion that these two species are distinct (Figs. 6.267-6.273). The radula and odontophore, although similar overall to those of *cumingii* (Figs. 6.211, 6.238, and 6.251), have several differences as discussed above.

Burgess and Sage (1992: 3) report that Kay borrowed the holotype of *astaryi* from the Museum fur Naturkunde der Humboldt-Universitat in Berlin, Germany. Kay, Burgess and Sage then compared the holotype with 14 cowries sent to Burgess for study by André Lefaiti of Papeete, Tahiti: all were found to be conspecific with Schilder's type of *astaryi*, and *lefaiti*, therefore, is a junior synonym of *astaryi*.

Schilder's formula: 17.59.23.25. New formula: 17.2/ 58.9/ 25/ 2.4/ 2.1.

Etymology: in honor of Dr. J.C. Astary of Vannes, France (Schilder, 1971).

Material examined: Paratype of *Cribrarula fischeri astaryi* Schilder, 1971 (= *Cribrarula astaryi* Schilder, 1971), Marquesas, Tahuata Is., Hanehevane Bay, 3-8 m, 09°57'S, 139°05'W, J. C. Astary!, Feb. 1968 (USNM 862332, 1 specimen); Marquesas, Atuona, Homeotype, gift from Lefait to C. M. Burgess, 1992, 09°00'S, 139°30'W, Lefait!, 1992 (CMB NL 7, 1 specimen); Marquesas, Atuona, Homeotype, 09°00'S, 139°30'W, H. Boswell, 1984 (CMB NB 1, 1 specimen); Marquesas, Farahiva, 3 m on dead coral, 09°00'S, 139°30'W, ex WH Harmon, 28 Feb. 1978 (AMNH 270682, 1 specimen); Marquesas, Nuku Hiva, 08°56'S, 140°06'W, ex Fleischner, 8 Apr. 1971 (AMNH 273214, 1 specimen); Marquesas, Tahuata Is., 90 ft., 09°57'S, 139°05'W, ex Kienle coll., Feb. 1985 (DMNH 196056, 1 specimen); Marquesas, Ua Pou Is., 09°23'S, 140°03'W, D. Pisor!, 9 Jun. 1984 (HBR P10, 2 specimens); Marquesas, 3-5 m under dead coral, ex Kienle coll., Sept. 1978 (DMNH 196057, 1 specimen); Vanuatu, New Hebrides (DMNH 196058, 1 specimen).

9. *Cribrarula taitae* (Burgess, 1993) (Figs. 6.177-6.188, 6.210, 6.236, and 6.249).

Cypraea taitae Burgess, 1993: 174-177. Type locality: The reef near the village of Lepua directly across Pago Pago Harbor from Tutuila, American Samoa, 140°W, 19.6°S, by original designation.

Cribraria (*Cribraria*) *gaskoini fischeri* Vayssière, 1910 – Schilder and Schilder, 1952: 174-175.

Cypraea fischeri Vayssière, 1910 – Schilder, 1933: 4, 7. Purtymun, 1977: 7.

Cypraea astaryi (Schilder, 1971) – Burgess, 1985: 250 (the two photos of the shell illustrated are actually of the holotype of *taitae* (Burgess, pers. comm., 1998)).

Cribrarula gaskoinii [sic] *taitae* (Burgess, 1993). Lorenz and Hubert, 1993, pl. 70: figs. 15-16.

Cribrarula taitae (Burgess, 1993) – Lorenz, 1995: 78-79, figs. Lorenz and Hubert, 2000, pl. 70: figs. 15-16, pl. 127: figs. 15-16, 486. Lorenz, 2002: 126, 287 (species No. 211, 2 unnumbered figures). Moretzsohn, 2002b: 1.

Description – Shell (Figs. 6.177-6.188): Usually small (mean length 13.1 mm), elongate and rostrate, superficially similar to those of *cumingii* but with coarser and fewer teeth, steep fossula, and shorter extremities than in *cumingii*. Shells of *taitae* may also resemble those of male specimens of *gaskoinii* (i.e., with a small, elongated shell), but with larger and less numerous marginal spots.

Radula (Fig. 6.210): Most similar to that in *cumingii* and *astaryi*, but with a more distinct shallow groove along the outer margin of the marginal teeth. The central tooth is trapezoidal in profile, apparently intermediary in profile between that of *astaryi* (wide base) and *cumingii* (narrower base).

Odontophore (Figs. 6.236 and 6.249): Typical *Cribrarula* odontophore, most resembling that of *cumingii* but slightly less curved (VA/OH), and higher (OT/OL) (Table 6.6).

Animal: Burgess (1993: 174) provides a good description of the animal of *Cypraea taitae*: "Mantle brilliant dark carmine, thin, not obscuring dorsal pattern. Papillae fingerlike, blunt, arising from circular area of discrete black dots. Other papillae prominent, widely spaced, resembling three or four beads on a string, decreasing in size from their bases. Some papillae white, bearing several tufts arising from terminal bead, forming two vertical rows equally spaced along full length of mantle. Siphon carmine, finely fringed with short processes shaped as are interstices between them. Tentacles darker carmine, clubbed, with still darker tips. Foot of same color as mantle, studded, as is mantle, with discrete black spots; crawling surface pale orange." T. Kurth wrote on the label of Paratype E (see below) that even the feces of the cowrie were orange, the same color as the mantle.

Distribution: This species was described from American Samoa, and has also been recorded from other parts of Melanesia and Western Polynesia (Fig. 6.189).

Discussion: In the past shells of *taitae* have been confused with *Cypraea fischeri* (= *gaskoini*), *astaryi* and *cumingii*. The species was finally recognized and described as a new species by Burgess (1993), who reviews the history of name usage associated with the species. Lorenz and Hubert (1993) did not originally recognize *taitae* as valid, and listed the species as a subspecies of *gaskoini*, but after material became available, Lorenz (1995, 2002) and Lorenz and Hubert (2000) accepted *taitae* as a full species. The radula in *taitae* (Fig. 6.210) is most similar to those of *astaryi* (Fig. 6.212) and *cumingii* (Fig. 6.211), but the odontophore of *taitae* (Figs. 6.236 and 6.249) is more like that of *cumingii* (Figs. 6.238 and 6.251) than that of *astaryi* (Figs. 6.230 and 6.243), which is the largest among the three species.

Schilder's formula: 13.58.22.23. New formula: 13.1/ 57.8/ 23/ 1.7/ 1.1.

Etymology: in honor of Grace Tait Burgess, C. M. Burgess' wife.

Material examined: Holotype of *Cypraea taitae* Burgess, 1993 (= *Cribrarula taitae* (Burgess, 1993)) (illustrated here in Figs. 6.177-6.182), American Samoa, Pago Pago, Lepua, Pago Pago, Tutuila, 014°16'S, 170°43'W, CM Burgess!, 1965 (BPBM 9966, 1 specimen); W. Samoa, Lepua, Paratype "C", 013°49'S, 171°46'W, Purtymun! (CMB 756-2, 1 specimen); W. Samoa, Asau, Paratype "E", 013°40'S, 172°30'W, T. Kurth!, Feb. 1975 (CMB Paratype E, 1 specimen); Marquesas, Ua Pou Is., Baie Hikeu, N. Side, 09°23'S, 140°03'W, Pele Expedition!, 1967 (USNM 798522, 2 specimens); American Samoa, Ta'u, Samoa, 014°15'S, 169°27'W, W. Harris!, 25 Apr. 1937 (BPBM 187296-298, 1 specimen); W. Samoa, Apia Harbor, Apia Harbor, dredging, 013°40'S, 172°30'W, W. Cernohorsky!, 3 Sept. 1966 (USNM 773698, 2 specimens).

10. *Cribrarula pellisserpentis* Lorenz, 1999 (Figs. 6.190-6.195).

Cribrarula pellisserpentis Lorenz, 1999. Type locality: Tulear to Fort Dauphin, Southern Madagascar, by original designation.

Cribrarula esontropia (Duclos, 1833) (previously identified as *esontropia* (in part)) – Lorenz, 1999.

Cribrarula pellisserpentis Lorenz, 1999 – Lorenz and Hubert, 2000: 179, pl. 127: figs. 7-9, pp. 485-486, fig. A4. Lorenz, 2002: 126, map 32 (with shell figure), pl. 33 (Figs. 6.5), 281 (species No. 173, 2 unnumbered figures). Moretzsohn, 2002b: 1.

Description: Shells (Figs. 6.190-6.195) are callous and inflated, most resembling some shells of *cribraria* and *esontropia*, but with finer teeth, especially on the columella. The dorsal pattern consists of large lacunae that overlap and anastomose, different from the dorsal spotting in all other species in the complex. Size: most between 20 and 25 mm in length (Lorenz and Hubert, 2000).

Distribution: This recently described species seems restricted to Southern Madagascar (Lorenz, 2002) (Fig. 6.196).

Discussion: Shells of *pellisserpentis* are distinct from those of other species in the complex, most resembling those of *esontropia* and *gaskoinii* the most (Fig. 6.268). The dorsal netting in *pellisserpentis* is different from the dorsal spotting pattern in the congeneric species. The dorsal line angle is among the highest in the genus (Fig. 6.281), as is that of the number of labral spots (Fig. 6.284).

Schilder's formula (based on one specimen measured): 19.67.17.19. New formula: 18.6/ 67.5/ 19/ 3.6/ 2.0.

Etymology: The name *pellisserpentis* (Latin: *pellis* = skin; *serpens* = snake) refers to the narrow dorsal netting of the shells, resembling the scaly skin of a snake (Lorenz, 1999).

Material examined: Madagascar, Faux Lap, 25°32'S, 45°30'E, 1999 (DAN, no catalog number, 1 specimen), Madagascar, 2000 (TAK, no catalog number, 2 specimens).

11. *Cribrarula garciai* Lorenz and Raimes, 2001 (no figures).

Cribrarula astaryi Schilder, 1971. Anon., 1988: 28 (A shell from the Marquesas, apparently conspecific with *garciai*, was identified by Lorenz in 1988 as *astaryi*).

Cribrarula garciai Lorenz and Raimes, 2001 – Lorenz, 2002: 126, fig. 32, 267, 3 unnumbered figures (species No. 90). Moretzsohn, 2002b: 1, 10, 13.

The following is adapted from the original description of *garciai* by Lorenz and Raines, 2001, with additional information from Felix Lorenz (pers. comm., 2002):

Description - Shell: Holotype oval, extremities blunt. Extremely callused at extremities and margins. Spire small, depressed, covered with callus. Base convex, very thick. Aperture narrow, of equal width throughout, slightly curved left in posterior third. Labral teeth (25) not deeply carved, extending toward middle of the labrum, columellar teeth (24) not extending on to base, reaching deep into the shell forming a distinctly denticulate columellar peristome and fossula. Terminal ridge thick, rather long. Base, marginal callus, extremities, and dorsal lacunae white. Dorsum covered with a bright orange-brown coat forming regular round lacunae of variable size. An indistinct dorsal line runs the length of the dorsum along the labral side. Margins densely covered with large black spots reaching base and dorsum, where they form a row of slightly elevated black spots. The smaller paratype resembles the holotype in these features. Soft parts not recorded, radula unknown.

Distribution: Known range west coast of Easter Island, near Hanga Roa (Fig. 6.197). Michael Garcia (for whom the species was named) collected the type specimens side by side on the roof of a cave at 30 m depth. See discussion below regarding a possible record from the Marquesas.

Discussion: Lorenz and Raines (2001) compared *garciai* with *cumingii* and *astaryi* (as *cumingii astaryi*), and assign *garciai* to the *cumingii*-group because of the fine dentition, finely denticulate fossular area, and narrow aperture. Shells of *garciai* are easily separated from those of *gaskoinii* by the dentition, finely denticulate fossula, and large, sparse marginal spots (particularly dense and fine in *gaskoini*). The dorsal spots are much larger and sparser than in *gaskoini*. Shells of *catholicorum* may have a similar strong marginal callus, but the teeth are coarser and the fossula steep with only four to seven coarse denticles. The marginal spots are fine and inconspicuous. The western Polynesian *taitae* is barely callused, with coarse dentition resembling that in *catholicorum*. The recently described *pellisserpentis* Lorenz, 1999 from Madagascar may be similar in size, callosity of the margins, and size of the marginal spots, but in that species the aperture is wide, the teeth comparatively coarse and with a short, coarsely denticulate fossula.

A specimen, of which two photographs were published in *La Conchiglia* (Nov./Dec. 1987), may be conspecific with *garciai* was collected in the Marquesas. The shell has dorsal spots similar to those on shells of *garciai*, but the dark rings that surround the dorsal spots are offset. Felix Lorenz identified the specimen as *astaryi* Schilder, 1971 (Anon., 1988). If this record is accurate, it represents a considerable range extension for *garciai* into the Marquesas.

Measurements (L x W x H; CT/LT): Holotype: 26.4 x 17.4 x 13.7; 24/25; paratype: 22.3 x 14.3 x 10.8; 23/24. Subsequently more specimens have been collected, most of them smaller but typical, with extremely produced margins and large marginal spots (Lorenz, pers. comm., 2002).

Schilders' formula: 24.65.25.24 (Lorenz and Raines, 2001). New formula (estimated from photographs in original description): 24.4/ 65.0/ 24/ 3.4/ 3.0.

Etymology: In honor, Michael Garcia, who first collected the species (Lorenz and Raines, 2001).

Material examined: no shells were examined by the author, but information was obtained from photographs in the original description: Easter Is. (Holotype and paratype of *Cribrarula garciai* Lorenz and Raines, 2001), cave, 30 m, 27°07'S, 109°22'W, M. Garcia! (LACM Holotype, 1 specimen; paratype in Lorenz collection, 1 specimen).

12. *Cribrarula gravida* Moretzsohn, 2002 (Figs. 6.199-6.204, and 6.216).

Cribrarula gravida Moretzsohn 2002b: 1-16, original description. Type locality (by original designation): Fish Rock, S. side, 2 km SE of Smoky Cape, outside cave, 18 m, 030°56.4'S, 153°5.9'E, V. Taylor!, Nov. 1972 (AMS-C 91000) (Moretzsohn, 2002b).

Cypraea cribraria Linnaeus, 1758 – The holotype of *gravida* was identified as *cribraria* by Ian Loch, of the Australian Museum, in 1980.

Cribrarula gravida Moretzsohn, 2002 – Moretzsohn 2002b: 1-15, figs. 1-6 (shell of the holotype), 22 (SEM of radula), 26 (graph and shell), 27 (map), 28 (shell and cast).

Diagnosis: Large inflated pyriform shell, rostrate extremities, with elliptical dorsal spots, no marginal spots, columellar teeth thicker than in congeneric species, dorsal anterior extremity flared.

Description – Shell (Figs. 6.198-6.203): Large for the genus (35.15 mm in length), pyriform in dorsal profile, extremities produced, thick marginal calluses. Base and labrum convex, considerably inflated dorso-ventrally (shell width/length ratio 62.9%, height/width ratio 82.6%). Aperture slightly constricted at the center (minimum width is 2.10 mm, maximum width 2.70 mm), curved left. Labral teeth (21) thick, extending about 64% of the labrum width. Columellar teeth (20) medium in thickness, not extending on to the base, reaching deeply into the aperture, forming a distinctly ribbed, sloped, concave, and wide fossula and peristome. Terminal ridge long, thick, and nearly parallel to the anterior extremity of the labrum. Gap between the terminal ridge and anterior columellar teeth similar in width to neighboring intertooth spaces. Base, labral and columellar margins, and extremities white. White marginal calluses obliterate dorsal pattern up to about half of the shell height. No marginal spots (common on most species of *Cribrarula*, but rare in shells of *cribraria*). Labrum thick, keeled, forming a marginal sulcus near the extremities. Anterior labral region declivous towards the aperture, labral margin upturned at the center. Both labral and columellar marginal calluses irregular, forming slightly crenulated margins. Dorsum distinctly convex; highest point 23 mm from the anterior extremity (67% of shell length). Dorsum light brown, densely peppered with 88 off-white elliptical spots of variable size (ranging in maximum diameter from 2.80 to 3.50 mm). Dorsal spots not so clear, no dark rings around the spots. Dorsal line unclear, but patches with overlaid "double exposure" pigmented layers define a dorsal line region. Smaller patches of overlaid pigmented layers occur elsewhere on the dorsum. Dorsal line region forms an angle of about 40° with the base of the shell (dorsal line angle) when seen from the anterior canal. Dorsal coat produced by both lobes of the mantle is similar in color, but dorsal spots (DS) produced by the right mantle lobe smaller than those produced by the left lobe. Spire region wide (c. 6.2 mm in diameter) and slightly umbilicated. Extremities rostrate, anterior and posterior canal margins thick. Dorsal part of the anterior canal flared up.

Animal: Soft parts dried inside the shell; part of the mantle showing inside the aperture bears apparently simple papillae: short, finger-like in the dry state, similar to those of other species of *Cribrarula.*

Radula (Fig. 6.216): Typical *Cribrarula* radula in the 'Cicercula' pattern of Bradner and Kay (1996: 125-147), but larger size, with at least two differences from the radula of *cribraria*: 1) central tooth has two rounded basal denticles (pointed in *cribraria* (Figs. 6.219-6.227)), and 2) marginal teeth have a small projection near the outer margin (not present in radulae of other species of *Cribrarula*, except in *catholicorum* (Fig. 6.217), in which a less pronounced projection is present). Average size of the central tooth 108.4 x 93.55 μm (n= 18), and L/W ratio 1.19 (n=14), larger than the average 68.5 x 54.4 μm, and L/W ratio 1.23 calculated for other species in *Cribrarula* (Bradner and Kay, 1996: 125). Average width of radular ribbon 595 μm; 11.4 rows of teeth per mm of radula (n= 29 rows).

Odontophore cartilage: Similar to those of congeneric species: falciform elongated, sponge-like texture, cream in color, larger than others, about double the size of the odontophores of other species in *Cribrarula* (estimated at about four mm long).

Type locality: Fish Rock, south side, 2 km SE of Smoky Cape, New South Wales, Australia, 30° 56.4'S, 153° 5.9'E (Fig. 6.204), collected at 18 m depth, outside a cave.

Schilders' formula: 35.63.19.18. New formula: 35.2/ 62.9/ 18/ 6.2/ 0. (a slightly different formula was used in the original description of *gravida* (Moretzsohn 2002b)).

Discussion: *Cribrarula gravida* is conchologically distinct from all other currently known taxa in *Cribrarula.* No apparent intermediate specimens were found connecting the holotype of *gravida* conchologically to specimens of other species. In some of the morphometric analyses, large specimens of *cribraria, esontropia, fallax*, and *gaskoinii* sometimes appeared close (in plots of principal components PC1 and PC2) to the holotype of *gravida*, probably because of the effect of shell size (judging by scores) had in the analyses. However, even with the exclusion of size-related characters, *gravida* remains distinctive (albeit less then when size-related characters were used – e.g. Fig. 6.269). Boxplots of size-related characters, such as shell length and spire diameter separate *gravida* from other congeneric species (Figs. 6.280 and 6.282). The large number of dorsal spots, and the lack of marginal spots (Figs. 6.285 and 6.284) can also be useful in separating *gravida* from the other species of *Cribrarula.*

The holotype of *gravida* shares some shell features with representatives of other species of *Cribrarula* (Table 6.5), but *gravida* can be easily separated from its congeners when a combination of characters is used. For example, the absence of marginal spots in *gravida* separates it from specimens of *esontropia* and *gaskoini*. Some shells of *exmouthensis* and *fallax* may also be large, pyriform and inflated, comparable to those of *gravida*, but those species occur in Western Australia, while *gravida* occurs in Eastern Australia. For more detailed discussion, see Moretzsohn (2002b).

The spire diameter in *gravida*, the widest among all species of *Cribrarula*, suggests that the protoconch is larger than those of congeneric species. Shells of *fallax* also have a wide spire (Fig. 6.282). One possible explanation for the restricted distribution of *fallax* and perhaps also that of *gravida* may be that both species have direct development, as in species of *Zoila* Jousseaume, 1884 in Southern Australia (Wilson, 1985, 1998). At this point, however, studies of live animals and development of egg masses are necessary to confirm this hypothesis.

Morphometrics

Materials and Methods

Of the 1298 specimens studied, 379 specimens were measured for a suite of 61 shell characters (Appendix 6.1) for morphometric analyses. Data from the remaining shells vary from almost complete (nearly all characters) to the basic measurements usually reported in the literature: shell length (L), width (W), height (H), numbers of columellar (CT) and labral teeth (LT).

A multivariate, principal component analysis (PCA) was performed with the statistics package Minitab (v. 12.1) to reveal groupings or splits in sets of taxa (Quicke, 1993). A suite of 61 shell characters and 1298 shells representing all taxa in the *Cribrarula* complex from different locales in the Indo-Pacific was used in an initial PCA analysis, but because of the large number of data points, it was difficult to see trends or groupings clearly. Characters that contributed least to the variation were then removed, based on PCA scores, and a subsequent analysis performed. This unorthodox strategy was adopted because the PCA algorithm in Minitab removes records with any missing variables from the analysis. Therefore, using fewer characters, in most cases, resulted in more specimens included in the analysis (e.g. Figs. 6.260 versus 6.261, 6.262 versus 6.263). Additionally, by removing characters, which contributed the least to variation, reduced noise, and groupings became more distinct. Additional PCA analyses were performed focusing on groups of taxa (e.g. Figs. 6.272 and 6.273), as well as geographical analyses (e.g. Figs. 6.276 and 6.277).

Finally, boxplots of selected shell characters of continuous nature are presented to show the range of variation in each taxon (12 species and 6 subspecies of *cribraria*).

Results

Plots of 13 PCA analyses are shown (Figs. 6.267-6.279), with different numbers of characters and species, to illustrate graphically the range of variation and overlap between the groupings of points representing specimens. Boxplots of selected continuous characters are shown in Figs. 6.280-6.285 to represent graphically the range of variation and mean values in each taxon recognized in this study.

Discussion

PCA analyses using all 61 characters measured produced plots of PC1 and PC2 with fewer data points than when fewer characters were used. In most cases, a larger number of points made the grouping more recognizable; in others, there was more overlap between the groupings than with fewer points.

When all 61 characters and all specimens were used (Fig. 6.267), 265 points appeared in the PCA plot, and two large groups could be recognized: one with *cribraria*, *fallax* and *gravida*, and the other with all other species. Within the latter group, subgroups with some overlap could be distinguished: *esontropia* and *cribellum* were well separated from one another; *taitae* and *cumingii* were distinguishable, but close to one another, and overlapping slightly with *astaryi* and *gaskoini*. In the next PCA (Fig. 6.268), a smaller set of characters (19) was used, and 291 points appeared with a wider spread of the groupings, but still showing similar grouping as in Fig. 6.267.

The next seven PCA analyses (Figs. 6.269-6.273) were restricted to Pacific Ocean specimens (including those from the Malaysian province). When 17 characters were used (Fig. 6.269), 198 points appeared, and two major groups were clear: one with *cribraria* and *gravida* (the latter separated from the former), and the second large group formed by the remaining species that occur in the Pacific Ocean. The latter group could be subdivided into smaller, overlapping groups. The next PCA analysis (Fig. 6.270) used 6 characters, which resulted in 321 points that could again be divided into two large groups, but now with more overlap than in Fig. 6.269 because of the larger number of points.

Next, all specimens of *cribraria* were removed from the analysis, and using 7 characters, 96 points appeared (Fig. 6.271). Now, points representing shells of *gaskoinii* formed a group that although overlapped with *catholicorum*, was distinct from the others; *taitae* also overlapped partially with *gaskoini*. Points representing *garciai* were well separated from the rest, and those representing *cumingii* and *astaryi* showed some overlap with one another, but separated from the rest.

A new PCA analysis was done after removing all specimens of *gaskoinii* (Fig. 6.272), and using all 61 characters, 30 points appeared, showing distinct groupings for *catholicorum* and *taitae*, but with *astaryi* and *cumingii* still overlapping. Although the name *garciai* is included in the legend, the points representing this species did not appear because missing characters excluded the points (specimens) from the analysis.

One last PCA focusing on Pacific Ocean specimens included only specimens of *astaryi* and *cumingii*, and, using four characters and 27 points, the two species could be almost completely separated from one another. In this case, the number of columellar and labral teeth was responsible for most of the variation in the analysis.

The next two PCA analyses were performed using only specimens of *cribraria* from the Pacific Ocean and three characters, which resulted in 293 points. Fig. 6.274 shows the groupings of points representing three subspecies of *cribraria*: *cribraria cribraria*, *gaspardi* and *melwardi*. The most distinct grouping is that of *melwardi*, but it still partially overlaps with the other two subspecies, while *gaspardi* cannot be separated from *cribraria cribraria* using only the three characters employed. Fig. 6.275 shows the same PCA analysis as Fig. 6.274, but coding some of the specimens as recognized by Lorenz (2002). Again, *melwardi* is the most distinct grouping, but all the other taxa overlap with one another, and groupings are not distinct.

The next two PCA analyses used only specimens from the East Indian Ocean (including specimens from Sri Lanka), and four characters, which resulted in 105 points. Fig. 6.276 shows the groupings representing four taxa as recognized in this study. The most distinct group is that of points representing *fallax*, followed by *exmouthensis*, which overlaps partially with *ganteri*. Only two points identified as *cribraria cribraria* appeared overlapped with *exmouthensis*. Fig. 6.277 shows the same PCA analysis as Fig. 6.276, but now coding the specimens according the Lorenz (2002). The most distinct grouping is that of *fallax*, as in Fig. 6.276, followed by *rottnestensis*, while points representing *australiensis* and *exmouthensis exmouthensis* (*sensu* Lorenz, 2002) overlap almost completely with one another, and with most points representing *abrolhensis*. This figure suggests that *australiensis* and *exmouthensis exmouthensis* cannot be separated from one another using only the four characters (L, W/L, CT and SD) that are the most useful in separating taxa in the *Cribrarula* complex (the fifth character, LSS does not apply because none of the taxa considered in this analysis has labral spots).

The last two PCA analyses used only specimens from the West Indian Ocean and seven characters, which resulted in 112 points. Fig. 6.278 shows the groupings of points representing taxa recognized in this study; the most distinct grouping is that representing *esontropia*, followed by *cribellum*, which does not overlap with *esontropia* in this analysis, thus suggesting that two species are represented. The points representing *cribraria cribraria* and *comma* partially overlapped with one another. Fig. 6.279 shows the same PCA analysis as in Fig. 6.278, but now coding specimens according to Lorenz (2002). Again, the most distinct groupings are those of *esontropia esontropia* and *esontropia cribellum*, while Lorenz's *esontropia francescoi* could not be distinguished from *comma*, and *cribraria cribraria* (*sensu* Lorenz, 2002) overlapped partially with *comma*. A single point representing *pellisserpentis* overlapped with the group formed by *esontropia esontropia*.

Boxplots of selected continuous characters are shown in Figs. 6.280-6.285 to represent graphically the range of variation in each taxon recognized in this study. Other continuous characters were also studied, but for the sake of space, only six of them are presented. Other continuous characters not shown have patterns of variation similar to those presented: e.g., distributions of shell width and height are similar to shell length (Fig. 6.280): number of labrals similar to columellar teeth (Fig. 6.283), and number of marginal columellar spots similar to labral spots (Fig. 6.284).

The distribution of shell length (L) (Fig. 6.280) was the widest in *cribraria cribraria*, while *melwardi*, *taitae* and *fallax* were the taxa with the least variation (not including *gravida* and *pellisserpentis* each of which only one specimen was measured). The taxa with the longest length (L) were *fallax* and *gravida*, although a few specimens of *cribraria cribraria* were the largest measured; *cumingii* had the lowest median length (11.70 mm), but a few large specimens of *cumingii* (usually identified as *cumingii cleopatra* in the shell trade) increased the standard deviation (3.64).

Boxplots of the dorsal line angle (DLA) (Fig. 6.281) show that in most taxa in the *Cribrarula* complex distributions are similar, ranging between 20° and 45°, but in *catholicorum* and *gaskoini*, the DLA ranged from about 45° to 65°. This measurement shows the relative proportion between length of the right and the left lobes of the mantle. When the DLA is 90° (as in a few specimens of *cribraria cribraria* and *catholicorum*), both lobes of the mantle have approximately the same length, but in most specimens examined, the right lobe is smaller than the left lobe (i.e., DLA is less than 90°).

Boxplots of the spire diameter (SD) (Fig. 6.282) show that shells of *fallax* and *gravida* have the widest spires in the complex, which suggest that they may also have the widest protoconchs. Boxplots of columellar teeth (Fig. 6.283) (and labral teeth, not shown) clearly separate *cumingii* from all others, because of the large number of teeth. Shells of *astaryi* and *taitae* also have large number of teeth, followed by *fallax*, while shells of *melwardi*, *cribellum* and *esontropia* have the lowest CT and LT.

Boxplots of the number of labral spots (LSN) (Fig. 6.284) show that labral spots are rare on shells of *Cribrarula cribraria* subspecies, although most shells of *cribraria ganteri* have marginal spots. Shells of *fallax* and *gravida* also lack marginal spots, but shells of the remaining species in the complex have marginally spotted shells, with those of *garciai*, *gaskoini*, *esontropia*, *cumingii* and *astaryi* having the largest LSN.

Finally, boxplots of the number of dorsal spots (DS) (Fig. 6.285) can separate the shells of *gaskoinii* and *esontropia* from shells of the other species. Shells of *cumingii* and *gaspardi* have the lowest DS (not considering the albinistic or partially albinistic shells of some specimens of *melwardi*, which may have no dorsal spots).

The number of dorsal spots (DS) on the shells of taxa in the *Cribrarula* complex seems to represent a record of the dorsal papillae at the time the dorsal pattern was laid by the mantle. The dorsal line angle (DLA) provides a measurement of the relative sizes of the lobes of the mantle. Therefore, study of DS and DLA (at least in this complex) can reveal information about the animal that produced the shell (Moretzsohn, 2002a). Figures 6.282, 6.284 and 6.285 show that each taxon in the complex has a species-specific range of DLA, LSN and DS, respectively. These non-traditional characters can be useful in separating species, and suggest that cowrie shells may be more informative than generally believed.

Recent molecular data (Meyer, in press) suggest that some populations are sufficiently genetically distinct from other populations to be considered different subspecies. Lorenz (2002) used Meyer's molecular data to support some of his splitting decisions, describing five new subspecies in *Cribrarula* alone (and many more in other genera). However, because of: 1) the limited number of specimens examined that could be classified as Lorenz (2002)'s new taxa; 2) morphometric analyses of shell characters did not reveal distinct groupings coinciding with Lorenz (2002)'s new taxa; and 3) my molecular dataset (Moretzsohn, unpublished) is not so comprehensive as Meyer's, I prefer to be more conservative and do not recognize any of the five subspecies of *Cribrarula* proposed by Lorenz (2002). When more data (e.g. on the radulae, odontophore, photos of live specimens, Meyer's comprehensive molecular data, etc.) are available, some of those taxa may be recognized as valid.

Conclusions

Twelve species are recognized in the genus *Cribrarula* Strand, 1929 based on the study of a large number of specimens (1298) representing all taxa currently recognized in the genus, analysis of the radula and odontophore cartilage, multivariate analyses of shell characters, and review of the literature. The nominal species, *cribraria*, is the most widespread, common and morphologically variable. Consistent shell features distinguish six populations of *cribraria* as subspecies.

Table 6.1. History of the classification of taxa in the *Cribrarula* complex (*sensu* Lorenz and Hubert, 2000) and species that were considered allied by the Schilders in early studies; n/a denotes that the species was not described at the time.

Species	Author	Original genus	Sowerby 1870	Sch-Sch, 1971	Lorenz and Hubert, 2000
cribraria	Linnaeus, 1758	*Cypraea*	*Cypraea*	*Cribrarula*	*Cribrarula*
cumingii	Sowerby, 1832	*Cypraea*	*Cypraea*	*Cribrarula*	*Cribrarula*
esontropia	Duclos, 1833	*Cypraea*	*Cypraea*	*Cribrarula*	*Cribrarula*
gaskoinii	Reeve, 1846	*Cypraea*	*Cypraea*	*Cribrarula*	*Cribrarula*
cribellum	Gaskoin, 1849	*Cypraea*	*Cypraea*	*Cribrarula*	*Cribrarula*
fallax	Smith, 1881	*Cypraea*	n/a	*Cribrarula*	*Cribrarula*
catholicorum	Sch-Sch, 1938	*Cribraria*	n/a	*Cribrarula*	*Cribrarula*
astaryi	FA Schilder, 1971	*Cribrarula*	n/a	n/a	*Cribrarula*
taitae	Burgess, 1993	*Cypraea*	n/a	n/a	*Cribrarula*
pellisserpentis	Lorenz, 1999	*Cribrarula*	n/a	n/a	*Cribrarula*
garciai	Lorenz and Raines, 2001	*Cribrarula*	n/a	n/a	n/a
gravida	Moretzsohn, 2002	*Cribrarula*	n/a	n/a	n/a

Table 6.2. Schilders' formulae from the literature, calculated from specimens measured by Kay (unpublished) and in this study

Taxon	Sch-Sch 1938-39	Schilder M, 1967	Kay's data	Lorenz, 2002	This study
astaryi	*	*	16.59.22.21	n/a	17.59.23.25
catholicorum	14.63.21.20	14.63.17.15	15.63.17.11	n/a	15.63.19.20
cribellum	14.56.18.16	14.56.14.14	14.58.15.15	17.56.15.15	15.57.16.17
cribraria **	23.57.19.18	21.58.18.17	23.59.16.16	n/a	22.59.17.18
crib. cribraria	n/a	n/a	n/a	22.58.16.16	22.58.18.19
crib. comma	24.61.19.16	n/a	n/a	22.60.17.18	20.62.17.17
crib. exmouthensis	n/a	n/a	n/a	28.57.16.16 ***	23.61.17.16
crib. ganteri	*	*	*	n/a	24.60.17.19
crib. gaspardi	*	*	*	n/a	19.57.18.20
crib. melwardi	22.57.20.19	n/a	n/a	22.64.15.15	22.63.17.17
cumingii	11.54.40.34	11.56.27.23	13.56.29.27	n/a	13.57.33.32
esontropia	26.61.17.16	24.61.17.16	24.62.15.15	18.63.15.16	23.62.16.18
fallax	30.60.17.17	n/a	29.64.18.18	31.59.20.21	31.59.20.22
garciai	*	*	*	n/a	24.65.25.24
gaskoinii	n/a	20.63.20.18	17.64.18.18	n/a	17.64.20.20
gravida	*	*	*	n/a	35.63.19.18
pellisserpentis	*	*	*	n/a	19.67.17.19
taitae	*	*	n/a	n/a	13.58.22.23

* Taxon not described at the time; ** Data pooled for all subspecies of *C. cribraria*; *** Lorenz 2002 considers *exmouthensis* a different shell than recognized in this study (see discussion under *exmouthensis*).

Table 6.3. Schilders' formula versus the new formula calculated from specimens measured in this study.

Taxon	Schilders' formula	New formula
astaryi	17.59.23.25	17.2/ 58.9/ 25/ 2.4/ 2.1
catholicorum	15.63.19.20	14.9/ 62.7/ 20/ 2.2/ 1.0
cribellum	15.57.16.17	14.7/ 56.5/ 17/ 2.2/ 1.3
cribraria *	22.59.17.18	22.2/ 59.2/ 18/ 3.2/ 0.1
crib. cribraria	22.58.18.19	22.5/ 58.2/ 19/ 3.3/ 0.1
crib. comma	20.62.17.17	19.6/ 62.0/ 17/ 3.0/ 0.1
crib. exmouthensis	23.61.17.16	23.0/ 60.6/ 16/ 3.3/ 0
crib. ganteri	24.60.17.19	24.5/ 60.3/ 19/ 3.2/ 0.7
crib. gaspardi	19.57.18.20	19.3/ 56.8/ 20/ 2.5/ 0
crib. melwardi	22.63.17.17	21.7/ 63.2/ 17/ 3.4/ 0
cumingii	13.57.33.32	12.9/ 56.8/ 32/ 1.9/ 1.6
esontropia	23.62.16.18	23.2/ 62.0/ 18/ 3.2/ 2.1
fallax	31.59.20.22	31.3/ 59.4/ 22/ 4.5/ 0
garciai **	24.65.25.24	24.4/ 65.0/ 24/ 3.4/ 3.0
gaskoinii	17.64.20.20	17.3/ 63.2/ 20/ 2.6/ 1.3
gravida	35.63.19.18	35.2/ 62.9/ 18/ 6.2/ 0
pellisserpentis	19.67.17.19	18.6/ 67.5/ 19/ 3.6/ 2.0
taitae	13.58.22.23	13.1/ 57.8/ 23/ 1.7/ 1.1

* Data pooled for all subspecies of *C. cribraria*; ** Lorenz and Raines, 2001

Table 6.4. Comparison of shell characters in subspecies of *C. cribraria*, showing average figures or most common conditions.

	crib. comma	***crib. cribraria***	***crib. exmouth.***	***crib. ganteri***	***crib. gaspardi***	***crib. melwardi***
Shell shape	Ovate-pyriform	Ovate, not inflated	Pyriform-rhomboidal	Ovate	Oval rostrate	Ovate callous
Shell length (Ave/range)	19.6/ 11.5-28.6	22.5/ 10.0-40.8	23.0/ 17.6-36.4	24.5/ 18.0-29.4	19.3/ 12.0-29.6	21.7/ 18.2-25.0
Marginal calluses	Slightly callused	Some shells callused	Some shells callused	Some shells callused	Not callused	Very callused
Marginal spots (Color/Ave.)	Faint, a few	No spots	No spots	Black-brown/ 3.1	No spots	No spots
Columellar teeth (Ave./ thickness)	16.2/ fine	18.2/ fine	15.7/ medium-fine	23.5/ fine	18.6/ very fine	16.1/ medium-fine
Labral teeth (Ave/ thickness.)	15.8/ medium	17.2/ medium	16.2/ medium	24.5/ medium	16.5/ medium-fine	16.3/ medium
Dorsal coat color	Dark brown	Orange brown to brown	Brown to dark brown	Brown	Light brown	White to light brown
Shell extremities	Not rostrate	Slightly rostrate	Slightly rostrate	Slightly rostrate	Rostrate	Blunt

Table 6.4. (Continued) Comparison of shell characters in subspecies of *C. cribraria*

	crib. comma	***crib. cribraria***	***crib. exmouth.***	***crib. ganteri***	***crib. gaspardi***	***crib. melwardi***
Fossula (inclination/ concavity)	Steep, flat	Steep, concave	Abrupt, flat	Sloped, concave	Steep, concave	Steep, concave
Spire diameter (Ave/ umbilic.)	3.0/ slightly projecting	2.8/ umbilicated	3.3/ umbilicated	3.2/ umbilicate	2.5/ flat	3.4/ umbilicated
Dorsal flare (anterior extremity)	Flared	Flared	Most shells flared	Convex	Flared	Convex in most shells
No. Dorsal Spots (DS) (Ave./range)	54/ 44-103	50/ 25-120	42/ 35-77	51/ 30-70	36/ 15-90	28/ 0-90
DS shape/ min.-max. diameter	Elliptical/ 1.0-1.9	Round/ 1.2-2.2	Elliptical/ 1.1-2.3	Round/ 1.1-2.3	Round/ 1.4-2.4	Elliptical/ 0.7-1.2
DS density/ sharpness	Medium-high/ some unclear	Medium/ sharp	Low to high/not sharp	Medium/ sharp	Medium/ sharp	Medium/ some incomplete
Schilders formula	20.62.17.17	22.58.18.19	23.61.17.16	24.60.17.19	19.57.18.20	22.63.17.17
New formula	19.6/ 62.0/ 17/ 3.0/ 0.1	22.5/ 58.2/ 19/ 3.3/ 0.1	23.0/ 60.6/ 16/ 3.3/ 0	24.5/ 60.3/ 19/ 3.2/ 0.7	19.3/ 56.8/ 20/ 2.5/ 0	21.7/ 63.2/ 17/ 3.4/ 0

Table 6.5. Comparison of shell characters among species of *Cribrarula*, showing average figures or most common conditions.

	astaryi	*catholicorum*	*cribellum*	*cribraria*	*cumingii*	*esontropia*
Shell shape	Pyriform	Ovate	Cylindrical	Ovate, not inflated	Ovate elongated	Ovate to rhomboidal
Shell length (Ave/range)	17.2/ 15.6-20.5	14.9/ 12.0-20.0	14.7/ 11.5-19.3	22.2/ 10.0-40.8	12.9/ 8.1-24.6	23.2/ 14.1-32.6
Marginal calluses	Most shells not callused	Medium calluses	Not callused	Some shells callused	Most shells not callused	Very callused
Marginal spots (Color/Ave.)	Black/ 21	Light brown/ 5	Light brown/ 9	No spots	Black/ 17	Light brown/ 20
Columellar teeth (Ave./ thickness)	21.8/ very fine	16.7/ fine	14.6/ fine	18.2/ fine	24.6/ very fine	17.2/ fine-medium
Labral teeth (Ave/ thickness.)	20.3/ fine	15.9/ medium-fine	14.0/ medium-fine	16.8/ medium	25.6/ very fine	16.1/ medium-thick
Dorsal coat color	Orange-light brown	Caramel	Light brown	Orange brown to brown	Dark yellow-light brown	Light to medium brown
Shell extremities	Rostrate anteriorly	Blunt extremities	Slightly rostrate anteriorly	Slightly rostrate	Rostrate to very rostrate	Slightly rostrate

Table 6.5. (Continued) Comparison of shell characters among species of *Cribrarula.*

	astaryi	*catholicorum*	*cribellum*	*cribraria*	*cumingii*	*esontropia*
Fossula (inclination/ concavity)	Steep, grooved	Steep, concave	Inflected, flat	Steep, concave	Steep-abrupt, grooved	Steep-abrupt, flat
Spire diameter (Ave/ umbilic.)	2.4/ flat	2.2/ projecting	2.2/ slightly projecting	2.9/ some umbilicate	1.9/ slightly projecting	3.2/ flat
Dorsal flare (anterior extremity)	Not flared	Convex	Not flared	Flared	Not flared	Some shells flared
No. Dorsal Spots (DS)(Ave./range)	63/ 48-80	75/ 53-105	63/ 48-100	61/ 0-120	50/ 33-80	100/ 63-190
DS shape/min.-max. diameter	Round/ 0.8-1.6	Round/ 0.8-1.3	Round-elliptical/ 0.8-1.5	Round-elliptical/1.1-2.1	Round/ 0.6-1.2	Elliptical/ 1.0-2.1
DS density/sharpness	Low-medium/ sharp	Medium/ sharp	Medium-high/ sharp	Medium/ sharp	Low-medium/ sharp	High/sharp
Schilders' formula	17.59.23.25	15.63.19.20	15.57.16.17	22.58.18.19	13.57.33.32	23.62.16.18
New formula	17.2/ 58.9/ 25/ 2.4/ 2.1	14.9/ 62.7/ 20/ 2.2/ 1.0	14.7/ 56.5/ 17/ 2.2/ 1.3	22.2/ 59.2/ 18/ 3.2/ 0.1	12.9/ 56.8/ 32/ 1.9/ 1.6	23.2/ 62.0/ 18/ 3.2/ 2.1

Table 6.5. (Continued) Comparison of shell characters among species of *Cribrarula.*

	garciai	*gaskoinii*	*gravida*	*pellisserpentis*	*taitae*	*fallax*
Shell shape	Ovate	Ovate callous	Pyriform, inflated	Ovate callous	Pyriform-ovate	Pyriform, somewhat inflated
Shell length (Ave/range)	24.4/ 22.3-26.4	17.3/ 9.4-30	35.2	18.6	13.1/ 11.2-16.2	31.3/ 28.8-33.4
Marginal calluses	Very callused	Some shells very callused	Callused	Callused	Not callused	Somewhat callused
Marginal spots (Color/Ave.)	Brown/ 27	Brown/ 27	No spots	Brown/ 20	Light brown/12	No spots
Columellar teeth (Ave./ thickness)	23.5/ fine	17.5/ fine	20/ medium	17/ fine	18.9/ very fine	23.6/ fine
Labral teeth (Ave/ thickness.)	24.5/ medium	17.7/ medium-fine	21/ thick	16/ medium	18.0/ fine	21.9/ medium
Dorsal coat color	Orange brown	Orange brown	Light brown	Brown	Light brown	Light to dark yellow
Shell extremities	Blunt	Slightly rostrate	Rostrate	Blunt	Rostrate	Rostrate

Table 6.5. (Continued) Comparison of shell characters among species of *Cribrarula*.

	fallax	*garciai*	*gaskoinii*	*gravida*	*pellisserpentis*	*taitae*
Fossula (inclination/ concavity)	Sloped, concave	Sloped, concave?	Steep, concave	Sloped, concave	Steep, concave	Sloped, concave
Spire diameter (Ave/ umbilic.)	4.6/ umbilicate	3.4/ callus	2.7/ umbilicated	6.2/ flat	3.6/ projecting	1.8/ slightly projecting
Dorsal flare (anterior extremity)	Not flared	Convex	Flared	Flared	Not flared	Not flared
No. Dorsal Spots (DS) (Ave./range)	64/ 35-75	51/ 47-55	84/ 46-173	88	40	41/ 33-56
DS shape/min.-max. diameter	Elliptical/ 1.3-2.4	Round/ 0.6-1.9	Round/0.6-1.1	Elliptical/ 2.8-3.5	Irregular/ 1.4-2.4	Round-elliptical/ 0.6-1.1
DS density/sharpness	Low-medium/not sharp	Medium/ sharp	Medium-high/ sharp	High /not sharp	High/ sharp	Low-medium/ sharp
Schilders' formula	31.59.20.22	24.65.25.24	17.64.20.20	35.63.19.18	19.67.17.19	13.58.22.23
New formula	31.3/ 59.4/ 22/ 4.6/ 0	24.4/ 65.0/ 24/ 3.4/ 3.0	17.3/ 63.2/ 20/ 2.6/ 1.3	35.2/ 62.9/ 18/ 6.2/ 0	18.6/ 67.5/ 19/ 3.6/ 2.0	13.1/ 57.8/ 23/ 1.7/ 1.1

Table 6.6. Odontophore characteristics per taxon (Moretzsohn, in review A) [Chapter 3]: odontophore length (OL); odontophore thickness at center (OT); OT/OL ratio (percent); ventral arch/odontophore height (VA/OH) (percent); shell length (L), OL/L ratio (percent); color in light microscopy, and number of LM and SEM photos. Odontophores of all taxa of *Cribrarula* examined had similar spongy texture (medium of Moretzsohn, in review A).

Taxon	OL (mm)	OT (mm)	OT/OL (%)	VA/OH (%)	L (mm)	OL/L (%)	color	Photo LM/ SEM
astaryi	1.40	0.42	29.6	34.6	20.45	6.8	white	230/ 243
catholicorum	1.52	0.62	40.7	27.0	19.30	7.8	white	228/ 241
cribellum	1.13	0.33	29.2	25.9	15.50	7.3	white	240/ 253
crib. cribraria	1.04	0.43	41.4	30.3	21.30	4.9	white	229/ 242
crib. comma	1.43	0.41	28.8	25.1	25.50	5.6	white	234/ 247
crib. comma "abaliena"	1.20	0.35	29.2	23.1	14.85	8.1	white	259
crib. exmouthensis	1.33	0.42	31.6	16.1	22.50	5.9	yellow tint	231/ 244
crib. melwardi	1.12	0.29	26.3	30.0	18.30	6.1	faint yellow	233/ 246
cumingii	0.74	0.19	26.1	30.7	11.50	6.4	white	238/ 251
esontropia	1.28	0.41	31.8	23.5	19.90	6.4	orange	239/ 252
fallax	1.80	0.56	31.3	23.5	31.00	5.8	white	232/ 245
gaskoinii (female)	1.64	0.52	31.6	24.3	20.70	7.9	white	235/ 248
gaskoinii (male)	0.97	0.26	27.0	33.2	12.70	7.6	white	237/ 250
gravida	4.0 *	n/a	n/a	n/a	35.15	11 *	beige	n/a
taitae	0.87	0.26	29.6	25.0	13.00	6.7	white	236/ 249

* estimated; n/a = not available.

Figure Captions

Figures 6.1 to 6.3. *Cribrarula gaskoinii* (Reeve, 1846) from Oahu, Hawaii. Photo of live specimen in a tank in columellar side view, showing the red mantle partially exposed and the numerous fingerlike red verrucose papillae, including a few white ones (*Courtesy of Wes Thorsson, 1998*). **6.2 and 6.3.** *Cribrarula cribraria gaspardi* Biraghi and Nicolay, 1993, photos of live specimens *in loco* in Kwajalein, Marshall Is., showing the bright orange to red color of the mantle. The dorsal spots on the shell can be seen through the mantle. **6.2.** Individuals in species of *Cribrarula* are often found on or near sponges similar in coloration to their mantle; and **6.3.** Specimens with the mantle down (left) and fully extended (right). (*Courtesy of Scott Johnson, 2002*).

Figure 6.4. Distribution map of the twelve species in *Cribrarula*, based on the localities of the specimens studied here, and on the published distribution (Schilder and Schilder, 1971; Burgess, 1985; Lorenz and Hubert, 2000; Lorenz and Raines, 2001; Moretzsohn 2002b; and references in the systematic part of this review).

Figure 6.5. Graphic representation of the "cowrie classification pendulum" at the generic level, swinging between the opinions of lumpers (left) and splitters (right) regarding the number of living genera in the Cypraeidae. The figures in bold represent the number of genera recognized by each author in a revision, monograph or taxonomic work (*based on the works cited in the figure*).

Figures 6.6 and 6.7. Plots of the first two components (PC1 and PC2) of PCA analyses, based on specimens examined in this study, using figures from the: **6.6)** "New Cowrie Formula" (characters: L; W/L; CT, SD; and LSS) (Moretzsohn, unpublished); and **6.7)** Schilders' Formula (characters: L; W/L; LT and CT) (Schilder and Schilder, 1938-1939).

Figures 6.8 to 6.19. Shells of *Cribrarula cribraria cribraria* (Linnaeus, 1758). **6.8 to 6.13.** Specimen from Okinawa, Japan (USNM 670743); **6.14 to 6.19.** Specimen (usually identified as "*zadela*") from Cebu, Philippines (USNM 773378). Bar scale = 10 mm. In these and all following shell figures, each shell is illustrated in six views, in this order: dorsal, labral side, ventral (or apertural), columellar side, anterior extremity (top), and posterior extremity view (bottom). **Figure 6.20.** Map of distribution and records of *C. cribraria cribraria.* The number of specimens examined from each location is given next to (●). The bold line represents the distribution of the subspecies according to Lorenz and Hubert (2000).

Figures 6.21 to 6.32. Shells of *Cribrarula cribraria comma* (Perry, 1811). **6.21 to 6.26.** Specimen from Mauritius (FMNH 63255); **6.27 to 6.32.** Specimen from the Cape region, South Africa (DMNH 155472). Bar scale = 10 mm. **Figure 6.33.** Map of distribution and records of *C. cribraria comma.* The number of specimens examined from each location is given next to (●). The bold line represents the distribution of the subspecies according to Lorenz and Hubert (2000).

Figures 6.34 to 6.45. Shells of *Cribrarula cribraria exmouthensis* (Melvill, 1888). **6.34 to 6.39.** Specimen from Broome, Western Australia (DMNH 196958); **6.40 to 6.45.** Specimen from the Exmouth Gulf, Western Australia (DMNH 196197). Bar scale = 10 mm. **Figure 6.46.** Map of distribution and records of *C. cribraria exmouthensis.* The number of specimens examined from each location is given next to (●). The symbol (✪) represents the type locality, and the bold line the distribution of the subspecies according to Lorenz and Hubert (2000).

Figures 6.47 to 6.58. Shells of *Cribrarula cribraria melwardi* (Iredale, 1930). **6.47 to 6.52.** Holotype of *Nivigena melwardi* Iredale, 1930, from North West Island, Capricorn Group, Queensland (AMS C. 57743); **6.53 to 6.58.** Specimen from Fairfax Is., Bunker Group, Queensland (AMS C. 363556). Bar scale = 10 mm. **Figure 6.59.** Map of distribution and records of *C. cribraria melwardi.* The number of specimens examined from each location is given next to (●). The symbol (✪) represents the type locality, and the bold line the distribution of the subspecies according to Lorenz and Hubert (2000).

Figures 6.60 to 6.65. Shell of *Cribrarula cribraria gaspardi* Biraghi and Nicolay, 1993 from Kwajalein, Marshall Islands (DMNH 196199); **6.66 to 6.71.** Specimen from Truk, Micronesia (DAN, no catalog number), tentatively identified as *C. cribraria gaspardi.* Bar scale = 10 mm. **Figure 6.72.** Map of distribution and records of *C. cribraria gaspardi.* The number of specimens examined from each location is given next to (●).

The symbol (✪) represents the type locality, (▲) specimens tentatively identified as *gaspardi* (Figs. **6.**66 to **6.**71), and the bold line the distribution of the subspecies according to Lorenz and Hubert (2000).

Figures 6.73 to 6.84. Shells of *Cribrarula cribraria ganteri* Lorenz, 1999. **6.73 to-78.** Typical specimen from Sri Lanka (FMNH 85809); **6.79 to 6.84.** Specimen from Sri Lanka with strong marginal calluses (AMNH 292276). Bar scale = 10 mm. **Figure 6.85.** Map of distribution and records of *C. cribraria ganteri.* The number of specimens examined is given next to (✪), which represents the type locality. The bold line represents the distribution of the subspecies according to Lorenz and Hubert (2000).

Figures 6.86 to 6.97. Shells of *Cribrarula cumingii* (Sowerby II, 1832). **6.86 to 6.91.** Specimen from Raiatea, Society Islands (USMN 888207); **6.92 to 6.97.** Large specimen from Tahiti, Society Islands, usually identified as *C. cumingii cleopatra* (Schilder and Schilder, 1938) (DMNH 196210). Bar scale = 10 mm. **Figure 6.98.** Map of distribution and records of *C. cumingii.* The number of specimens examined from each location is given next to (●). The sign (▲) represents a questionable identification or record, and the bold line the distribution of the species according to Lorenz and Hubert (2000).

Figures 6.99 to 6.110. Shells of *Cribrarula esontropia* (Duclos, 1833). **6.99 to 6.104.** (FMNH 85773) from Mauritius; **6.105 to 6.110.** (AMS C. 84792) from Mauritius. Bar scale = 10 mm. **Figure 6.111.** Map of distribution and records of *C. esontropia.* The number of specimens examined from each location is given next to (●). The symbol (✪) represents the type locality, and the bold line the distribution of the species according to Lorenz and Hubert (2000).

Figures 6.112 to 6.123. Shells of *Cribrarula gaskoinii* (Reeve, 1846). **6.112 to 6.117.** Small and elongated shell, typical of male specimens (FM 912) from Oahu, Hawaii; **6.118 to 6.123.** Large and inflated shell, typical of female specimens (CMB 8-37) from Oahu, Hawaii. Bar scale = 10 mm. **Figure 6.124.** Map of distribution and records of *C. gaskoinii.* The number of specimens examined from each location is given next to (●). The bold line represents the distribution of the species according to Lorenz and Hubert (2000).

Figures 6.125 to 6.136. Shells of *Cribrarula cribellum* (Gaskoin, 1849). **6.125 to 6.130.** (USNM 866186) from Mauritius; **6.131 to 6.136.** (DMNH 196190) from Mauritius. Bar scale = 10 mm. **Figure 6.137.** Map of distribution and records of *C. cribellum.* The number of specimens examined from each location is given next to (●). The symbol (✪) represents the type locality, and the bold line the distribution of the species according to Lorenz and Hubert (2000).

Figures 6.138 to 6.149. Shells of *Cribrarula fallax* (Smith, 1881) from Denmark, Australia. **6.138 to 6.143.** Specimen from Parry's Beach, Denmark (AMS C. 313993); **6.144 to 6.149.** Paratype of *Cribraria haddnightae* Trenberth, 1973 (AMNH 268523) (shell “photographed” with a flatbed scanner (Moretzsohn, in press B). Bar scale = 10 mm. **Figure 6.150.** Map of distribution and records of *C. fallax.* The number of specimens examined from each location is given next to (●). The bold line represents the distribution of the species according to Lorenz and Hubert (2000).

Figures 6.151 to 6.162. Shells of *Cribrarula catholicorum* (Schilder and Schilder, 1938). **6.151 to 6.156.** Specimen from Guadalcanal, Solomon Is. (DMNH 196108); **6.157 to 6.162.** Specimen from Nuku'alofa, Tonga (USMN 773694). Bar scale = 10 mm. **Figure 6.163.** Map of distribution and records of *C. catholicorum.* The number of specimens examined from each location is given next to (●). The symbol (✪) represents the type locality, and the bold line the distribution of the species according to Lorenz and Hubert (2000).

Figures 6.164 to 6.175. Shells of *Cribrarula astaryi* Schilder, 1971. **6.164 to 6.169.** Paratype of *Cribrarula astaryi* Schilder, 1971 from Tahuata Is., Marquesas (USNM 862332); **6.170 to 6.175.** Homeotype from Atuona, Marquesas (CMB NL-7). Bar scale = 10 mm. **Figure 6.176.** Map of distribution and records of *C. astaryi.* The number of specimens examined from each location is given next to (●). The symbol (✪) represents the type locality, (▲) a record with uncertain identity, and the bold line the distribution of the species according to Lorenz and Hubert (2000).

Figures 6.177 to 6.188. Shells of *Cribrarula taitae* (Burgess, 1993). **6.177 to 6.182.** Holotype of *Cypraea taitae* Burgess, 1993 from American Samoa (BPBM 9966). **6.183 to 6.188.** Specimen from Ua Pou, Marquesas (USNM 798522). Bar scale = 10 mm. **Figure 6.189.** Map of distribution and records of *C. taitae.* The number of specimens examined from each location is given next to (●). The symbol (✪) represents the type locality, and the bold line the distribution of the species according to Lorenz and Hubert (2000).

Figures 6.190 to 6.195. Shell of *Cribrarula pellisserpentis* Lorenz, 1999 from Faux Lap, Madagascar (DAN, no catalog number). Bar scale = 10 mm. **Figure 6.196.** Map of distribution and records of *C. pellisserpentis.* The number of specimens examined from each location is given next to (✪), which represents the type locality, and the bold line the distribution of the species according to Lorenz and Hubert (2000).

Figure 6.197. Map of distribution and records of *Cribrarula garciai* Lorenz and Raines, 2001. The symbol (✪) represents the type locality, (▲) a possible record reported by Aurora Richards in *La Conchiglia* 226-227 (1988), and the bold line the distribution of the species according to Lorenz and Raines, 2001.

Figures 6.198 to 6.203. Holotype of *Cribrarula gravida* Moretzsohn 2002, from Smoky Cape, New South Wales, Australia (AMS C. 91000). Bar scale = 10 mm. **Figure 6.204.**

Map of distribution of *C. gravida*. The symbol (✪) represents the type locality, Smoky Cape, New South Wales, Australia.

Figure 6.205. Schematic drawing of a cowrie shell in ventral view, showing some of the shell characters examined. CS –columellar spots; CSD – columellar spot diameter; CT – columellar tooth count; LT – labral tooth count; LS – labral spots; LSD – labral spot diameter; gap – gap between TR and anterior CT; TR – terminal ridge. **Figure 6.206.** Shell of *C. gaskoinii* in dorsal view, showing additional shell characters. DL – dorsal line; DLT – dorsal line thickness; DS –dorsal spots; DSmax – maximum DS diameter; DSmin – minimum DS diameter; L – shell length; LMC – labral marginal callus; MSu – marginal sulcus (not well defined in the shell shown); SD – spire diameter; W – shell width. **Figure 6.207.** Shell shape (half of the examples are of shells from other genera): 0) cylindrical; 1) ovate; 2) pyriform; 3) rhomboidal; 4) rostrate; and 5) globular. **Figure 6.208.** Dorsal coat color: 0) white/ivory; 1) beige; 2) dark yellow; 3) caramel; 4) orange brown; 5) brown/chocolate; 6) melanistic, and 7) other (not shown). **Figure 6.209.** Dorsal line angle (DLA). Shells seen at anterior extremity view. The dorsal line angle is defined as the angle formed by the general direction of the dorsal line and the plane of the base of the shell, using the anterior canal as the vertex of the angle.

Figures 6.210 to 6.218. SEM of radulae half-row. **6.210.** *Cribrarula taitae* (USNM 798522) from the Marquesas; **6.211.** *C. cumingii* (USNM 888207) from Raiatea, Society Islands; **6.212.** *C. astaryi* (DMNH 196056) from the Marquesas.; **6.213.** *C. gaskoinii*

(BPBM 241414), female from Oahu, Hawaii; **6.214.** *C. esontropia* (AMS C. 364815) from Mauritius; **6.215.** *C. cribellum* (USNM 866186) from Mauritius; **6.216.** *C. gravida* (AMS C. 91000) from New South Wales, Australia; **6.217.** *C. catholicorum* (USNM 773800) from the Solomon Islands; **6.218.** *C. gaskoinii* (FM 912-1) male from Maui, Hawaii. Scale bar in Figs 6.210 to 6.218 is 100 μm.

Figures 6.219 to 6.227. SEM of radulae half-row. **6.219.** *Cribrarula crib. cribraria* (ANSP 286678) from Phuket, Thailand.; **6.220.** *C. crib. cribraria* (FM-08) from Guam; **6.221.** *C. crib. cribraria* (ANSP 271247) melanistic specimen from New Caledonia.; **6.222.** *C. crib. cribraria* (AMNH 292279) from Okinawa, Japan; **6.223.** *C. crib. cribraria* (USNM 773496) from Fiji; **6.224.** *C. crib. gaspardi* (DMNH 196199) from Kwajalein, Marshall Is.; **6.225.** *C. crib. melwardi* (DMNH 31496) from Queensland, Australia; **6.226.** *C. crib. exmouthensis* (DMNH 196958) from Broome, Australia; **6.227.** *C. crib. comma* (AMNH 292286) from Mozambique. Scale bar in Figs 219-227 is 100 μm.

Figures 6.228 to 6.240. Odontophore cartilages in light microscopy. Orientation: dorsal is up, anterior to the right. Scale bar is 1.0 mm (odontophore length in mm). **6.228.** *Cribrarula catholicorum* (1.52 mm); **6.229.** *C. crib. cribraria* (1.11 mm); **6.230.** *C. astaryi* (1.40 mm); **6.231.** *C. crib. exmouthensis* (1.33 mm); **6.232.** *C. fallax* (1.80 mm); **6.233.** *C. crib. melwardi* (1.12 mm); **6.234.** *C. crib. comma* (1.43 mm); **6.235.** *C. gaskoinii* - female (1.64 mm); **6.236.** *C. taitae* (0.87 mm); **6.237.** *C. gaskoinii* - male

(0.97 mm); **6.238.** *C. cumingii* (0.74 mm); **6.239.** *C. esontropia* (1.75); **6.240.** *C. cribellum* (1.13 mm).

Figures 6.241-253. Odontophore cartilages in SEM. Orientation: dorsal is up, anterior is to the right. Scale bar is 1.0 mm (odontophore length in mm). **6.241.** *Cribrarula catholicorum* (1.52 mm); **6.242.** *C. crib. cribraria* (1.11 mm); **6.243.** *C. astaryi* (1.40 mm); **6.244.** *C. crib. exmouthensis* (1.33 mm); **6.245.** *C. fallax* (1.80 mm); **6.246.** *C. crib. melwardi* (1.12 mm); **6.247.** *C. crib. comma* (1.43 mm); **6.248.** *C. gaskoinii* - female (1.64 mm); **6.249.** *C. taitae* (0.87 mm); **6.250.** *C. gaskoinii* - male (0.97 mm); **6.251.** *C. cumingii* (0.74 mm); **6.252.** *C. esontropia* (1.75 mm); **6.253.** *C. cribellum* (1.13 mm).

Figures 6.254 to 6.257. Holotype of *Cribraria cribraria zadela* Iredale, 1939 from Queensland, Australia (junior synonym of *Cribrarula cribraria cribraria* (Linnaeus, 1758)) (AMS C. 60554). Scale bar 10 mm. **Figures 6.258 and 6.259.** *Cribrarula cribraria comma* "*abaliena*" (HBR, no catalog number). **6.258.** SEM of half row of radula (scale bar 100 μm); **6.259.** odontophore in light microscopy (scale bar 1.0 mm). **Figures 6.260 to 6.267.** Syntype of *Cypraea fischeri* Vayssière, 1910 (= *Cribrarula gaskoinii* (Reeve, 1846)), at the MNHN. **6.260 to 6.266.** Six views of the shells of the syntype, 10.90 mm in length (10.9/ 63.7/ 20.6/ 2.5/1), scale bar 10 mm. **6.266.** Specimen label indicating it is the type specimen.

Figures 6.267 and 6.268. PCA plot of all species of *Cribrarula* using: **6.267.** 61 characters (see list in Appendix 6.1) and 265 shells, and **6.268.** 19 characters (L, W/L, CT, SD, LSD, A-Rostr, Fs-Wide, Lab-Up, CSD, LS-col, Dk-Ring, Lab-MC, D-Band, LS-N, DS, U, DL-angl, Keel, and LS-Bas) and 291 shells. Notice the increase in the number of specimens of some taxa, such as *catholicorum*, as well in the percentage of variation explained by each principal component as the number of characters is reduced.

Figures 6.269 and 6.270. PCA plot of Pacific (including the Malayan province) species of *Cribrarula*, using: **6.269.** 17 characters (L, W/L, CT, SD, LSD, W, H, LT, Fs-Wide, CSD, Dk-Ring, Lab-MC, D-Band, LSN, D-Flare, DL-thick, and CT-Bas) and 198 shells, and **6.270.** 6 characters (L, W/L, CT, SD, LSD, and LSN) and 321 shells.

Figures 6.271 and 6.272. PCA plot of Pacific species of *Cribrarula*. **6.271.** Same data used for Fig. 6.263 minus all specimens of *cribraria*, using 7 characters (L, W/L, CT, SD, LSD, LSN, and Dk-Ring) and 96 shells. **6.272.** Same data as Fig. 6.264 minus all specimens of *gaskoini*, using 61 characters (Appendix 6.1), and 30 shells.

Figure 6.273. PCA plot of specimens of *astaryi* and *cumingii* using four characters (CT, LT*, SD and LSN) and 27 shells.

Figures 6.274 and 6.275. PCA plots Pacific Ocean subspecies of *cribraria* using 3 characters (L, W/L, and SD) and 293 shells. **6.274.** Taxa recognized in this study, and

6.275. taxa recognized by Lorenz, 2002. Note that shells of *melwardi* can be separated from other shells even without using shell color as a character.

Figures 6.276 and 6.277. PCA plots of East Indian Ocean taxa in the *Cribrarula* complex using 4 characters (L, W/L, CT and SD) and 105 shells. **6.276.** Taxa recognized in this study, and **6.277.** taxa recognized by Lorenz, 2002.

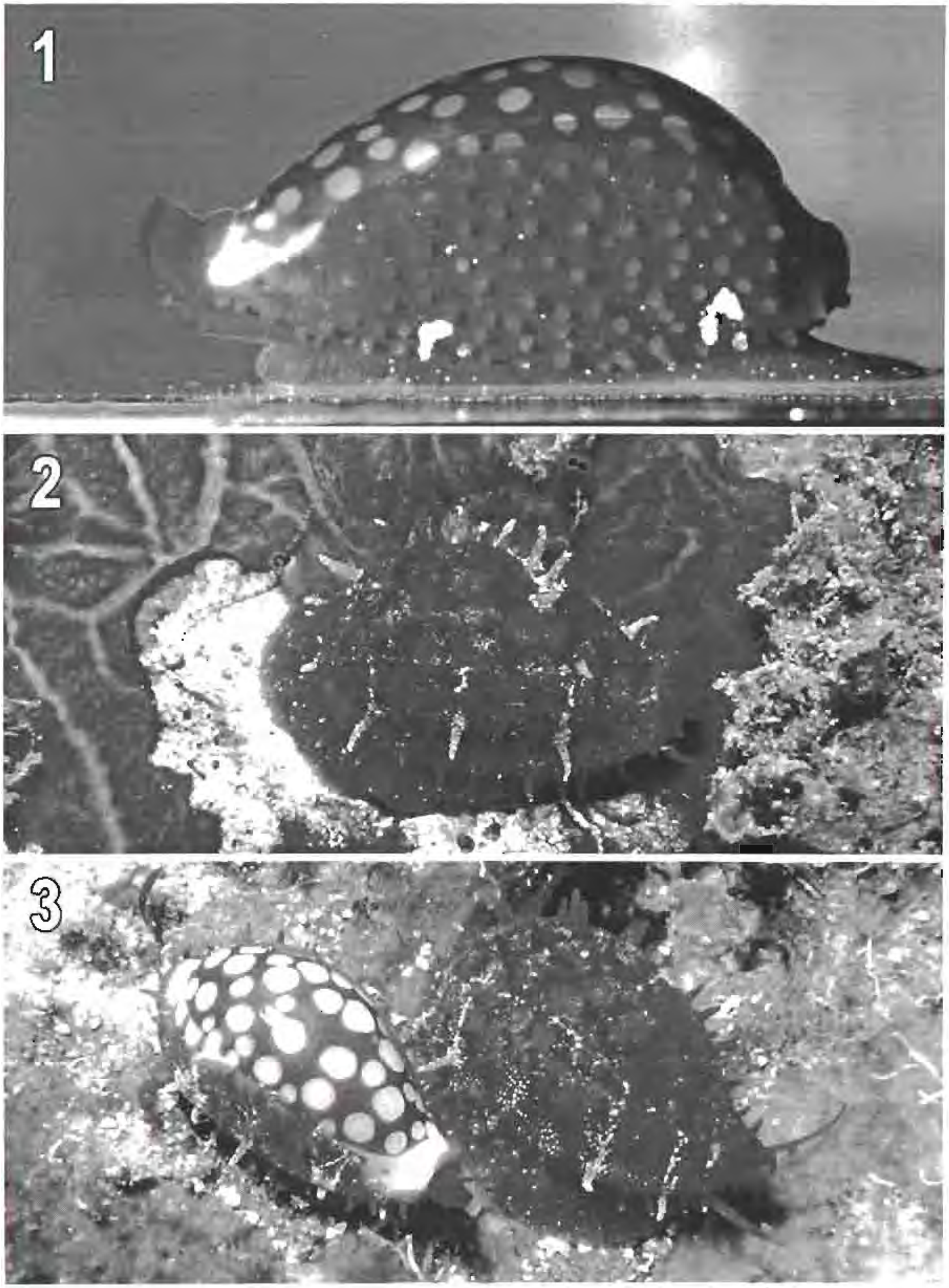
Figures 6.278 and 6.279. PCA plots of West Indian taxa in the *Cribrarula* complex using 7 characters (L, W/L, CT, SD, LSD, D-Band, and LSN) and 112 shells. **6.278.** taxa recognized in this study, and **6.279.** taxa recognized by Lorenz, 2002. Although seven specimens were identified as "abaliena", none is represented in the PCA because of missing characters.

Figures 6.280 to 6.282. Boxplots of selected shell characters showing the range of variation (Y axis) in each taxon in the *Cribrarula cribraria* complex, with taxa on the X axis (bottom of Fig. 6.282). **6.280.** shell length (L) (mm); **6.281.** dorsal line angle (not coded, in degrees), and **6.282.** spire diameter (SD) (mm).

Figures 6.283 to 6.285. Boxplots of selected shell characters showing the range of variation (Y axis) in each taxon in the *Cribrarula cribraria* complex, with taxa on the X axis (bottom of Fig. 6.285). **6.283.** number of columellar teeth (CT), transformed as in the

Schilders' formula; **6.284.** number of labral spots (LSN), and **6.285.** number of dorsal spots.

Figures 6.286 to 6.300. Types of taxa in the *Cribrarula cribraria* complex in The Natural History Museum, London (BMNH). Shells in dorsal (left) and ventral view (right). The scale bar in mm is shown below the shells (photos by Amelia Campbell, courtesy BMNH). **6.286 to 6.288.** Three syntypes of *Cypraea cribraria* Linnaeus, 1758, in the Linnaean Collection, no locality data. Label remarks: "Hanley [1855] has isolated three unmarked shells which he said were found in the Linnaean marked box" (Dance, S. P., 1963).(scale bar in mm, below label). **6.287 and 6.288.** Largest of the three syntypes from Fig. 6.286 shown in detail. **6.289 to 6.292.** Syntypes of *Cypraea cumingii* Sowerby II, 1832, from the Society Islands, deposited in the H. Cumming collection (BMNH, no catalog number). Note that the specimen in Figs. 6.289 and 6.290 is large (circa 27.6 mm), and thus *C. cumingii cleopatra* Schilder and Schilder, 1939 should be considered a synonym of *C. cumingii.* **6.293 and 6.294.** Holotype of *Cypraea compta* Pease, 1860, from Jarvis Island (Leg. Garrett, BMNH 1964276). **6.295 and 6.296.** Syntype of *Cypraea gaskoinii* Reeve, 1846, no locality data (BMNH 1988054). **6.297 and 6.298.** Holotype of *Cypraea fallax* Smith, 1881, from West Australia (purchased by G.B. Sowerby).(BMNH 1881.11.8.2). **6.299 and 6.300.** Syntype of *Cypraea cribraria exmouthensis* Melvill, 1888, from Exmouth Gulf, West Australia (Leg. & Pres. T.H. Haynes) (BMNH 1887.5.10.7).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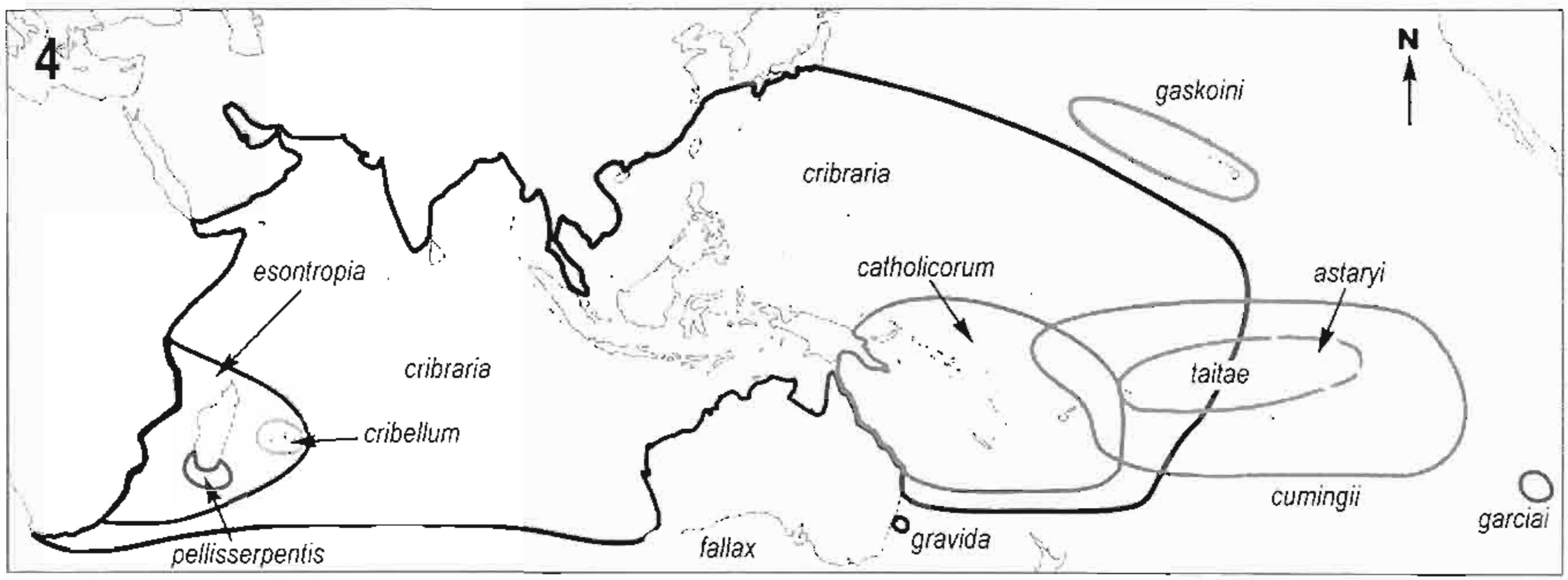
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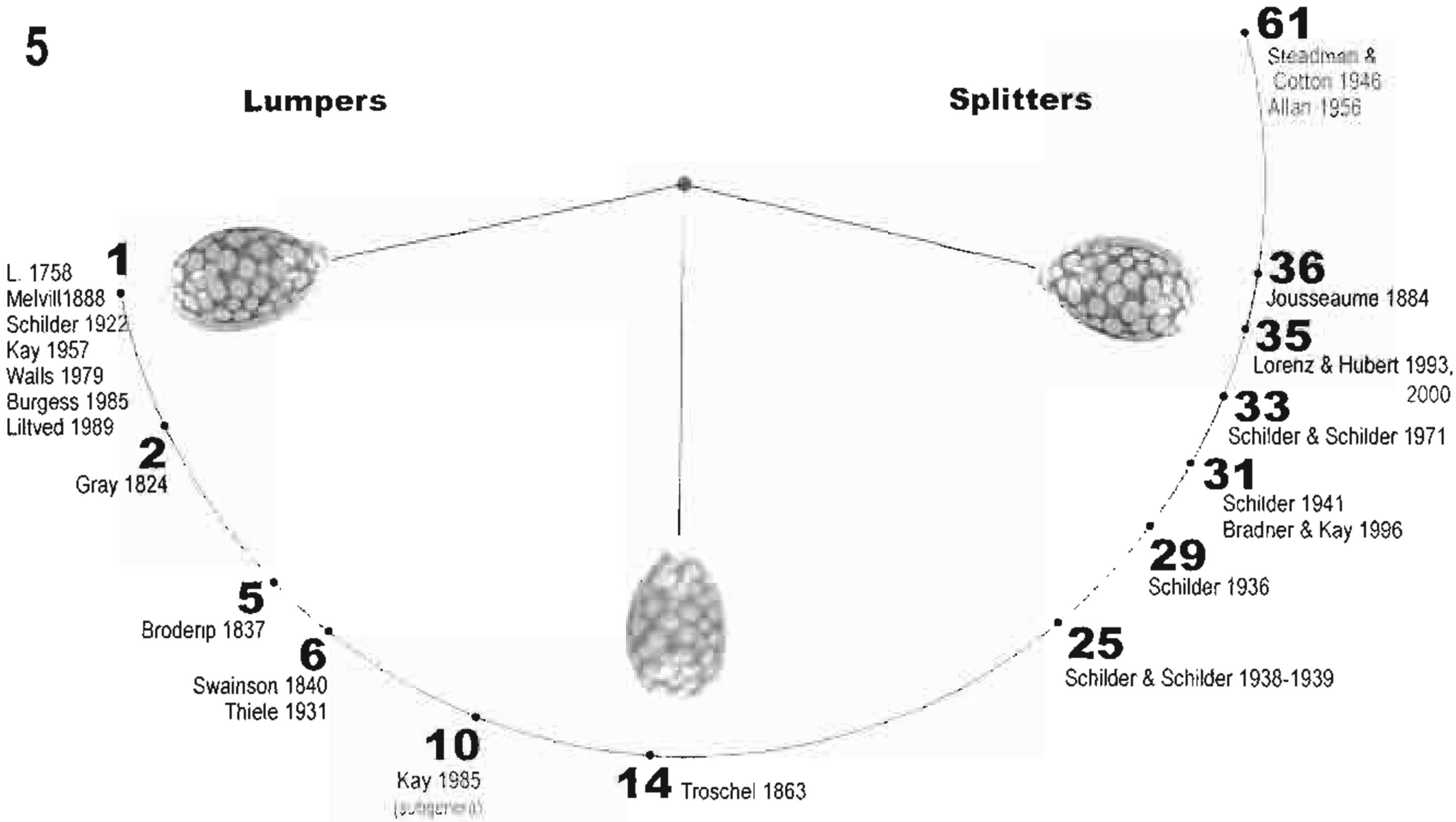

Lumpers
Splitters
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L. 1758
Melvill1888
Schilder 1922
Kay 1957
Walls 1979
Burgess 1985
Liltved 1989
2
Gray 1824
5
Broderip 1837
6
Swainson 1840
Thiele 1931
10
Kay 1985
14 Troschel 1863
25
Schilder & Schilder 1938-1939
29
Schilder 1936
31
Schilder 1941
Bradner & Kay 1996
33
Schilder & Schilder 1971
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Lorenz & Hubert 1993, 2000
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Jousseaume 1884
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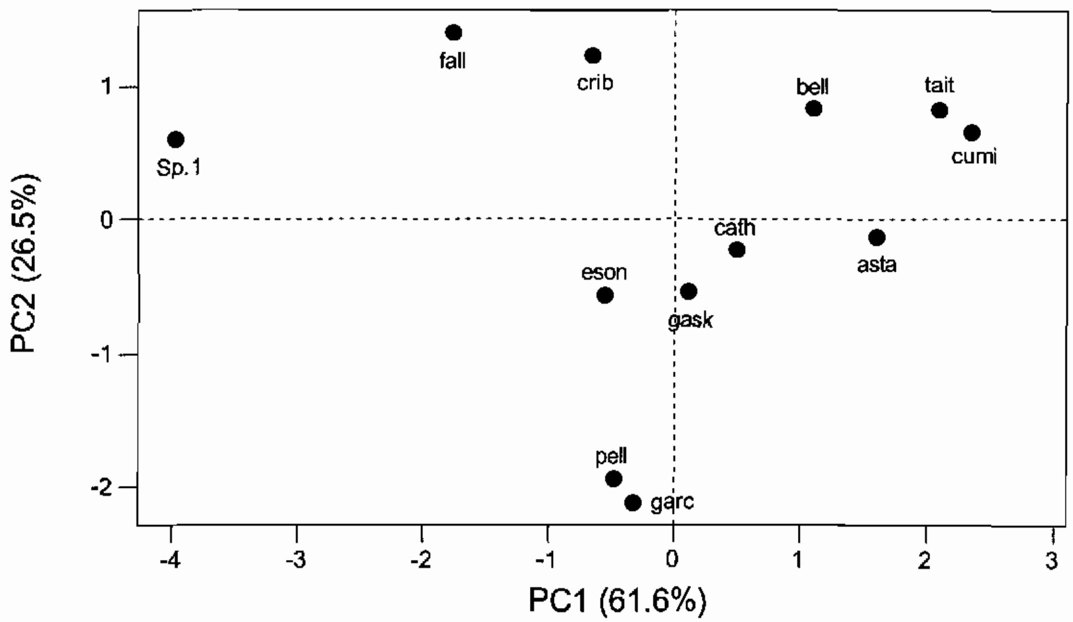
Steadman & Cotton 1946
Allan 1956

6

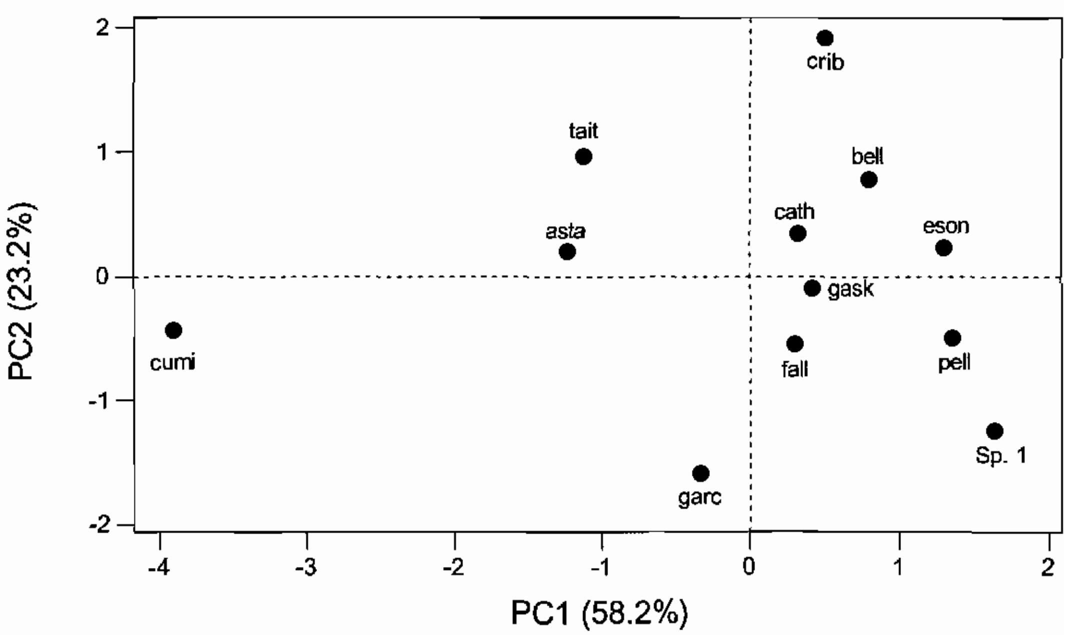
PCA using figures from the "New Formula"



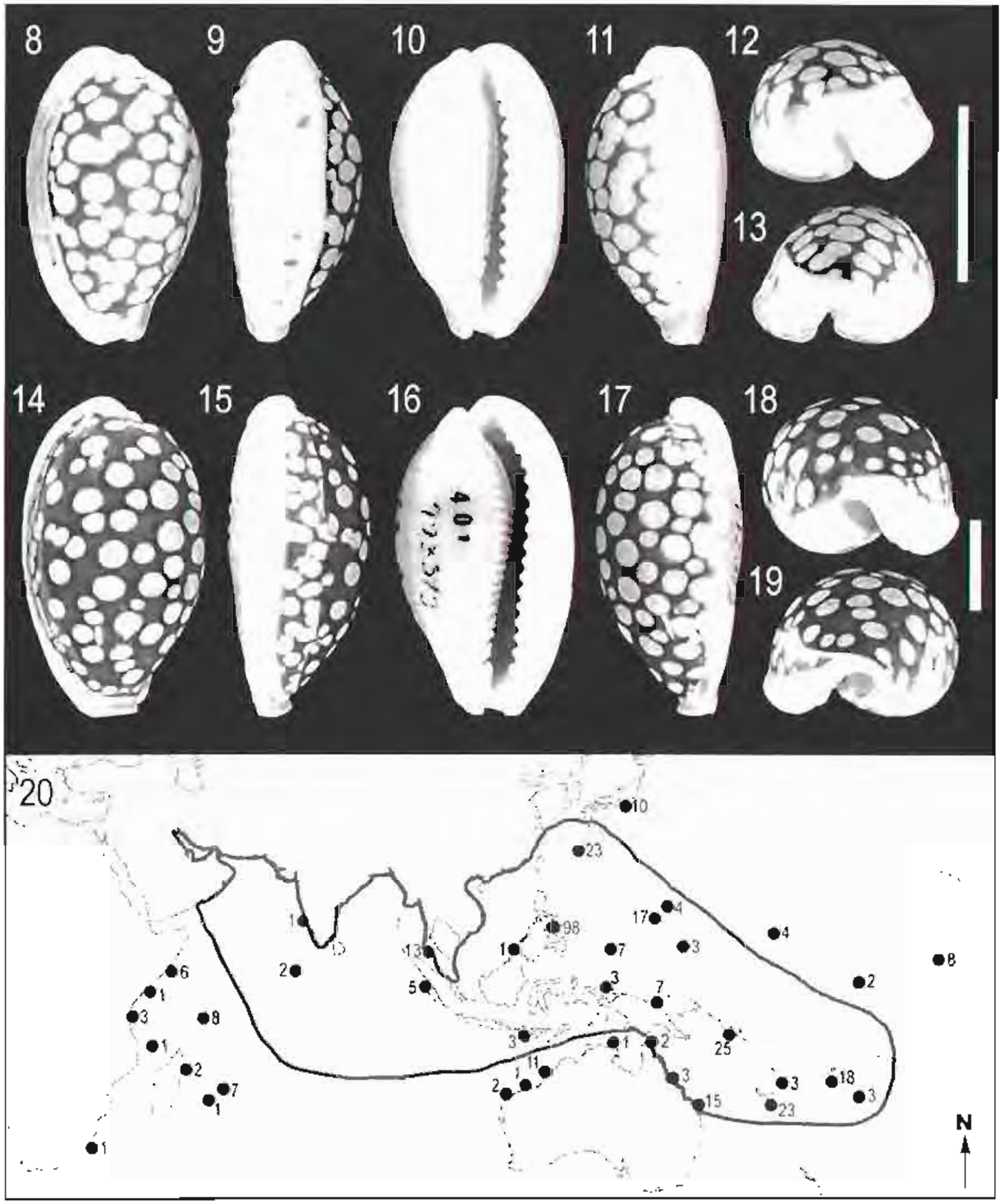
Characters: L, W/L; SPD; CTT; LSS

7

PCA using figures from the Schilders' Formula



Characters: L; W/L; LT; CT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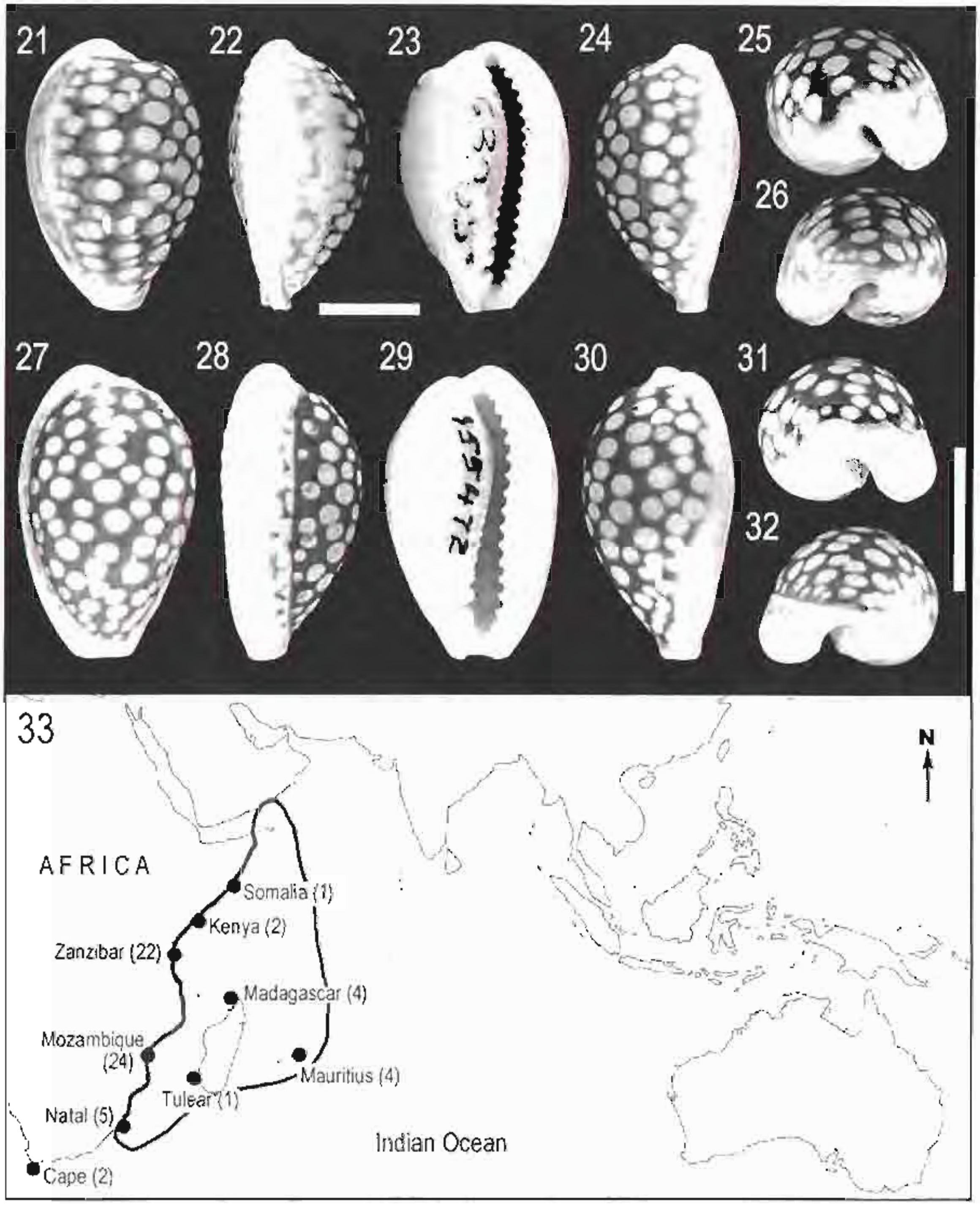
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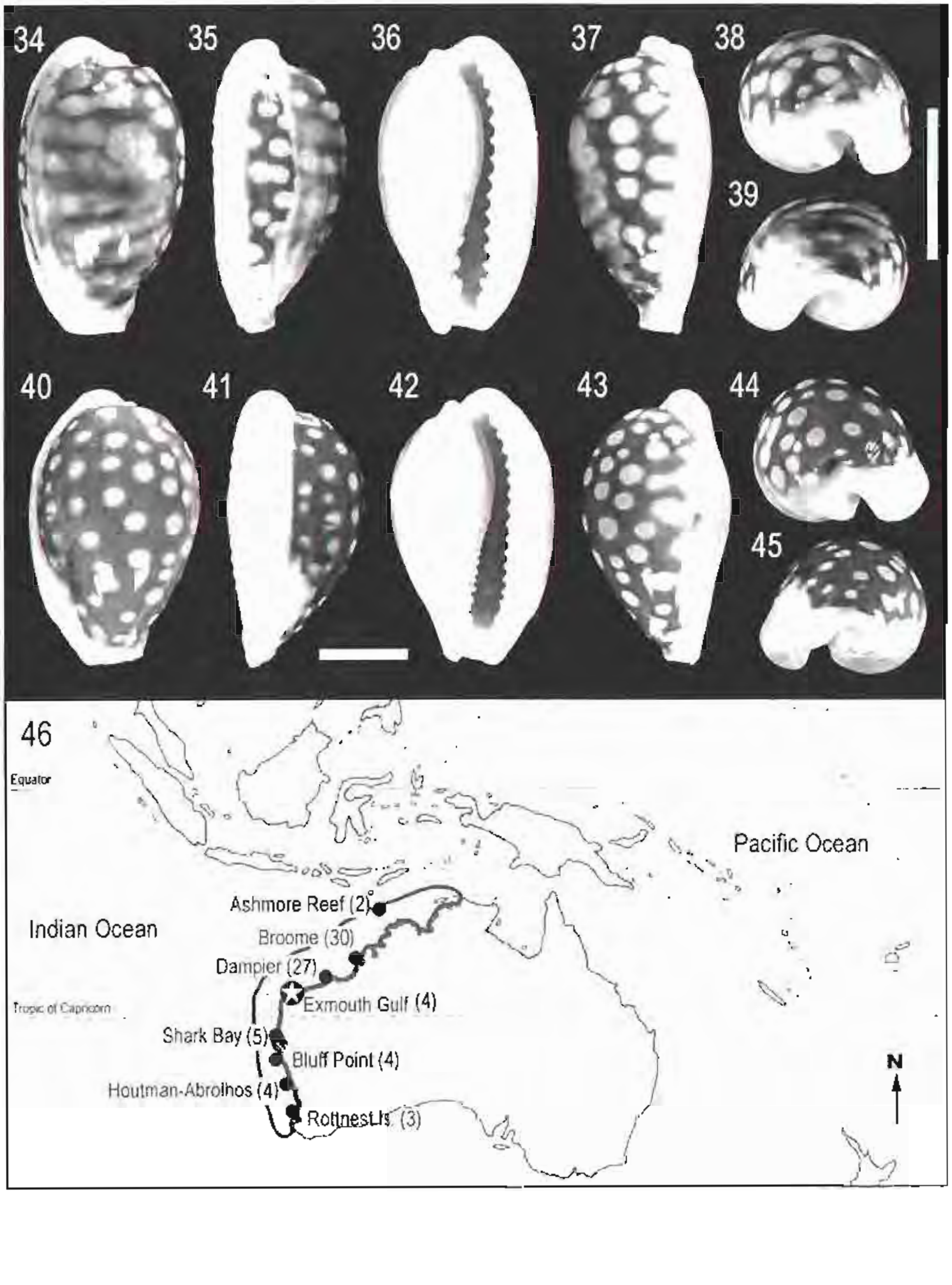

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Broome (30)
Dampier (27)
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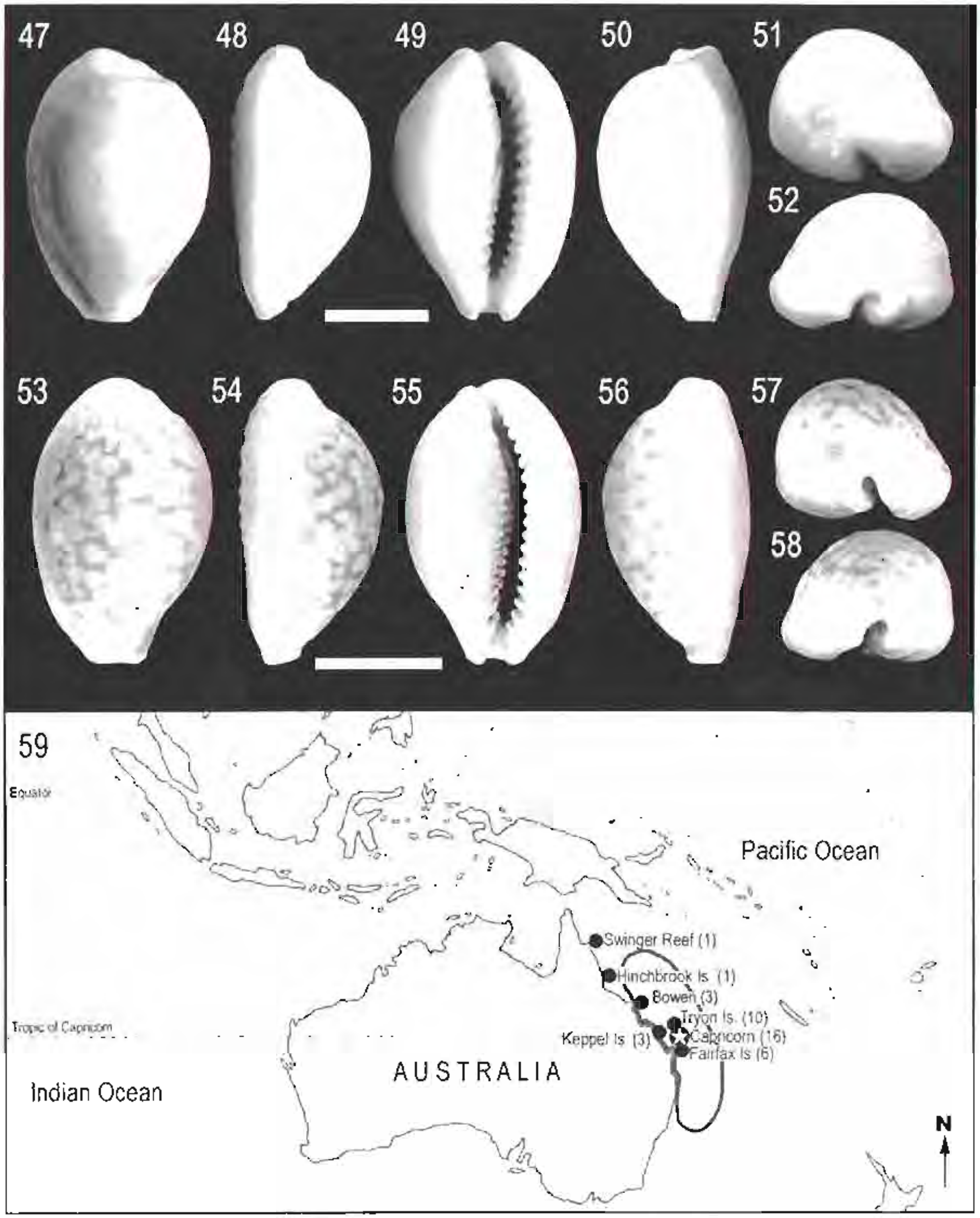
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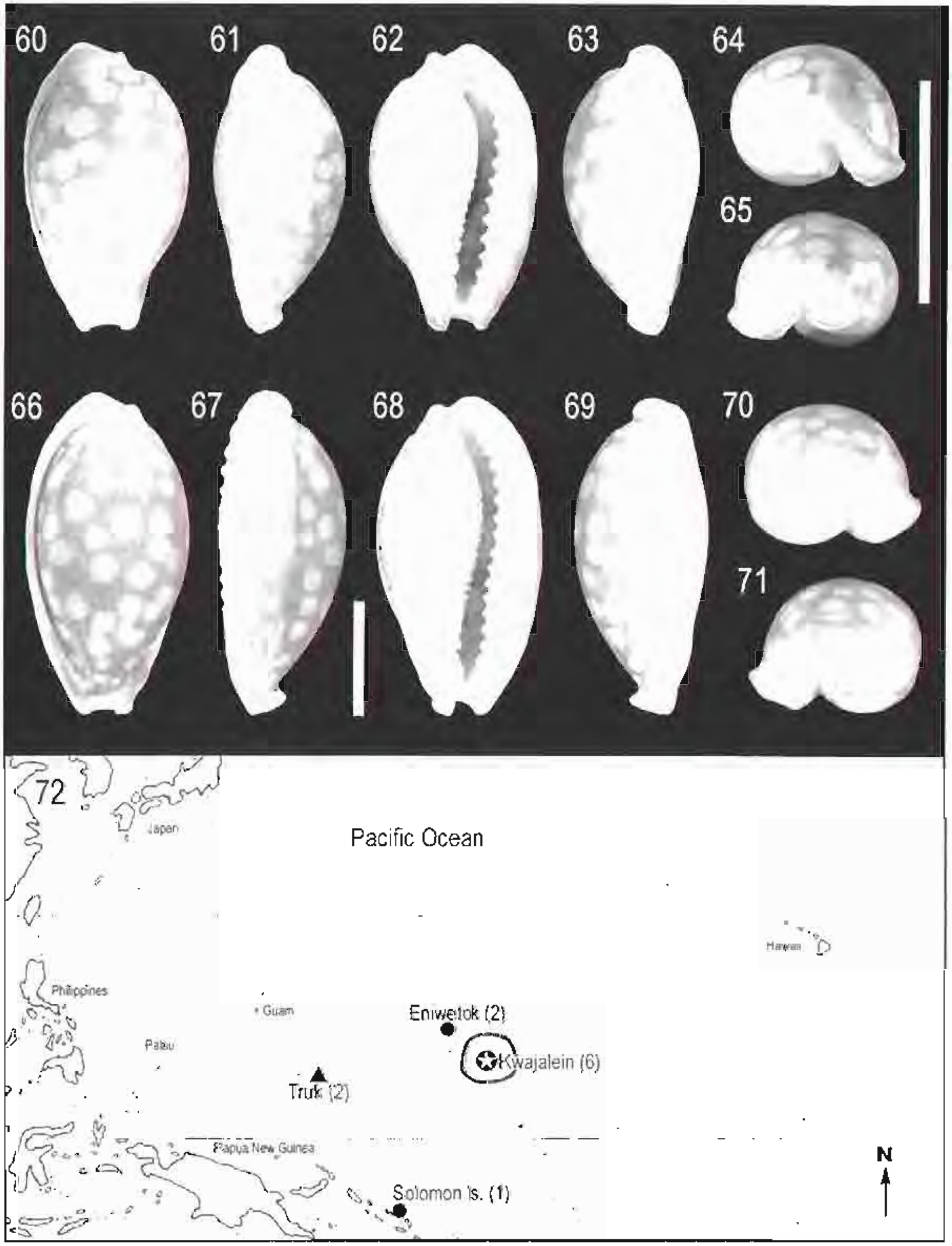
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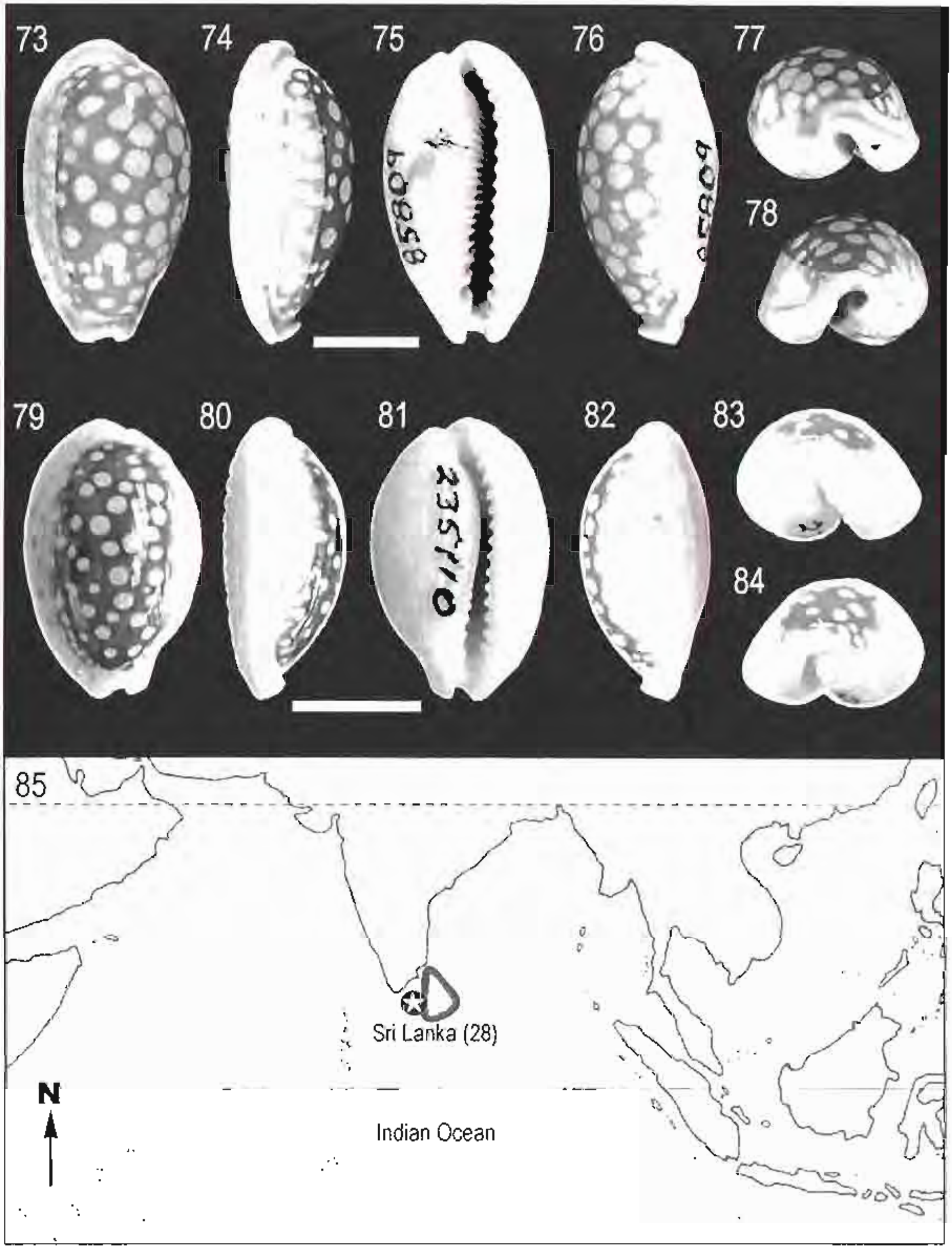
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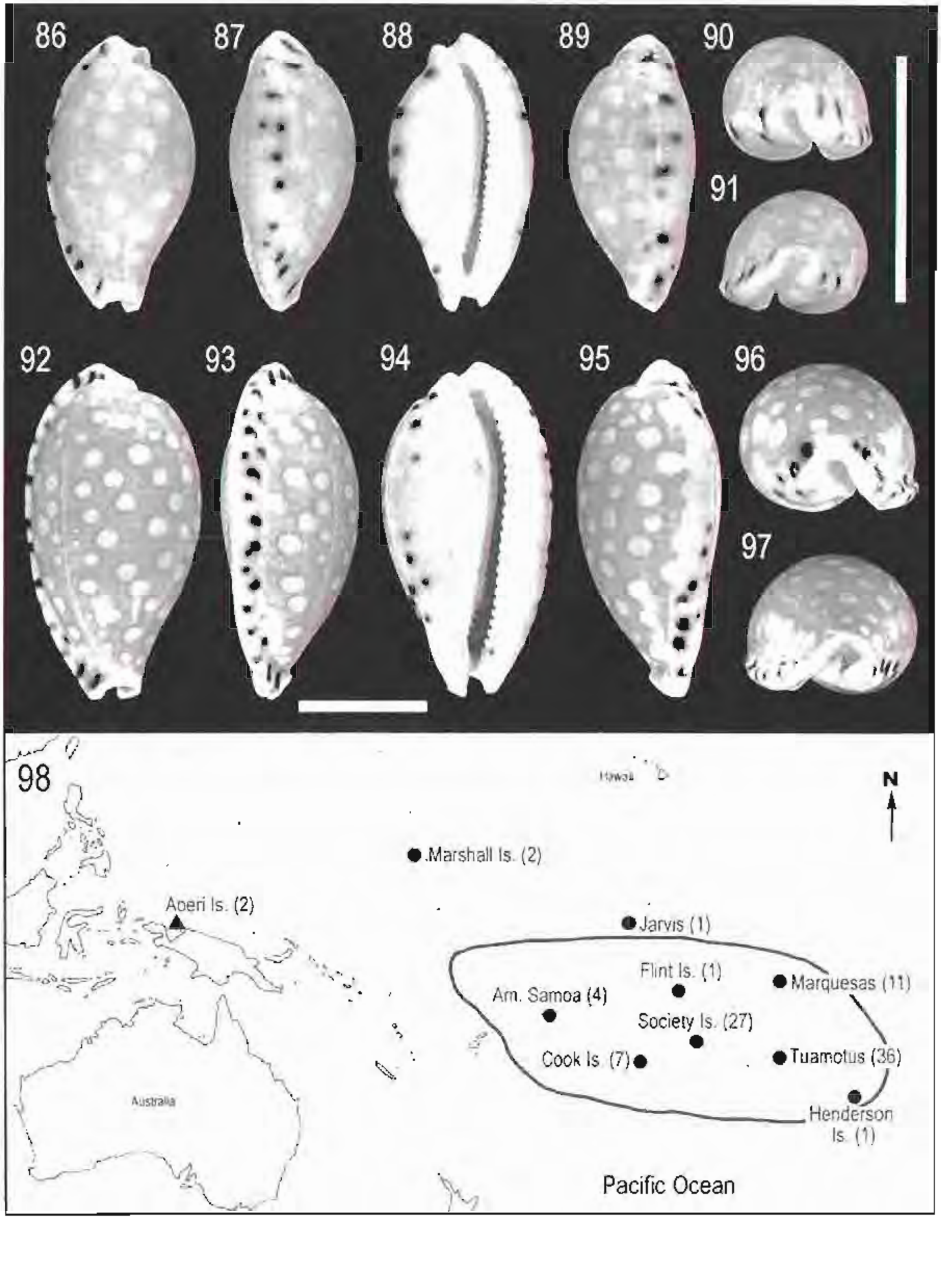
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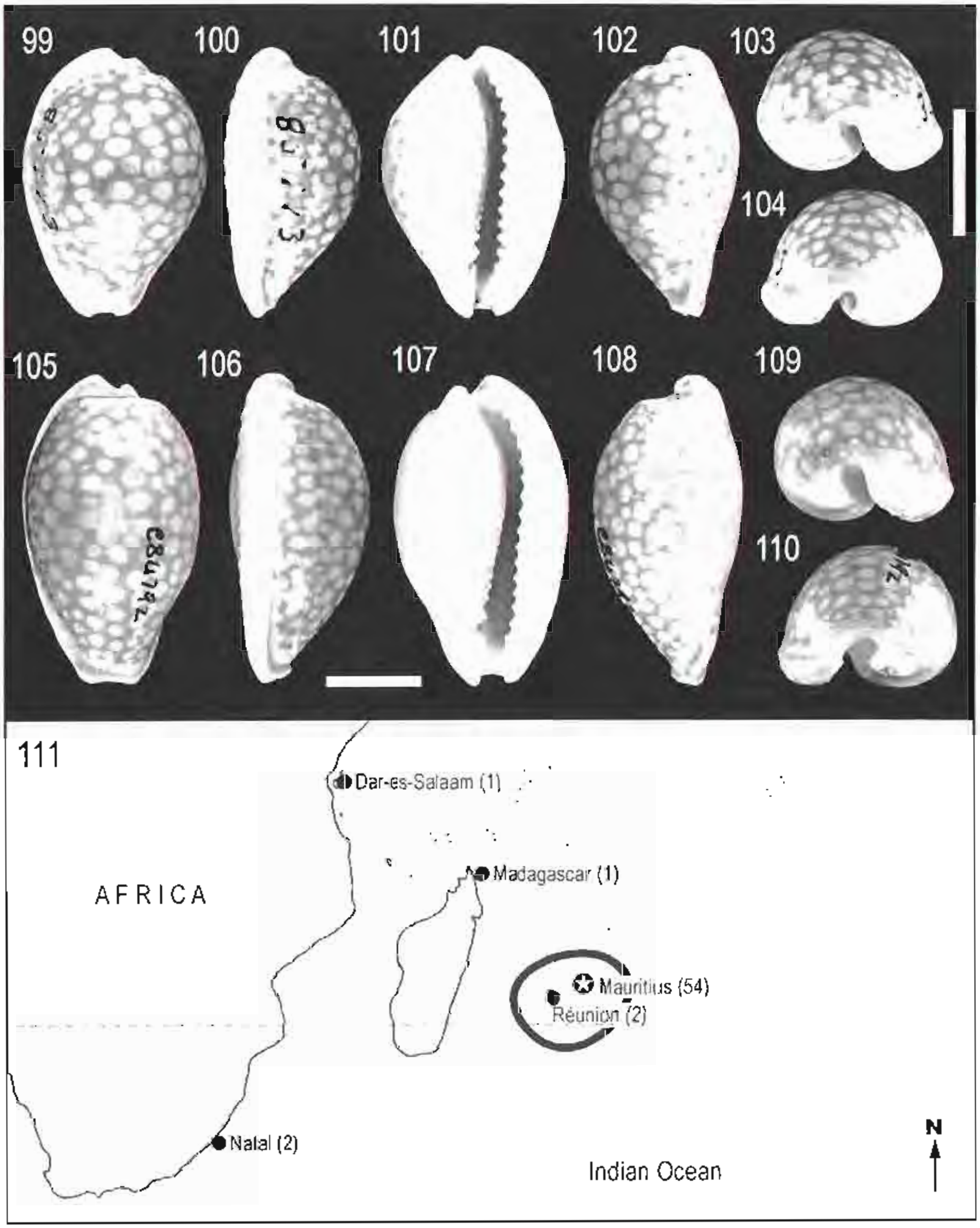
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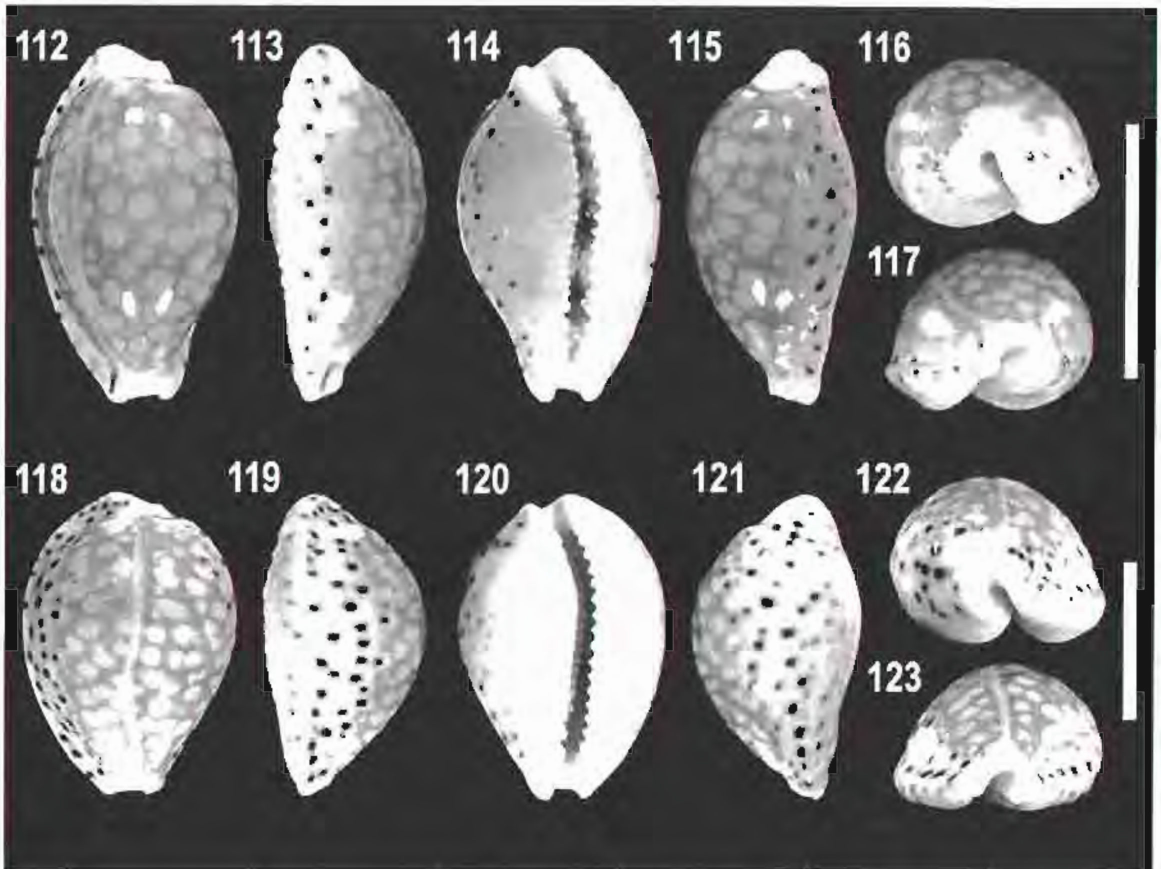
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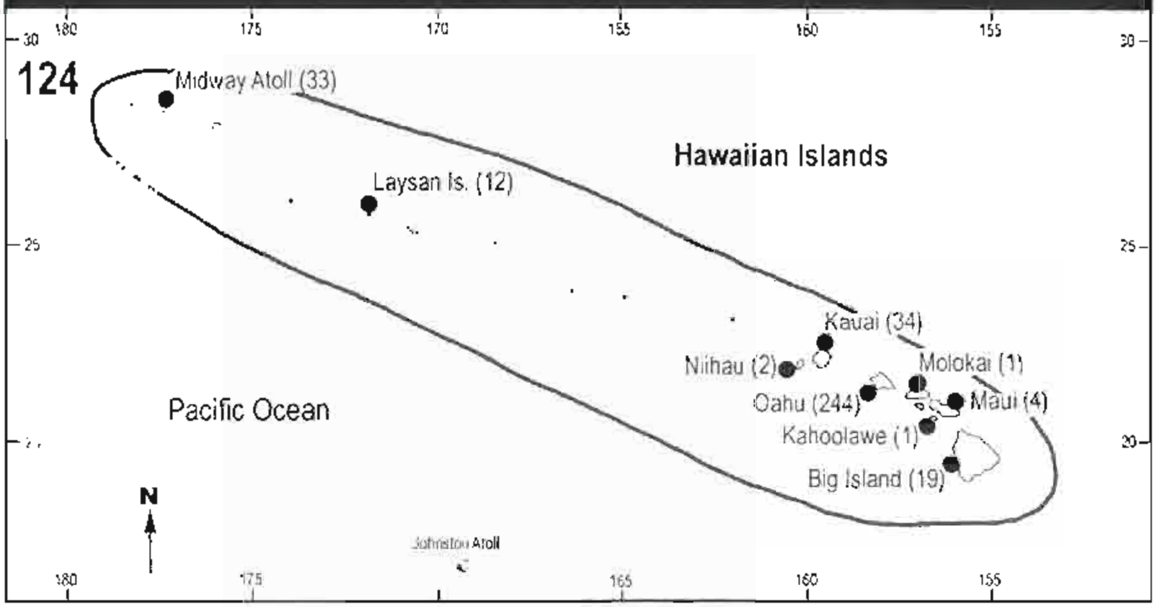
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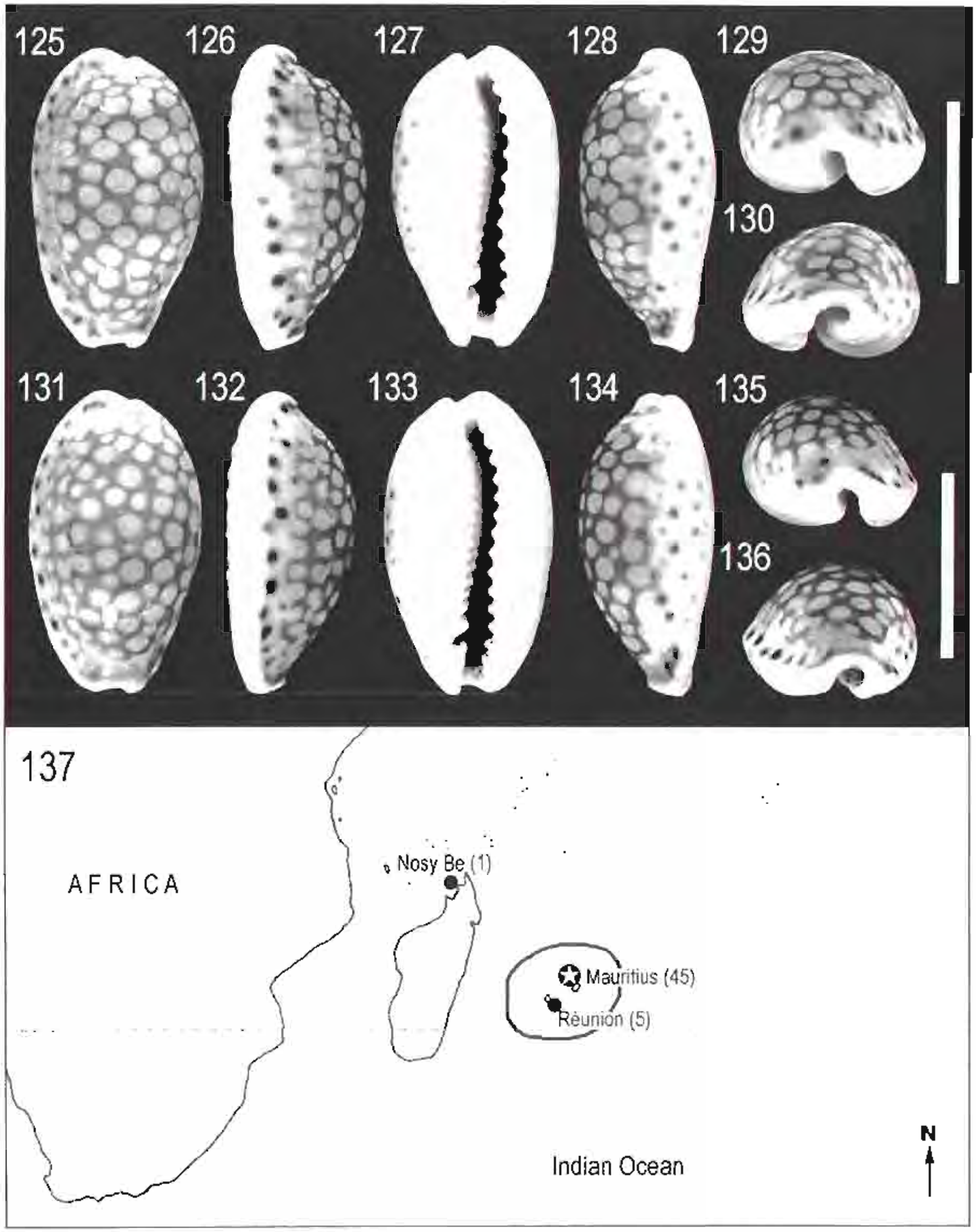
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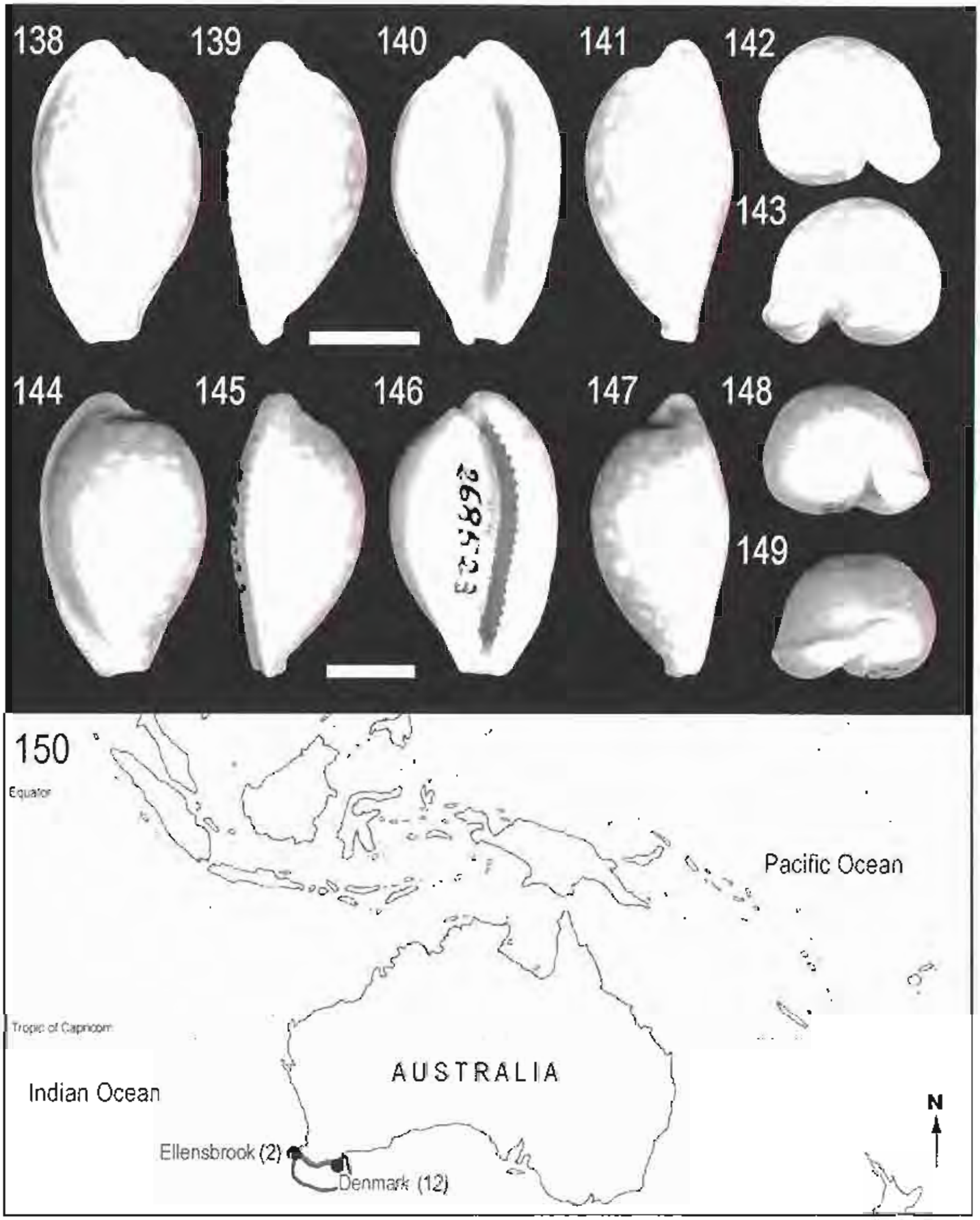
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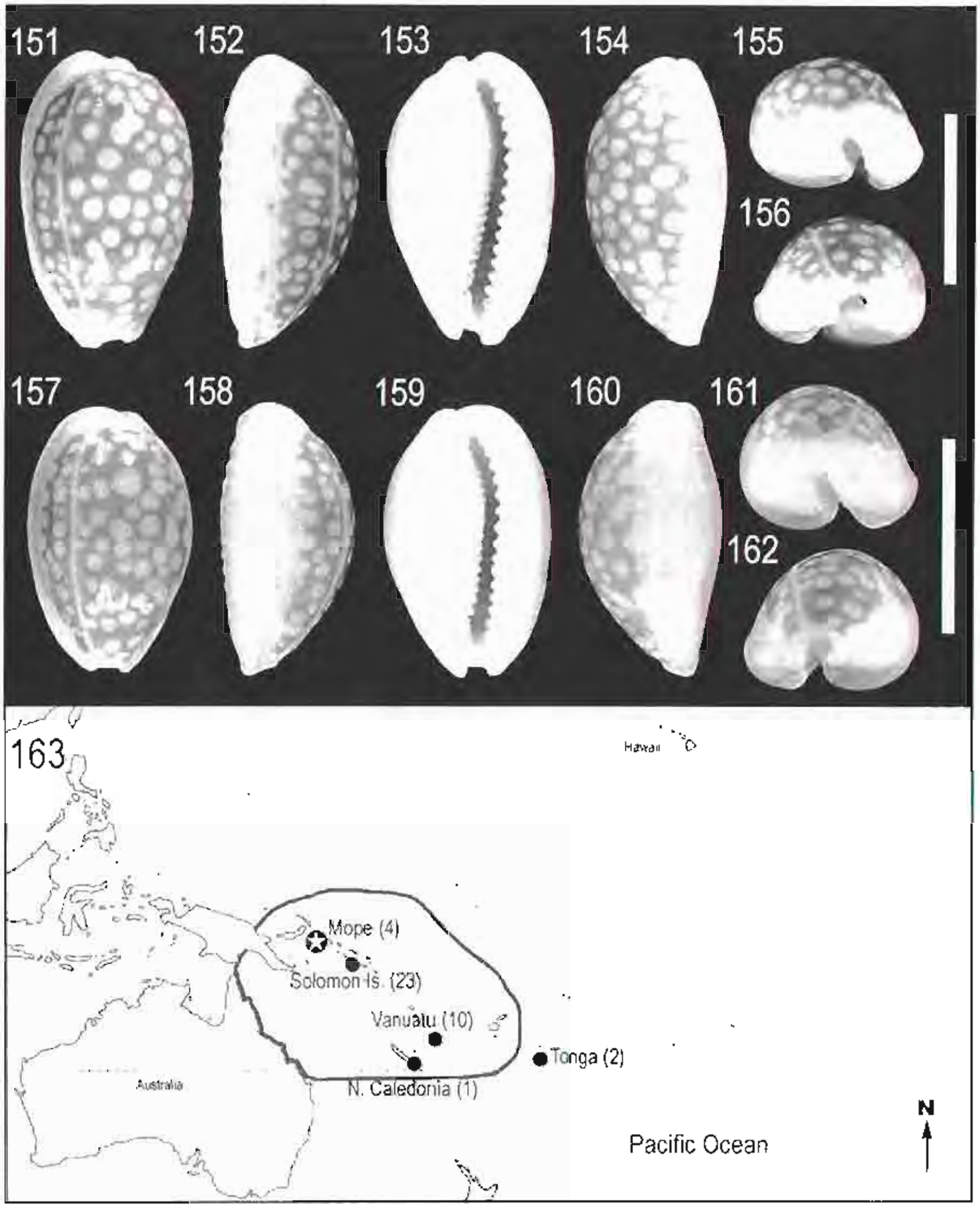
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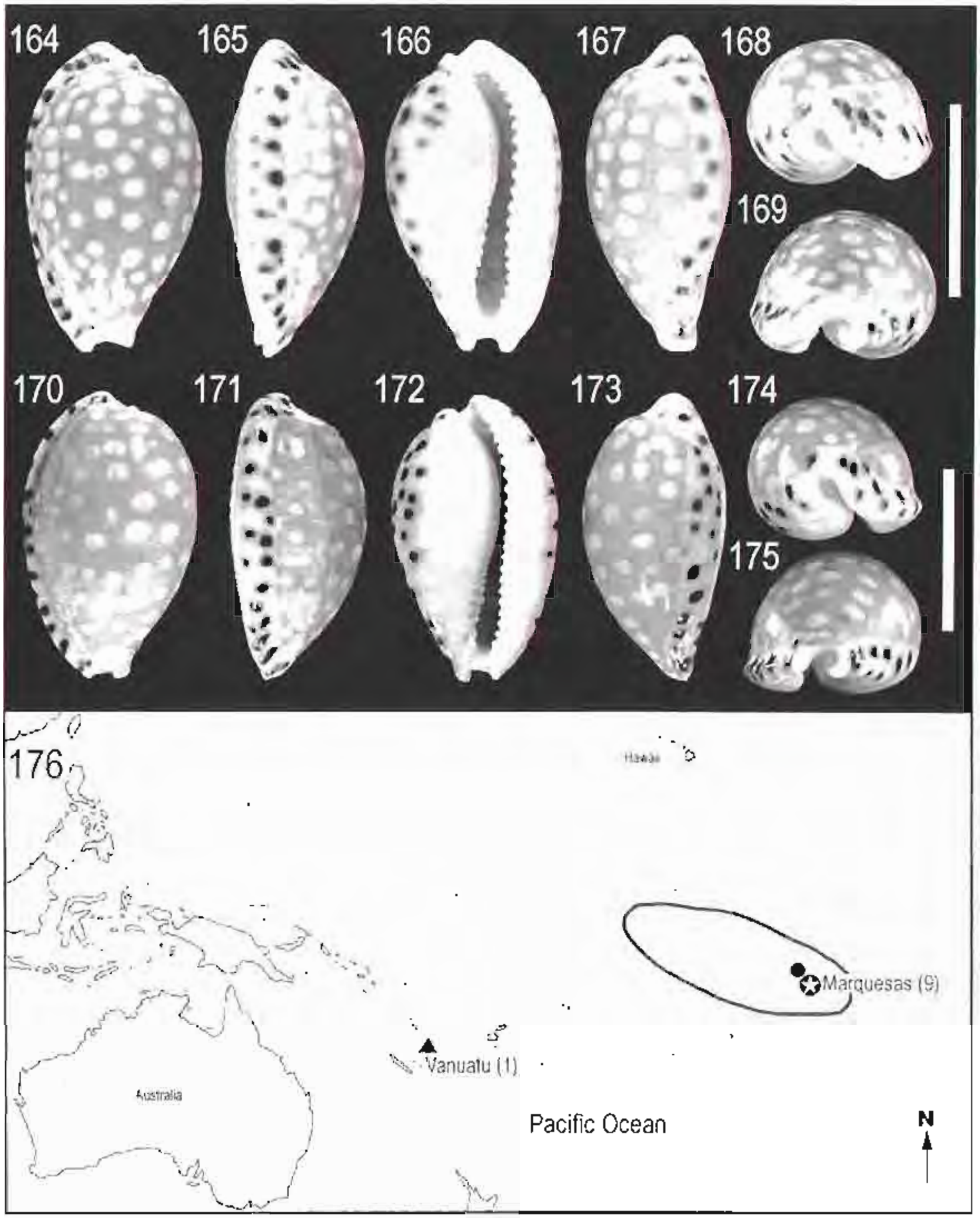
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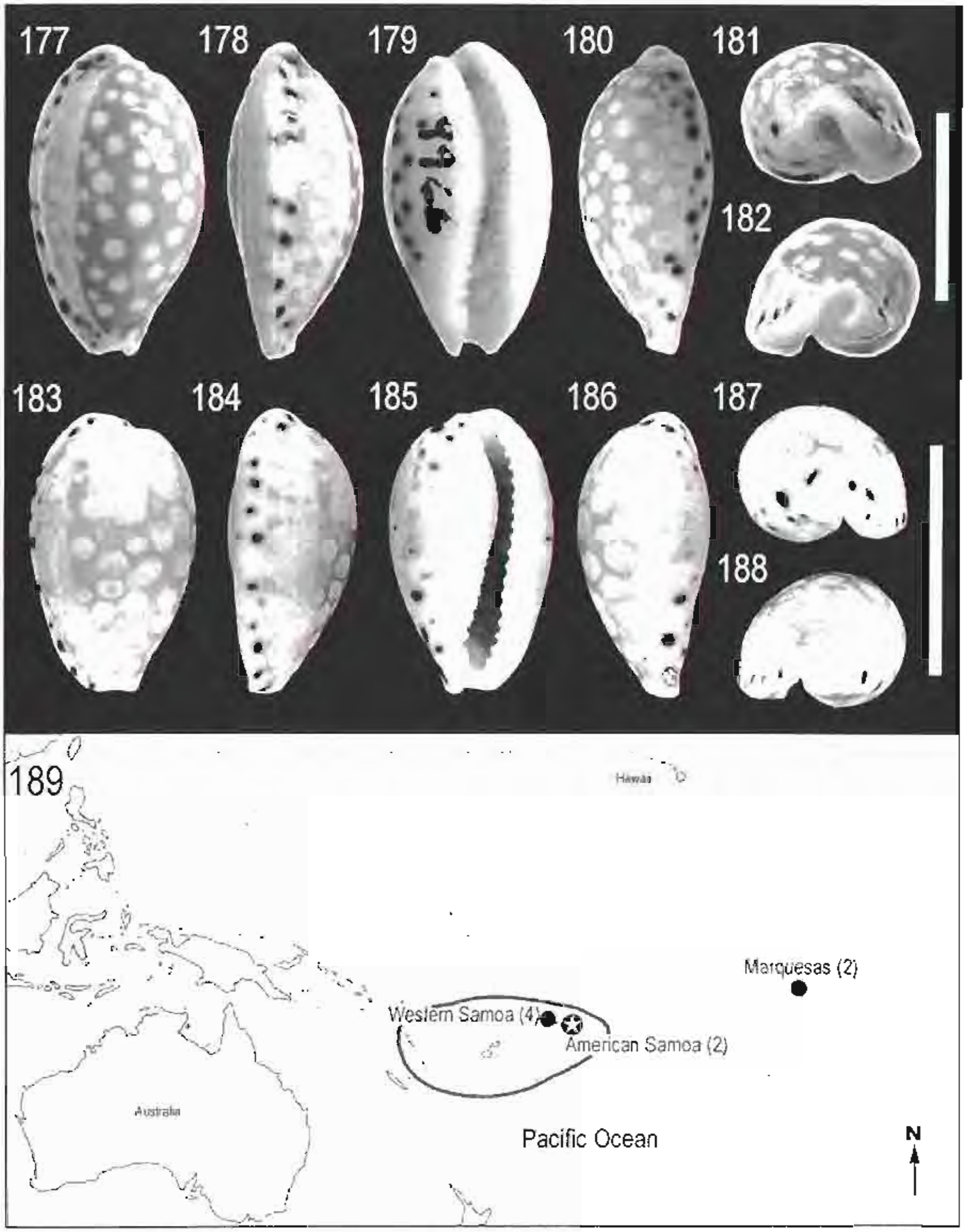
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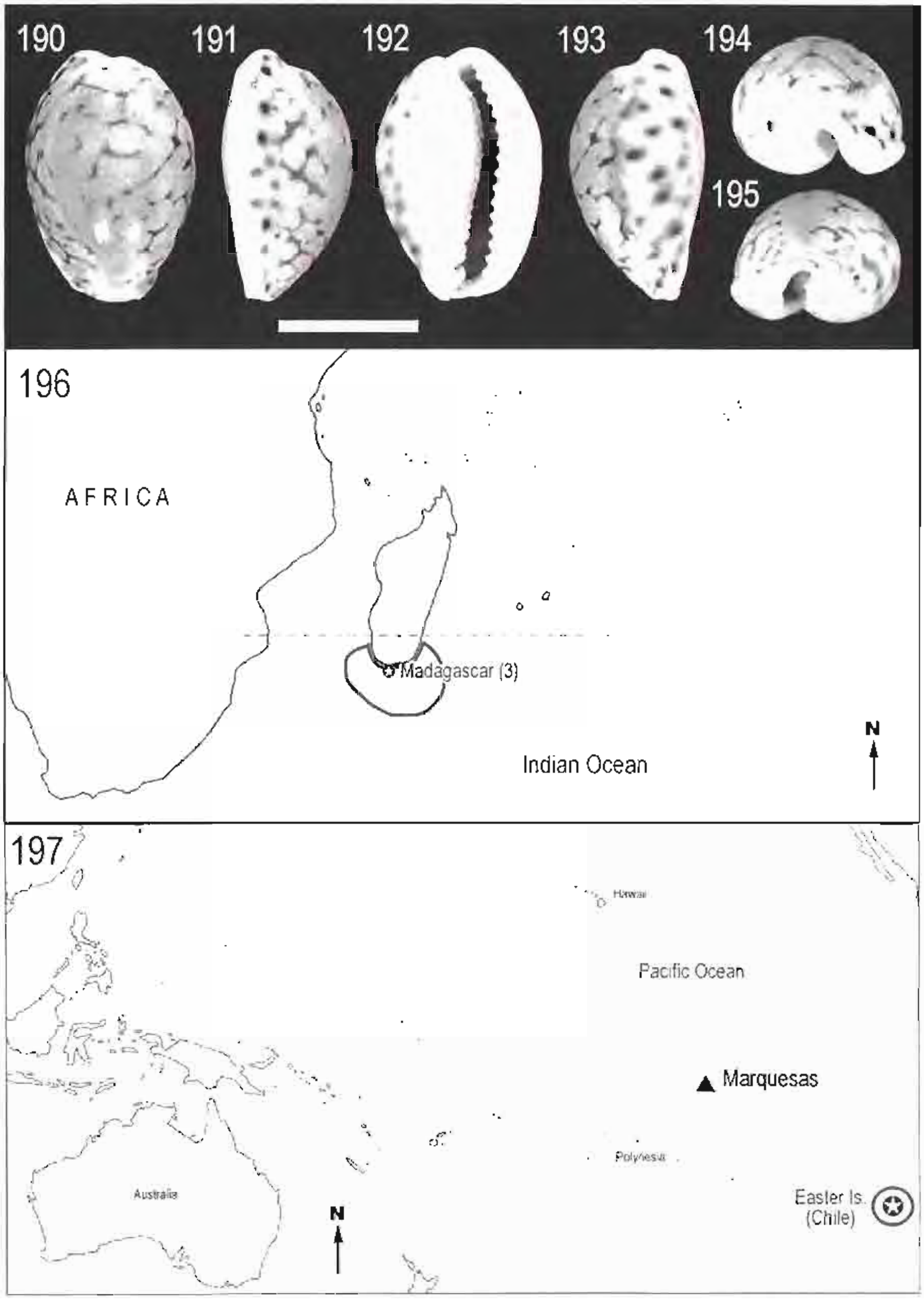
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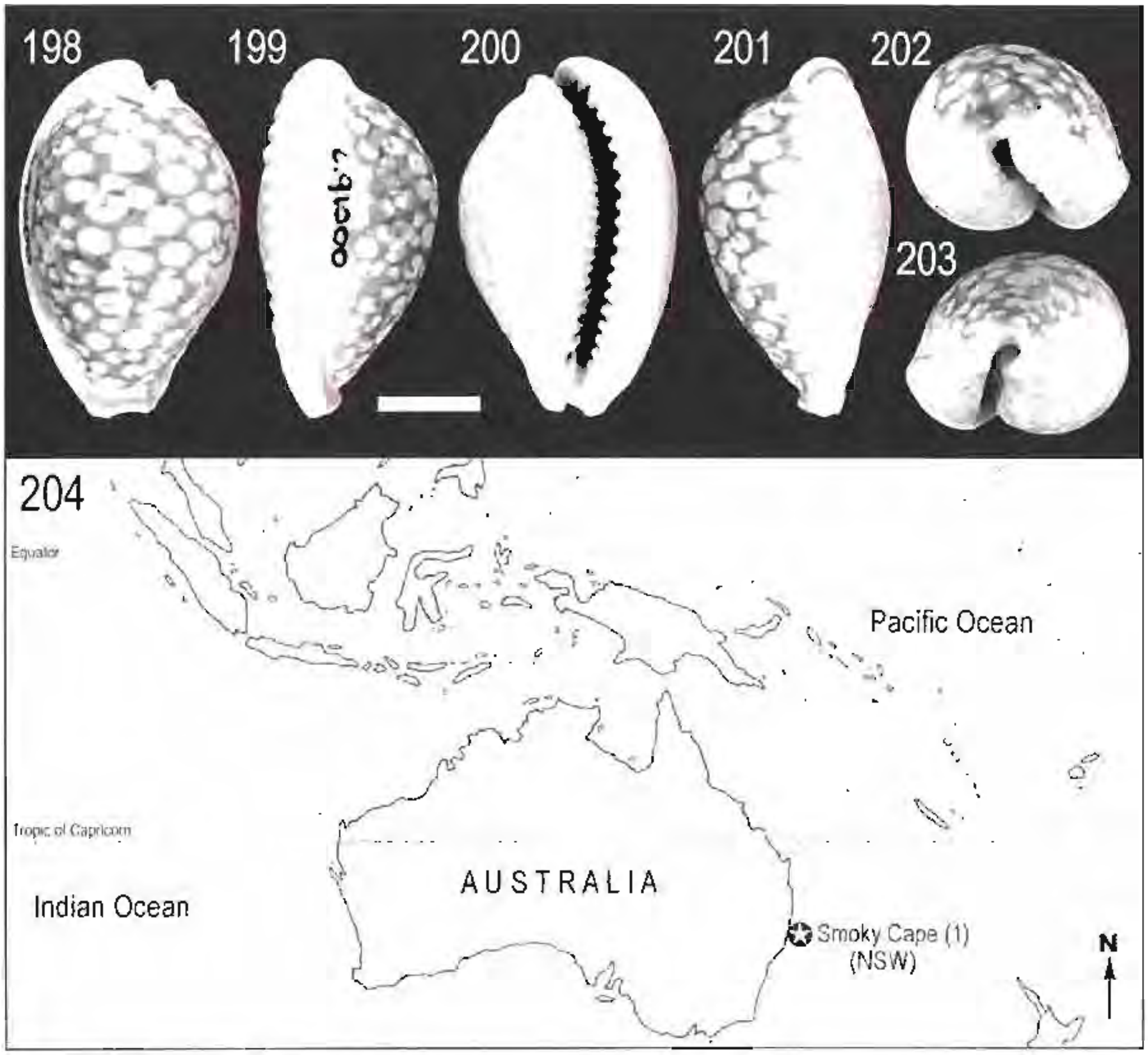
(Chile)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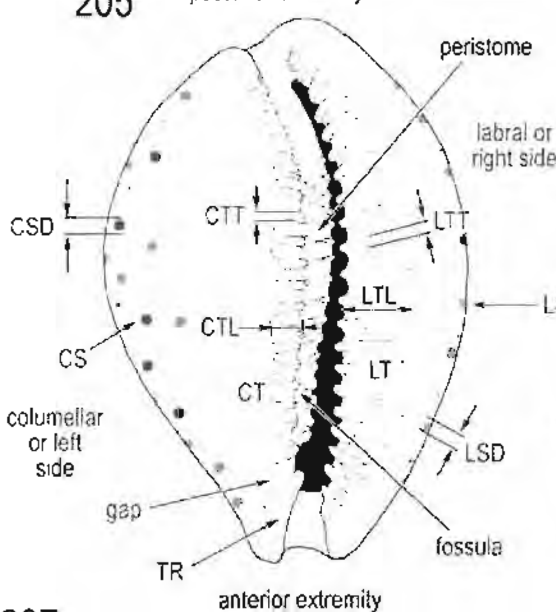

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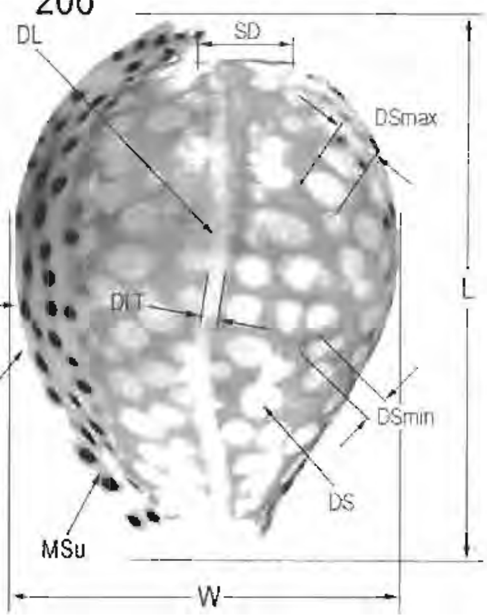

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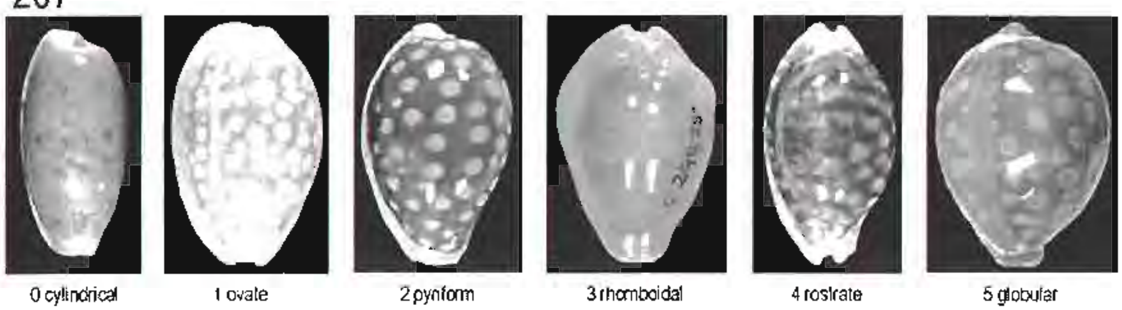

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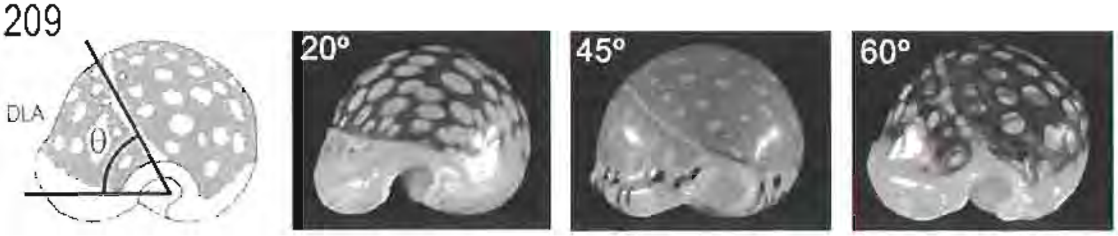

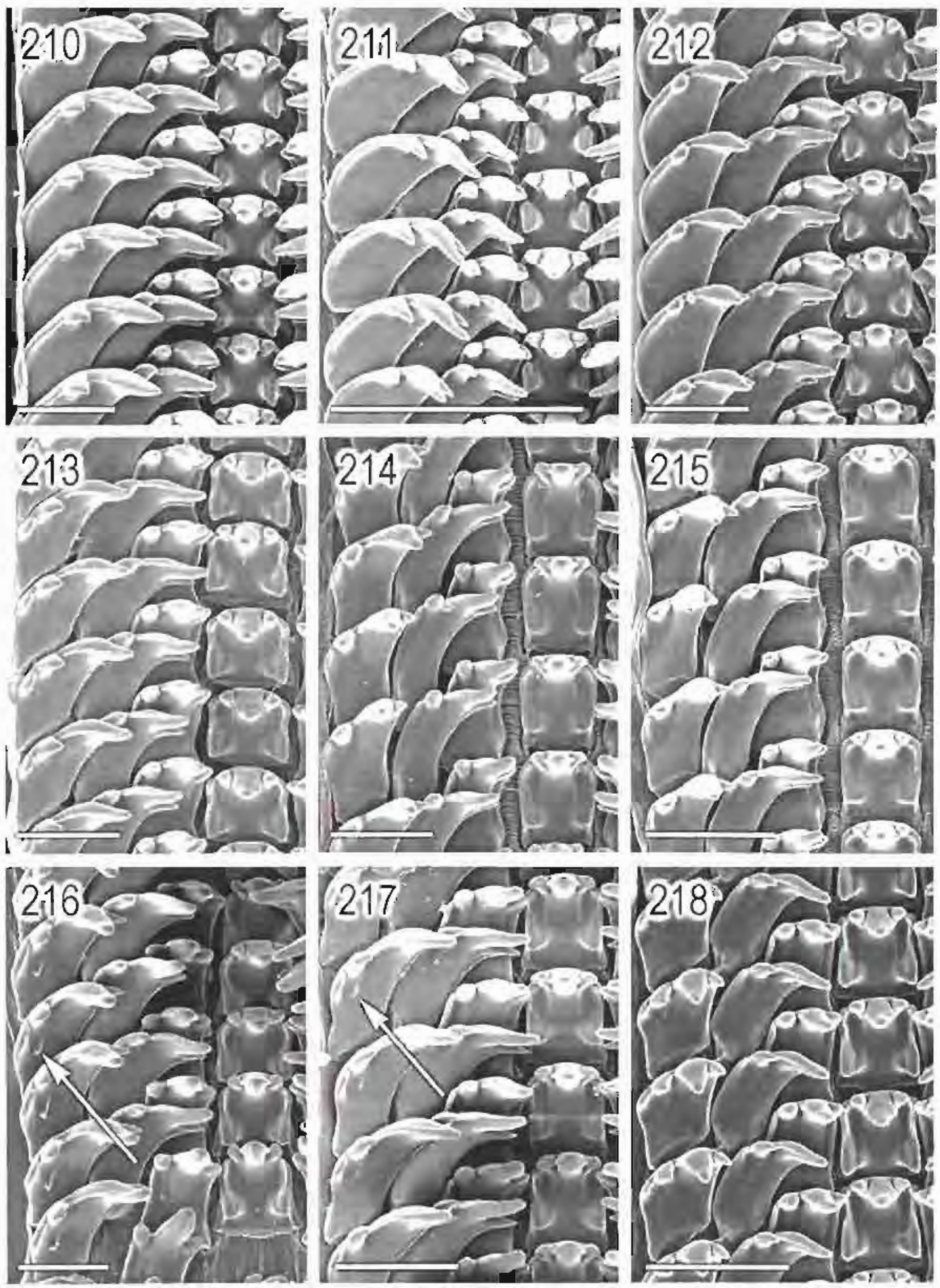
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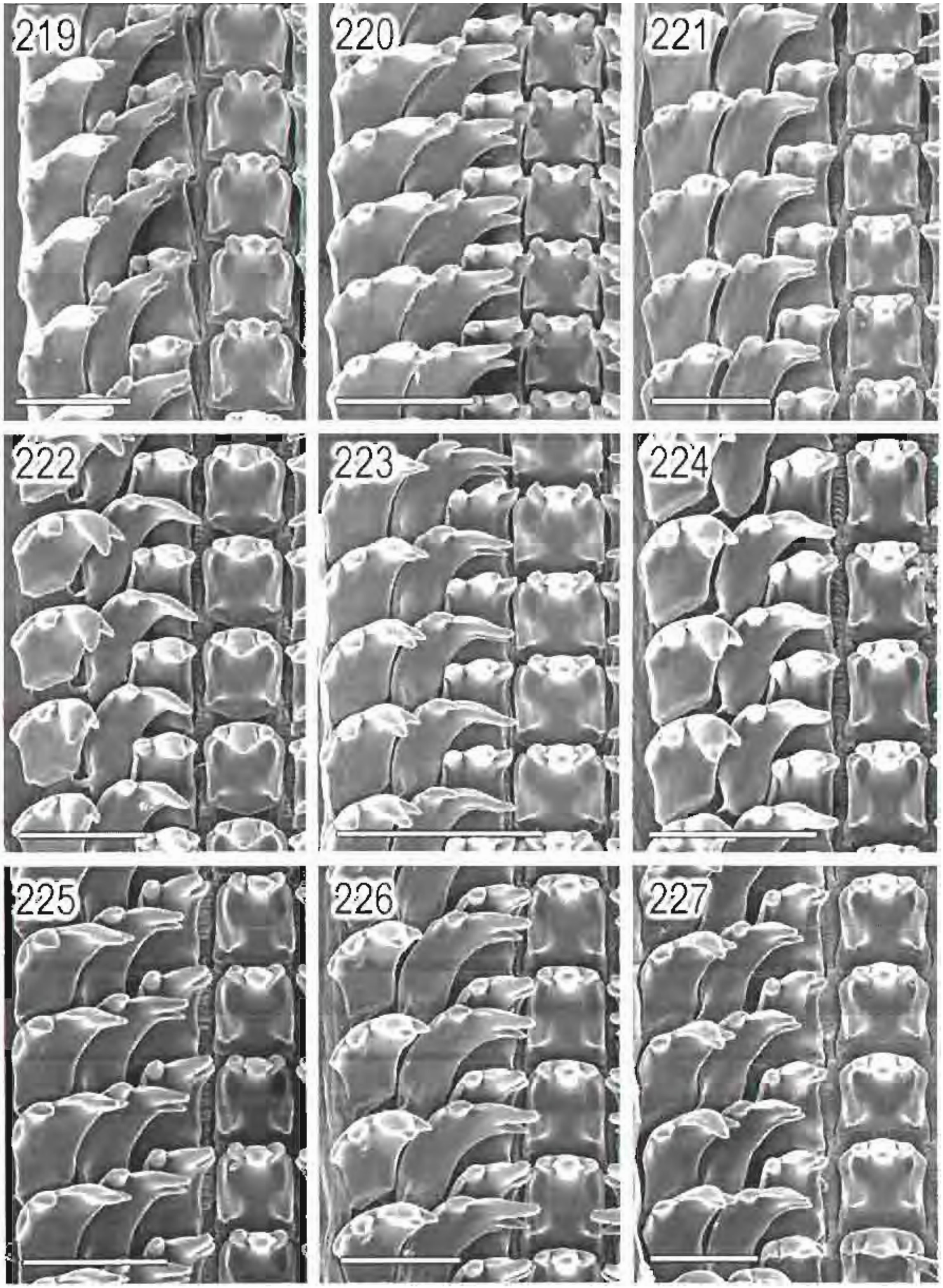
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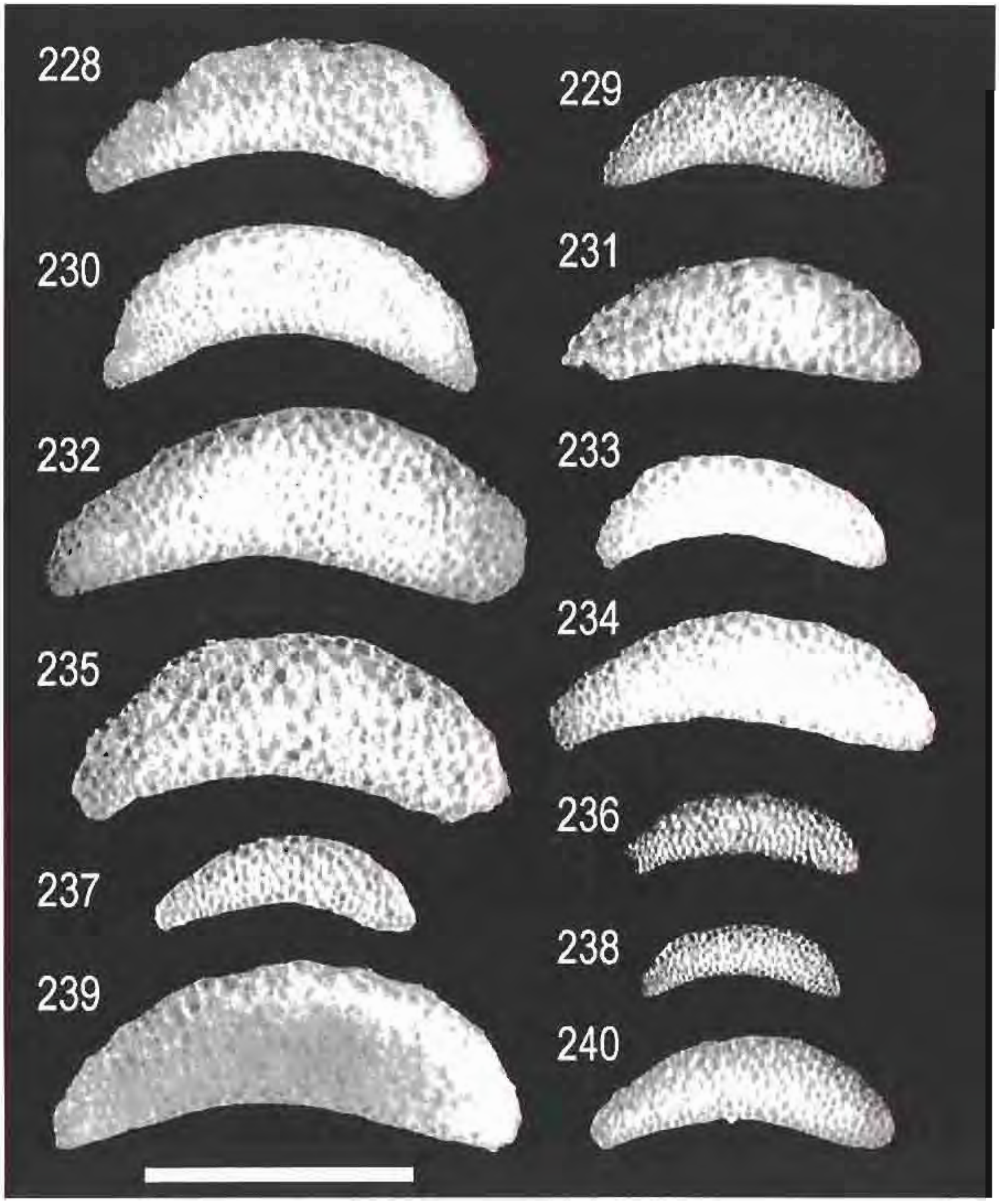
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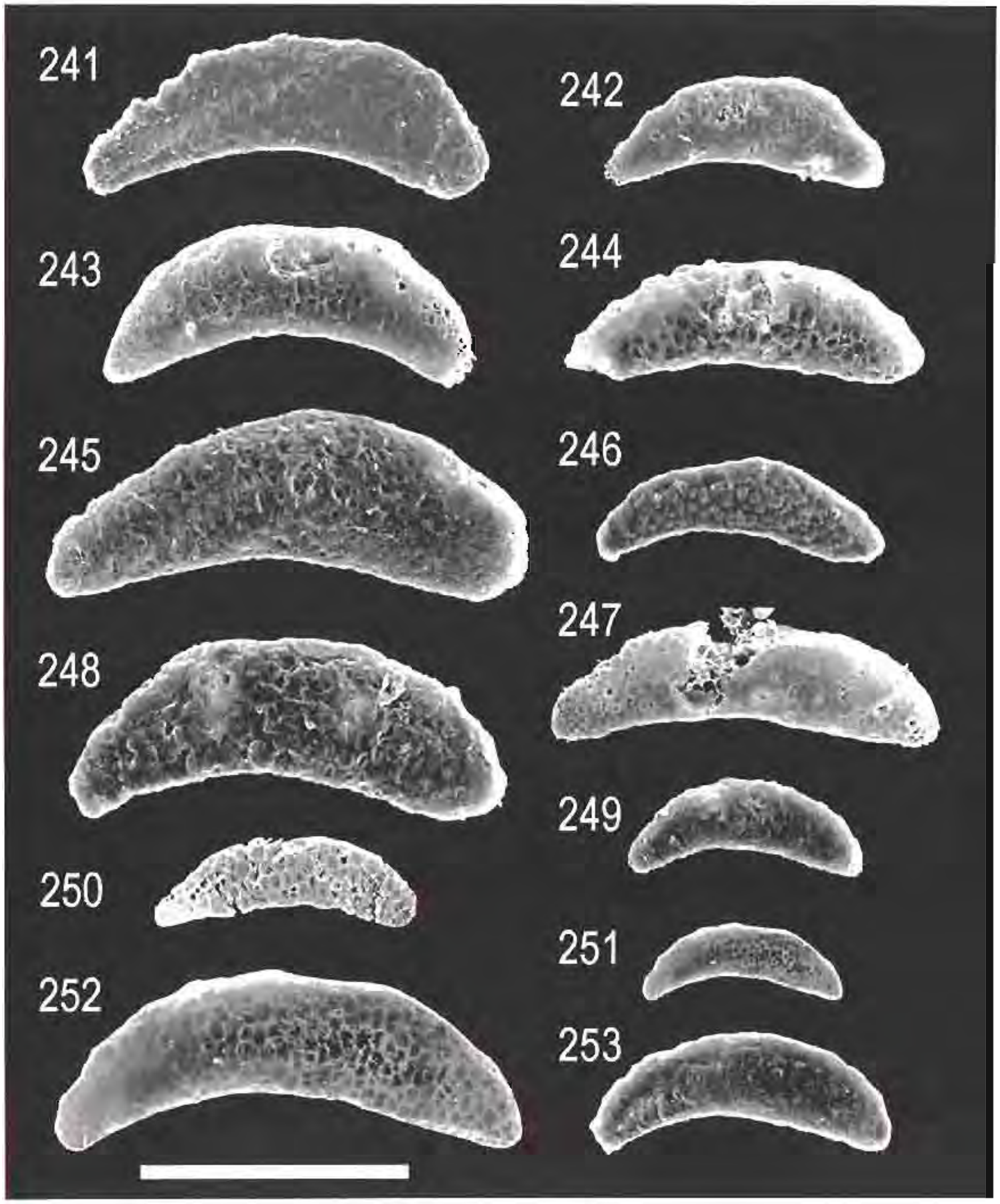

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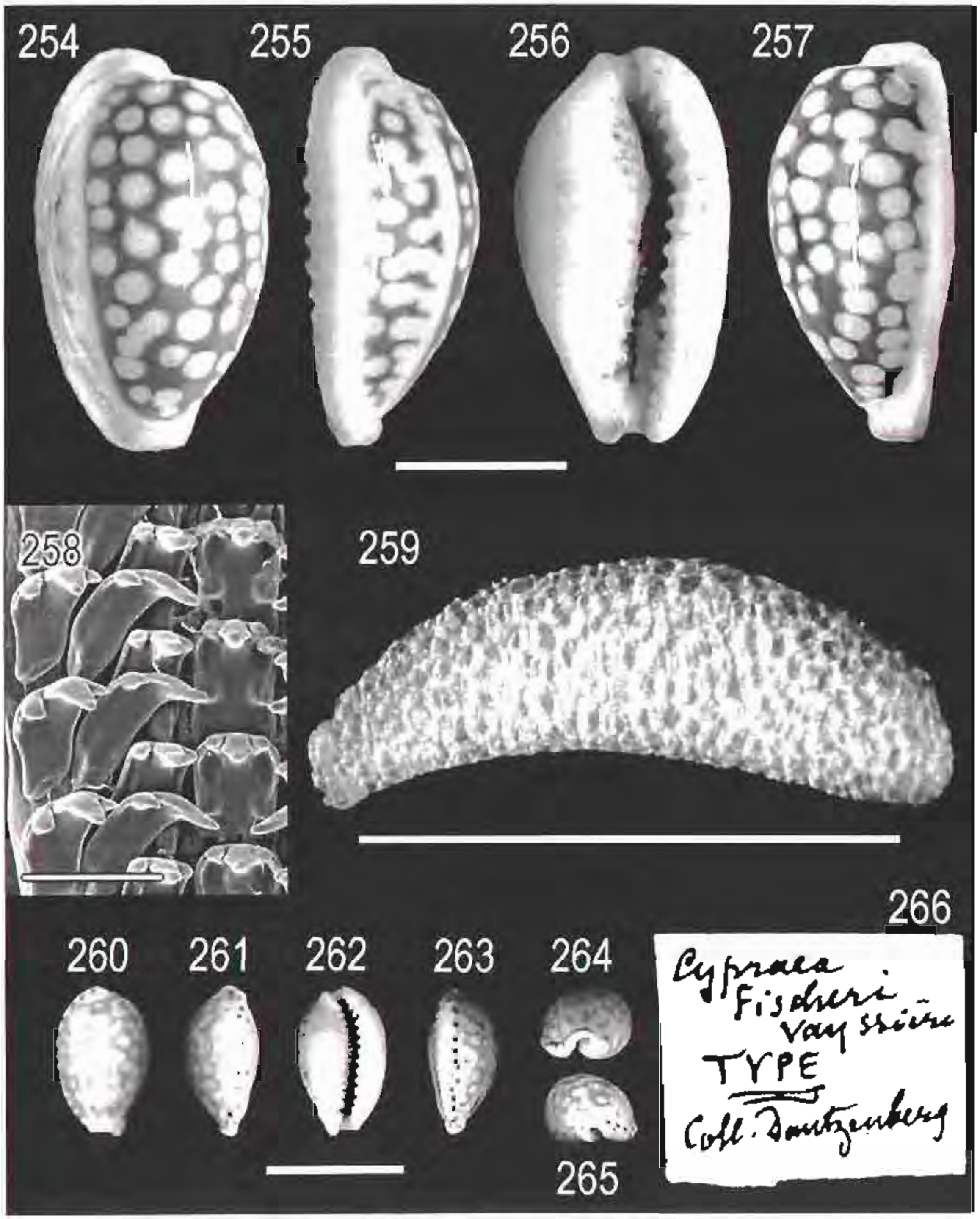
254
255
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266
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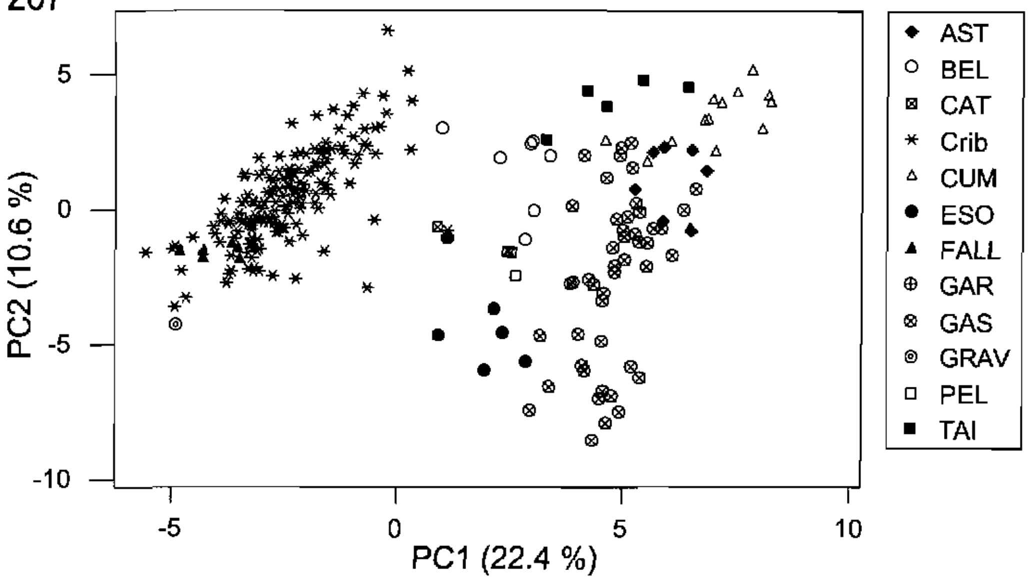
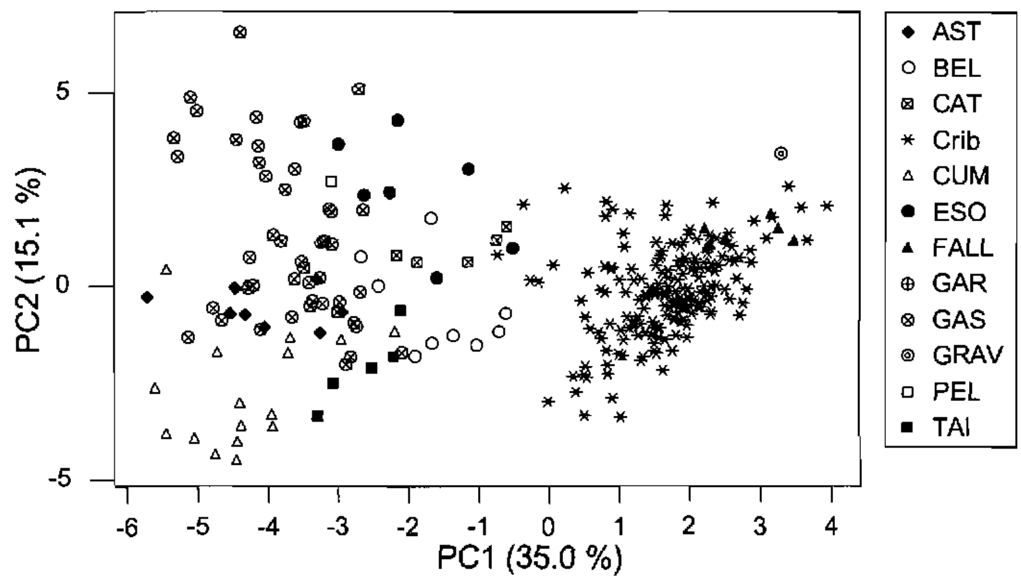
262
263
264
265
Cypraea
Fischeri
Vayssière
TYPE
Coll. Dautzenberg

267



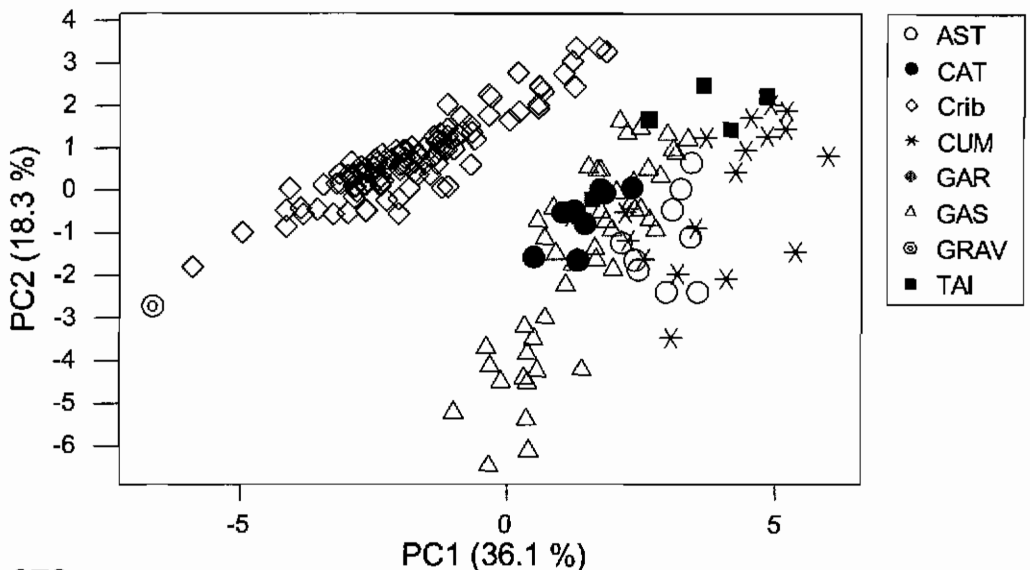
5
0
-5
-10
PC2 (10.6 %)
-5
0
5
10
PC1 (22.4 %)
AST
BEL
CAT
Crib
CUM
ESO
FALL
GAR
GAS
GRAV
PEL
TAI

268

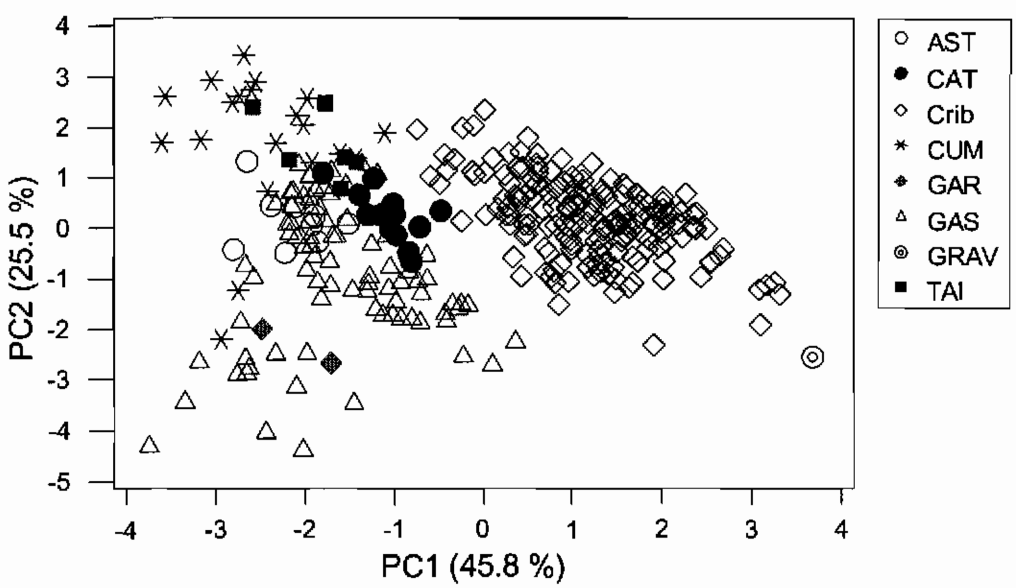


5
0
-5
PC2 (15.1 %)
-6
-5
-4
-3
-2
-1
0
1
2
3
4
PC1 (35.0 %)
AST
BEL
CAT
Crib
CUM
ESO
FALL
GAR
GAS
GRAV
PEL
TAI

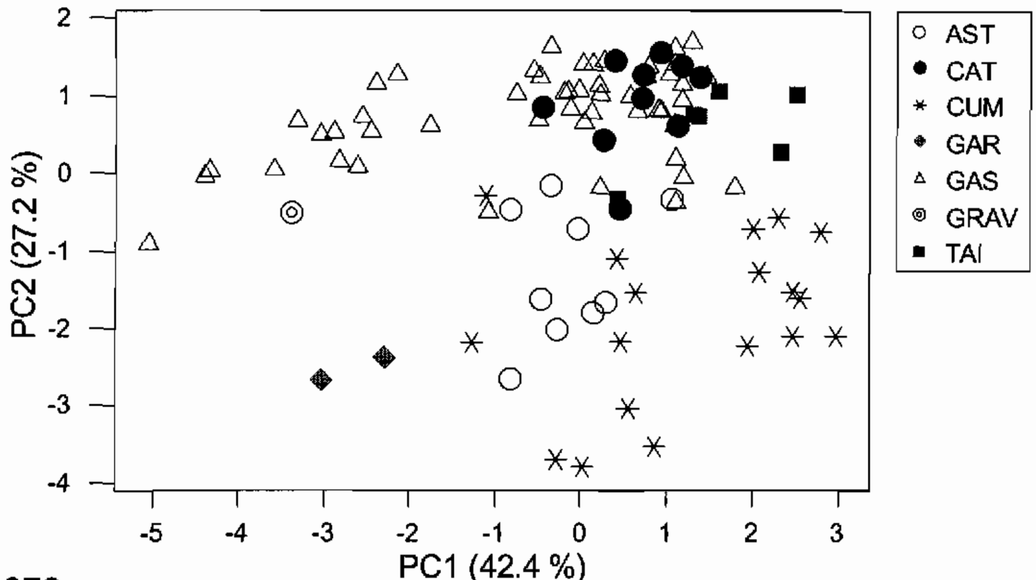
269


4
3
2
1
0
-1
-2
-3
-4
-5
-6
PC2 (18.3 %)
-5
0
5
PC1 (36.1 %)
AST
CAT
Crib
CUM
GAR
GAS
GRAV
TAI

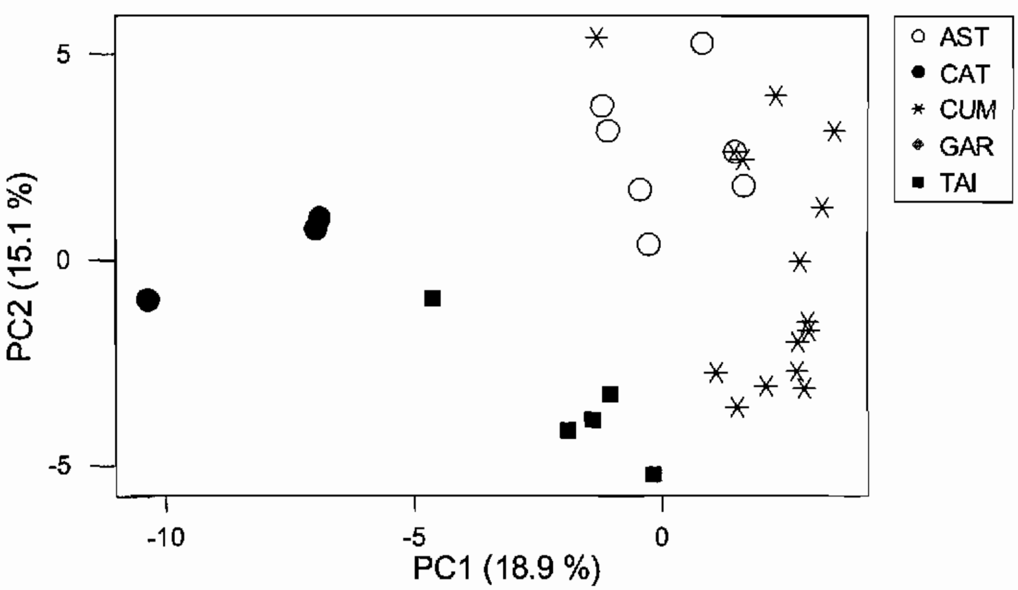
270


4
3
2
1
0
-1
-2
-3
-4
-5
PC2 (25.5 %)
-4
-3
-2
-1
0
1
2
3
4
PC1 (45.8 %)
AST
CAT
Crib
CUM
GAR
GAS
GRAV
TAI

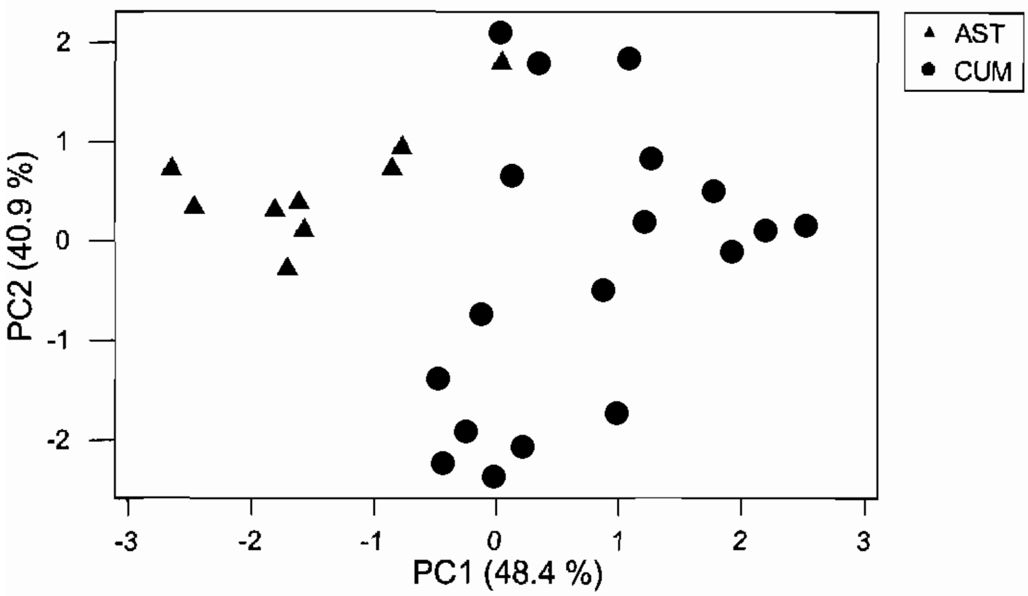
271


AST
CAT
CUM
GAR
GAS
GRAV
TAI
PC2 (27.2 %)
PC1 (42.4 %)
2
1
0
-1
-2
-3
-4
-5
-4
-3
-2
-1
0
1
2
3

272


AST
CAT
CUM
GAR
TAI
PC2 (15.1 %)
PC1 (18.9 %)
5
0
-5
-10
-5
0

273



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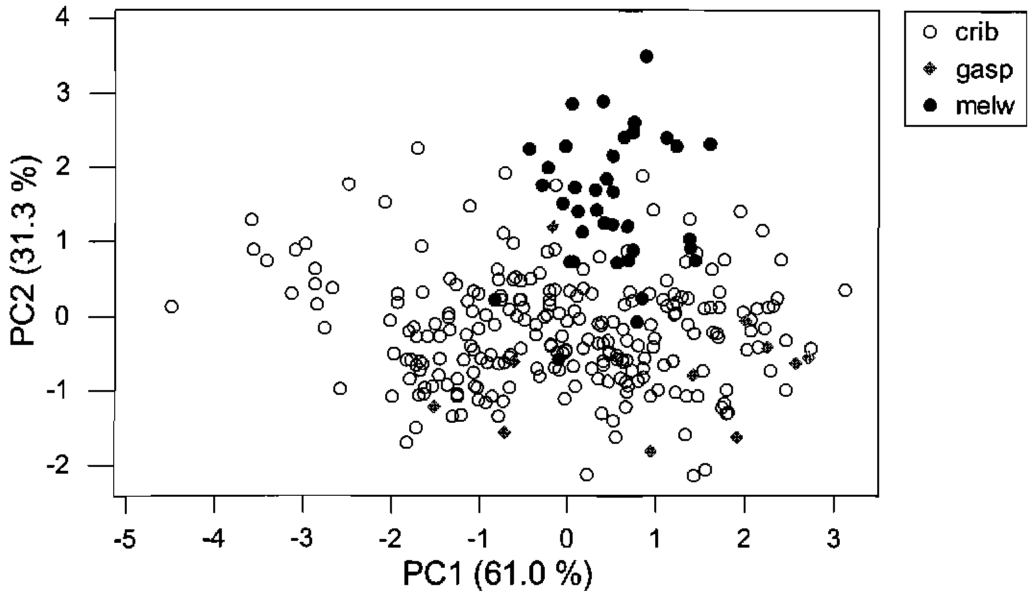
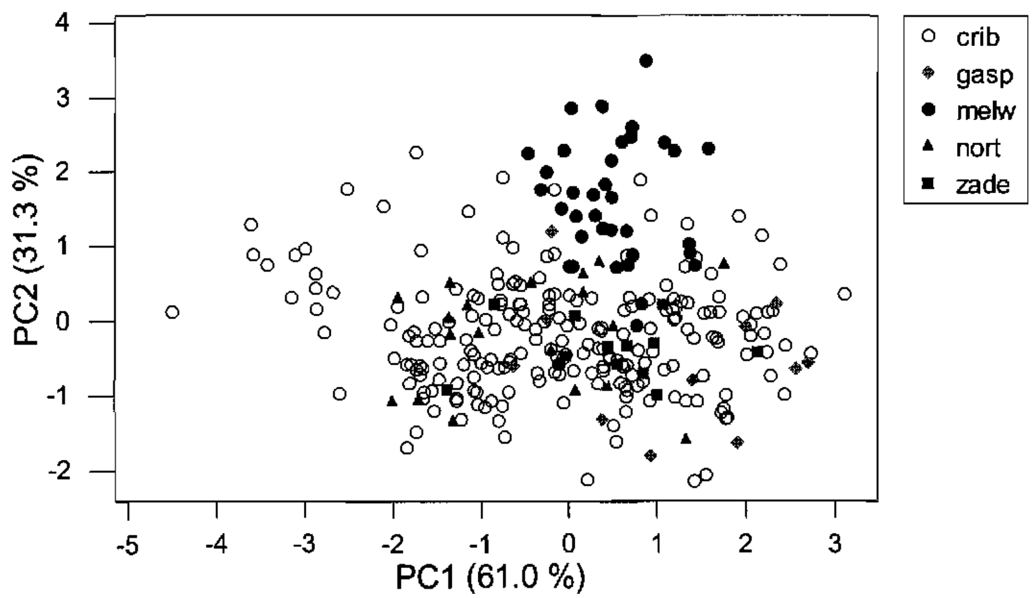


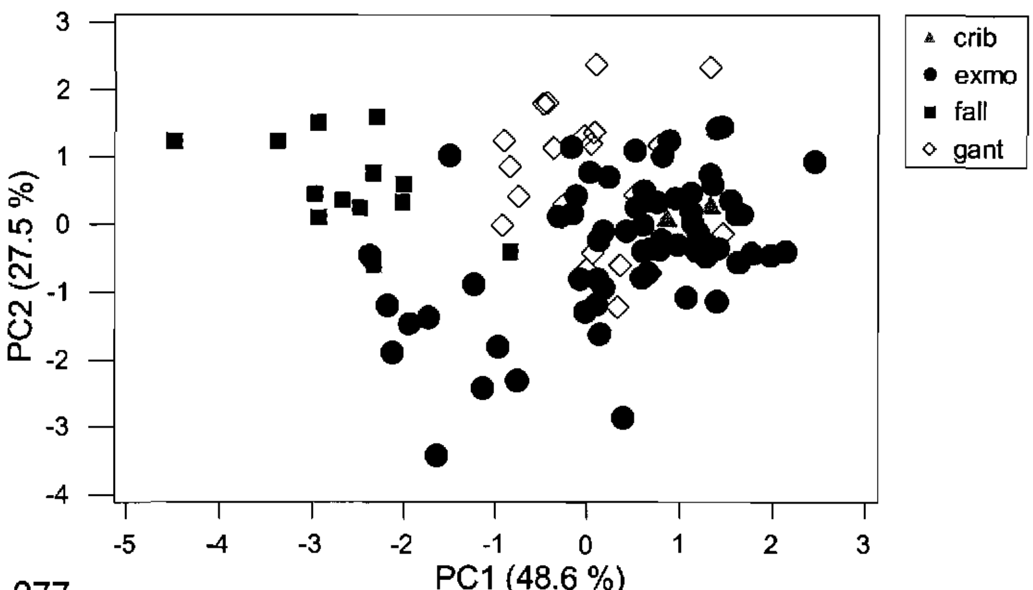
crib
gasp
melw
PC2 (31.3 %)
PC1 (61.0 %)

275

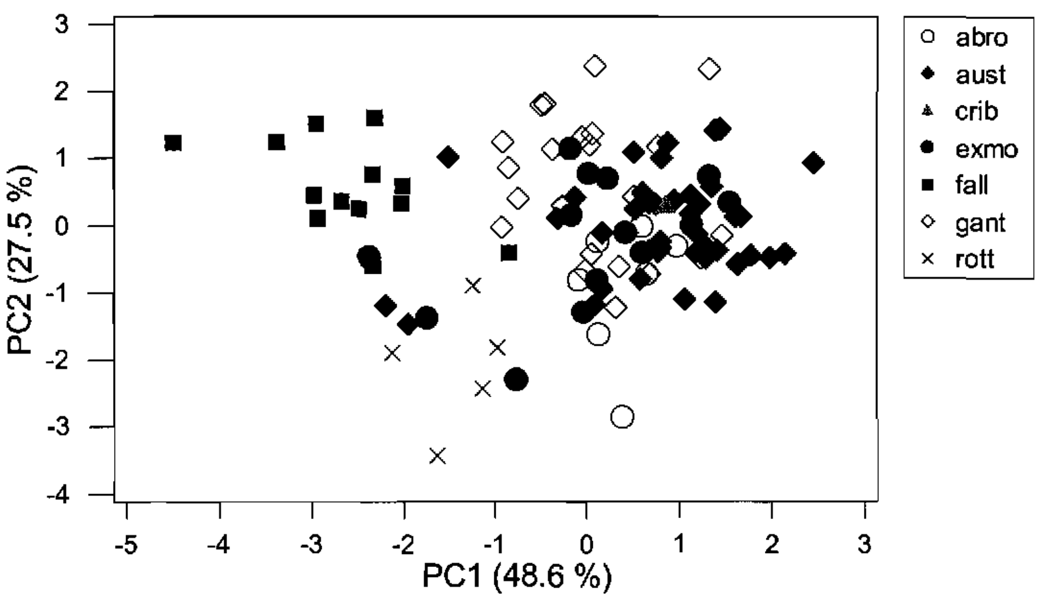


crib
gasp
melw
nort
zade
PC2 (31.3 %)
PC1 (61.0 %)

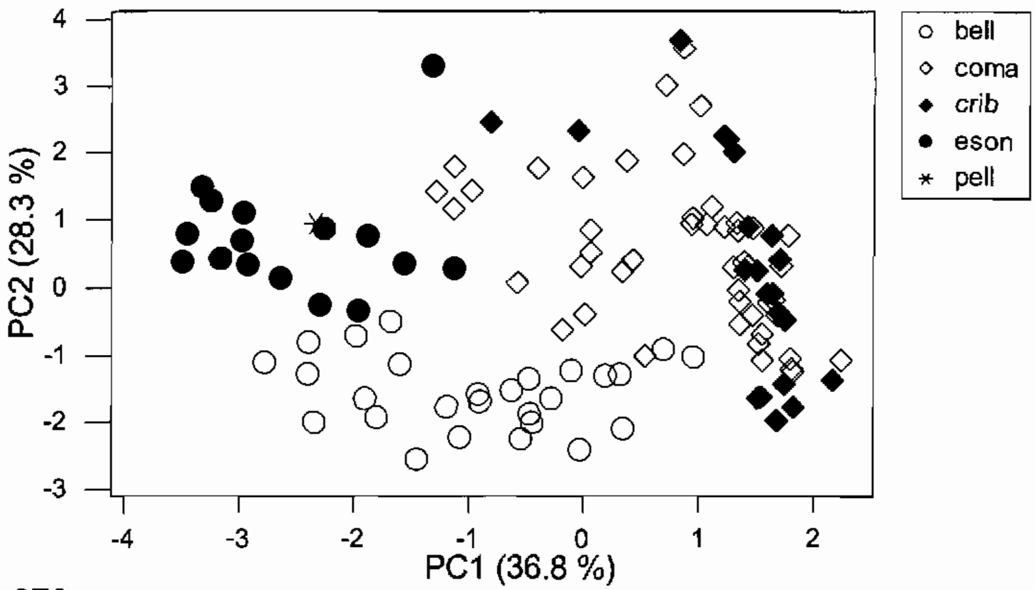
276


3
2
1
0
-1
-2
-3
-4
PC2 (27.5 %)
-5
-4
-3
-2
-1
0
1
2
3
PC1 (48.6 %)
crib
exmo
fall
gant

277

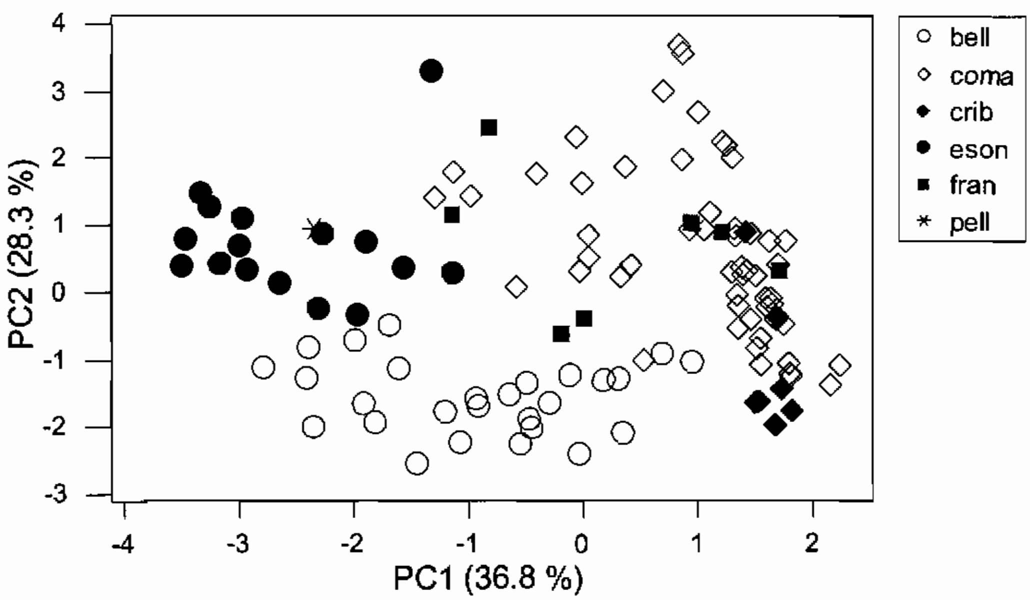

3
2
1
0
-1
-2
-3
-4
PC2 (27.5 %)
-5
-4
-3
-2
-1
0
1
2
3
PC1 (48.6 %)
abro
aust
crib
exmo
fall
gant
rott

278

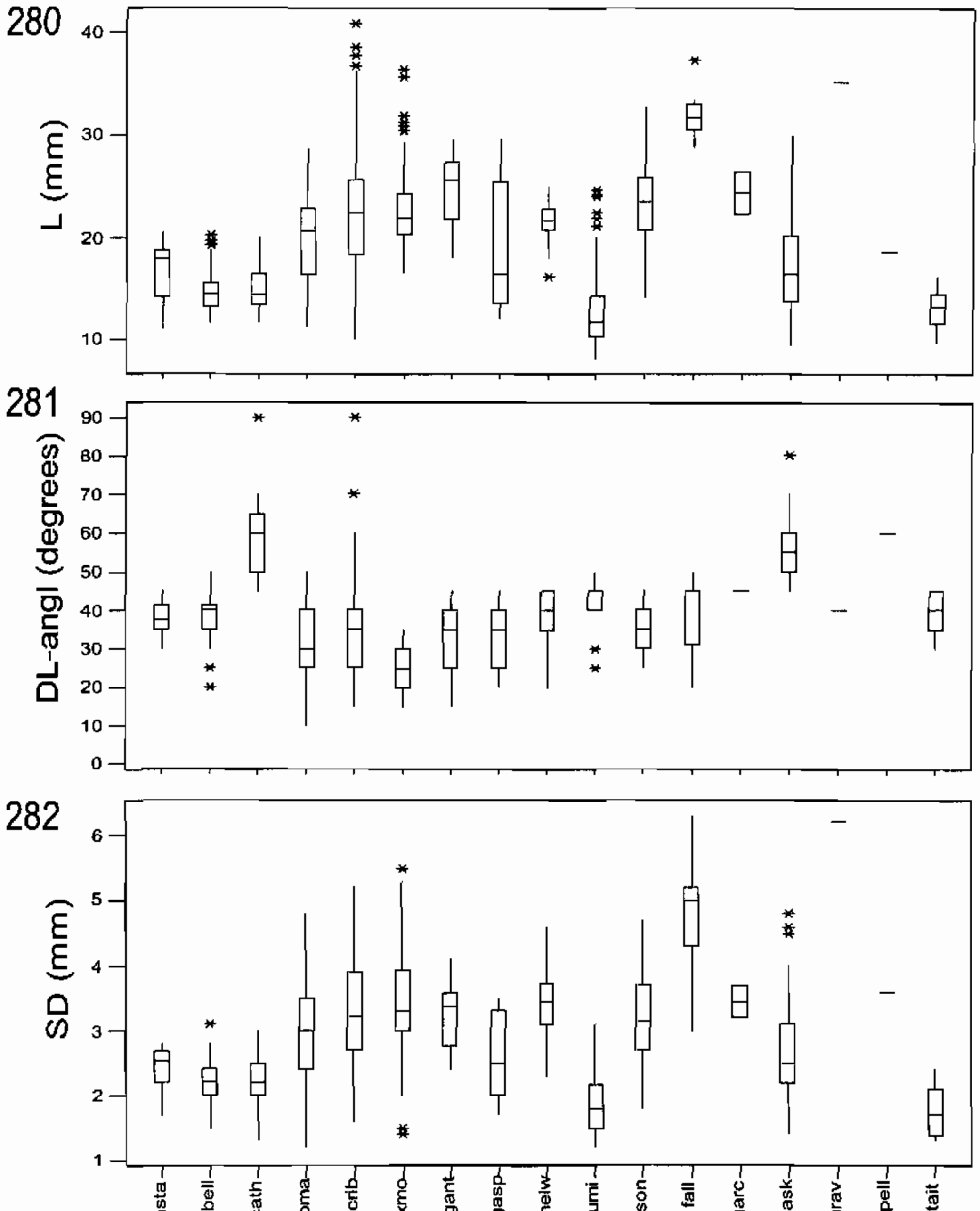


bell
coma
crib
eson
pell
PC2 (28.3 %)
PC1 (36.8 %)

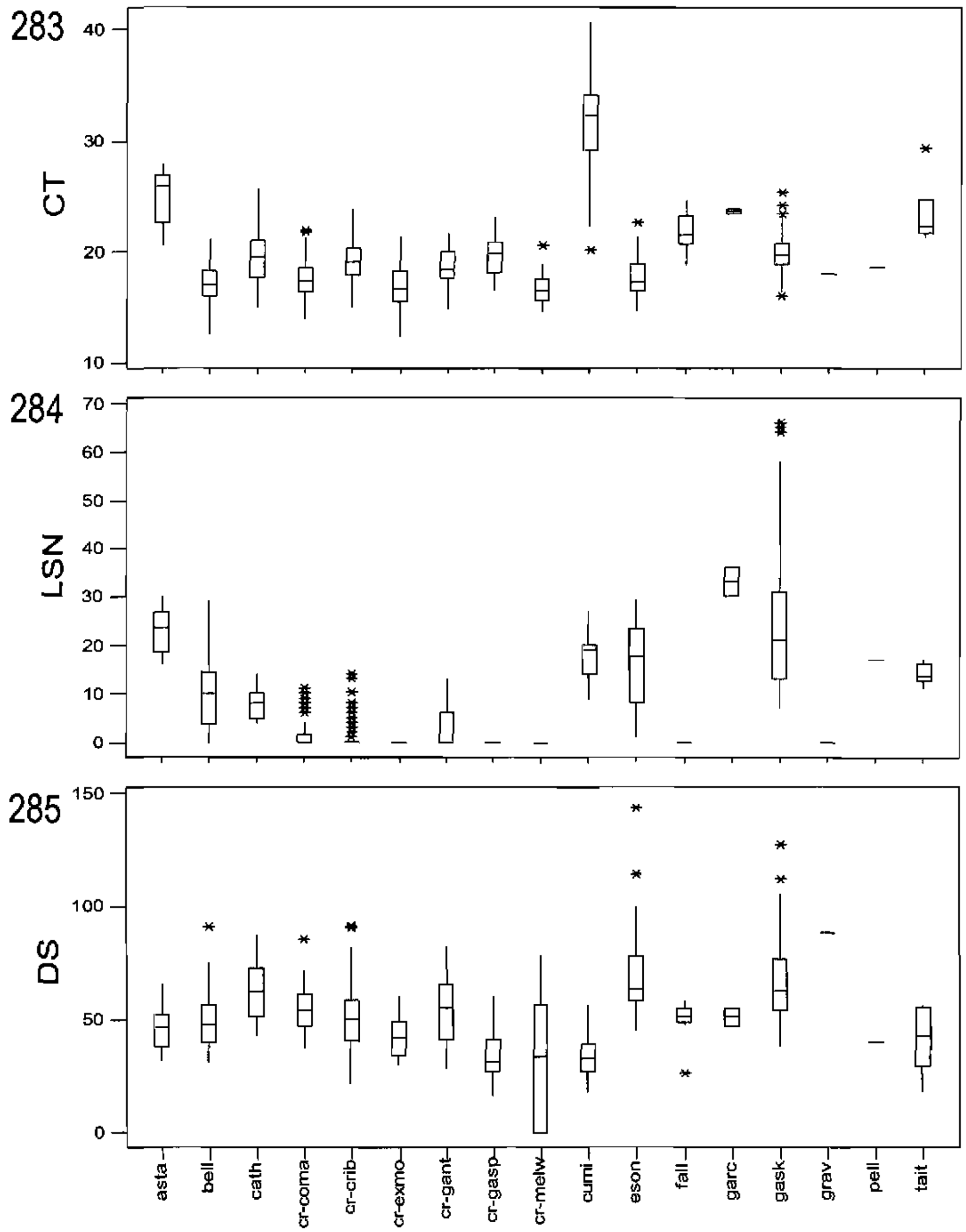
279

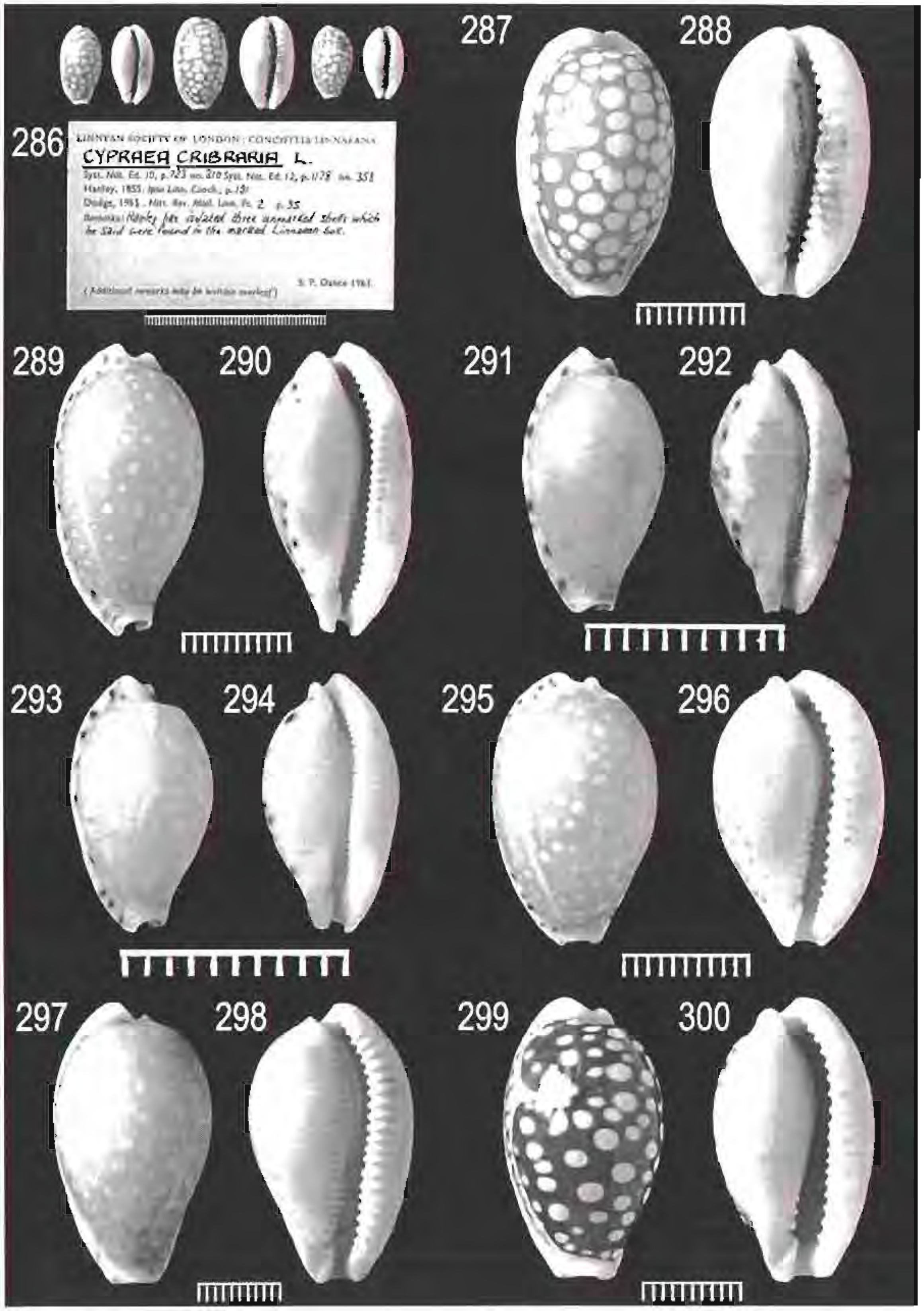


bell
coma
crib
eson
fran
pell
PC2 (28.3 %)
PC1 (36.8 %)



280
L (mm)
281
DL-angl (degrees)
282
SD (mm)
asta
bell
cath
cr-coma
cr-crib
cr-exmo
cr-gant
cr-gasp
cr-melw
cumi
eson
fall
garc
gask
grav
pell
tait


283
284
285
CT
LSN
DS
asta
bell
cath
cr-coma
cr-crib
cr-exmo
cr-gant
cr-gasp
cr-melw
cumi
eson
fall
garc
gask
grav
pell
tait


286
CYPRAEA CRIBRARIA L.
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299
300

APPENDIX 6.1. Shell characters and description of their character states. Additional character states may be needed to code shells of other cowries.

1. Shell length (**L**, Fig. 6.206). The longest dimension of the shell (in mm).
2. Shell width (**W**, Fig. 6.206). The widest dimension of the shell (in mm).
3. Shell height (**H**). Distance measured from base to highest point of shell dorsum (in mm).
4. Spire diameter (**SD**, Fig. 6.206). Measured in mm. This is an approximation of the diameter of the spire, because in many cases it is difficult to measure the exact diameter when there is a callus, the spire is flat, or it it umbilicated. In the last case, the shell can be placed under a light source to produce a reflection where the shell surface starts to umbilicate (the rim of the spire region). This overestimates the real diameter of the spire in flat or umbilicate spires, but works to separate species. It is easier to measure the diameter when the spire is projecting than when it is flat.
5. Spire umbilication (**U**). In most cowries, the spire is not visible in the adult shell. The character states are the following: (0) umbilicate; (1) flat; (2) projecting.
6. Shell width-length ratio (**W/L**). Expressed as percent.
7. Shell height-width ratio (**H/W**). Expressed as percent.
8. Labral spot diameter (**LSD,** Fig. 6.205). (0) none; (1) small; (2) medium; (3) large.

9. Columellar teeth count (**CT**, Fig. 6.205). Number of teeth (or clicks made by a needle sliding over) on the columella near the base of the shell (transformed as in the Schilders' formula). Denticulation on the fossula (inside the aperture) was not counted as CT.

10. Labral teeth count (**LT**, Fig. 6.205). Number of teeth on the labrum, counted and transformed as are CT.

11. Shell shape (**SS**) (Fig. 6.207). Six shapes are recognized in Recent cowries (Lorenz and Hubert, 2000): (0) cylindrical, (1) ovate, (2) pyriform, (3) rhomboidal, (4) rostrate, and (5) globular. Most shells of *Cribrarula esontropia* are rhomboidal or pyriform; those of the sympatric *cribellum* are usually cylindrical. Shells of *gaskoinii* are typically pyriform, those of *catholicorum* are oval. Shells of other taxa in the *cribraria* complex are usually oval or pyriform; some are rostrate (e.g. some shells of *cribraria* from New Caledonia). The character state "globular" does not occur in the *cribraria* complex (shell of *Lyncina leucodon* (Broderip, 1828) shown in Fig. 6.207-5).

12. Aperture constriction (**APC**) (0) center; (1) 2/3 posterior; (2) parallel; (3) extremities.

13. Anterior end rostratation (**AR**) (0) not rostrate/blunt; (1) slightly rostrate (2) rostrate.

14. Posterior end rostration (**PR**) (0) not rostrate/blunt; (1) slightly rostrate (2) rostrate.

15. Fossular inclination. The fossula (Fig. 6.205) is a region in the anterior columella that in some cowries can be differentiated from the rest of the columella (the peristome, Fig. 6.205). The fossula is here defined as the anterior 1/3 of the columella. Character states: (0) abrupt; (1) steep; (2) sloped; (3) inflected.

16. Peristomial inclination. The peristome is defined here as the posterior 2/3 of the columella. Character states: (0) abrupt; (1) steep; (2) sloped; (3) inflected.

17. Fossular concavity: (0) grooved; (1) concave; (2) flat; (3) convex.

18. Peristomial concavity: (0) grooved; (1) concave; (2) flat; (3) convex.

19. Fossular width: (0) narrow; (1) medium; (2) wide.

20. Number of denticles in the fossula similar to columellar teeth, or there are fewer or more denticles than CT: (0) same number; (1) 1+ CT; (2) 2+ CT; (3) 1- CT; (4) 2- CT.

21. Number of denticles in the peristome similar to columellar teeth, or there are fewer or more denticles than CT: (0) same number; (1) 1+ CT; (2) 2+ CT; (3) 1- CT; (4) 2- CT.

22. Callus on fossula: (0) absent; (1) present.

23. Gap between terminal ridge and first tooth (**gap**, Fig. 6.205) (0) less than width of 1st tooth; (1) about same width 1st tooth (up to 1.2); (2) larger than 1.3 widths of 1st tooth.

24. Terminal ridge (**TR**, Fig. 6.205) (adapted from Schilder and Schilder, 1938-1939: 125). (0) oblique; (1) oblique raised; (2) medium oblique (intermediary); (3) parallel; (4) parallel raised.

25. CT encroach on base. Length of columellar teeth on the labrum: (0) barely; (1) short; (2) long.

26. LT encroach on labrum. Length of labral teeth on the base: (0) barely; (1) short; (2) long.

27. Labrum keeled: (0) not keeled or round; (1) keeled; (2) keeled sharp; (3) prominent but rounded keel; (4) extremely keeled.

28. Marginal sulcus (**MSu**, Fig. 6.206): (0) none; (1) slightly sulcate; (2) sulcate.

29. Labrum upturned. Center of labrum in shells of *Cribrarula cumingii* (and other species) upturned, anterior declivous (character state 2). (0) no; (1) center up; (2) center up, anterior declivous; (3) anterior declivous.

30. Callus near spire: (0) none; (1) callus; (2) callus and spot; (3) spot only.

31. Columellar spots size (**CSD**, Fig. 6.205): (0) none; (1) small; (2) medium; (3) large.

32. Labral spot color (**LSC**): (0) none; (1) faint; (2) light brown/caramel/orange; (3) brown/dark brown; (4) black; (5) other.

33. Columellar spot color (**CSC**): (0) none; (1) faint; (2) light brown/caramel/orange; (3) brown/dark brown; (4) black; (5) other.

34. Labral spots encroach base. (0) no; (1) barely; (2) yes.

35. Columellar spots encroach base. (0) no; (1) barely; (2) yes.

36. Dorsal spot color: (0) none; (1) white; (2) ivory/gray; (3) beige/caramel; (4) melanistic; (5) other.

37. Dorsal spots of uniform size: (0) no dorsal spots; (1) most DS close to maximum diameter; (2) uneven; (3) bimodal.

38. Dorsal spot count (**DS**, Fig. 6.206). Number of dorsal spots (complete or nearly complete spots) counted on the shell; an approximation can be calculated by counting DS on a photograph of the dorsal view of a shell, then using a regression. In the *Cribrarula cribraria* complex the regression is: DS-Photo = 5.47 + 0.71 * DS-Shell (N= 363, R^2 = 0.84)

39. Dorsal spots density: (0) no spots; (1) low density; (2) medium; (3) high.

40. Ring around DS: (0) no ring; (1) dark ring around spot.

41. Dorsal spot shape: (0) no dorsal spots; (1) round; (2) elliptical; (3) irregular.

42. Dorsal Spot fusion: (0) no dorsal spot/no fusion; (1) some fusion/much fusion; (2) incomplete, netting.

43. Dorsal spot distinctive: Most shells of *Cribrarula cribraria* have distinct dorsal spots, but shells of *exmouthensis* and *comma* often have indistinctive DS: (0) no dorsal spot; (1) distinct; (2) indistinct; (3) smeared.

44. Dorsal coat overlay. Overlays in shells of *exmouthensis* and *comma* are common, but they may also occur on shells of other species: (0) no dorsal coating; (1) normal; (2) overlay, misregistration; (3) melanistic.

45. Dorsal coating color (Fig. 6.208). Color of the pigmented layer on the dorsum of the shell, between dorsal spots: (0) white/ivory; (1) beige; (2) dark yellow; (3) caramel; (4) orange brown; (5) brown or chocolate; (6) melanistic; (7) other.

46. Shell base color. Most species in the *cribraria* complex have shells with a white base, but some can be off-white or with some color. Character states: (0) white; (1) ivory/gray; (2) beige; (3) caramel.

47. Shell side color. The labral and columellar margins are often white in shells of species of *Cribrarula*: (0) white; (1) ivory/gray; (2) beige; (3) caramel.

48. Aperture curved. The aperture of cowrie shells is usually slightly curved to the left, but is sometimes straight: (0) curved; (1) straight.

49. Anterior terminus thickness: (0) delicate; (1) fine; (2) medium; (3) thick.

50. Posterior terminus thickness: (0) delicate; (1) fine; (2) medium; (3) thick.

51. Dorsal Anterior Flare: (0) flare; (1) horizontal/ not flared; (2) convex.

52. Labral marginal callus (**LMC**, Fig. 6.206): (0) none/absent; (1) callus; (2) strong callous.

53. Columellar marginal callus (**CMC**): (0) none/absent; (1) callus; (2) strong callous.

54. Dorsal line (**DL**, Fig. 6.206): (0) absent/inconspicuous; (1) present.

55. Dorsal line thickness (**DLT**, Fig. 6.206): (0) none; (1) thin; (2) medium; (3) thick.

56. Dorsal line curved: (0) irregular; (1) curved; (2) straight.

57. Dorsal line angle (**DLA**, Fig. 6.209): (0) 0° to 45°; (1) 46° or larger.

58. Dorsal bands (**DB**): (0) none; (1) one band; (2) two or more bands.

59. Marginal spots (either CS, LS) presence: (0) no marginal spots; (1) few spots; (2) distinctively marginally spotted.

60. Labral marginal spot count (**LS**, Figs. 6.205 and 6.206). Number of marginal spots on the labral margin.

61. Columellar marginal spot count (**CS**, Fig. 6.205). Number of marginal spots on the columellar side.

APPENDIX 6.2. List of names in the *Cribrarula cribraria* complex, in alphabetical order, including infrasubspecific taxa (based mostly on Schilder and Schilder, 1971; Walls, 1979; Burgess, 1985; Lorenz and Hubert, 2000, Lorenz, 2002). Names in bold are those I recognize as valid.

Taxon	Author	Year	Distribution	Status
abaliena	Lorenz	1989	Zanzibar	syn. of *comma*
abrolhensis	Lorenz	2002	SW Australia	syn. of *exmouthensis*
astaryi	Schilder	1971	NW Polynesia	**valid species**
australiensis	Lorenz	2002	NW Australia	syn. of *exmouthensis*
catholicorum	Schilder and Schilder	1938	Melanesia	**valid species**
cleopatra	Schilder and Schilder	1938	Polynesia	syn. of *cumingii*
comma	Perry	1811	W. Indian Oc.	**subsp. of *cribraria***
compta	Pease	1860	Polynesia	syn. of *cumingii*
cribellum	Gaskoin	1849	Mascarene Is.	**valid species**
cribraria	Linnaeus	1758	IWP	**valid species**
cumingii	Sowerby II	1832	Polynesia	**valid species**
esontropia	Duclos	1833	Mascarene Is.	**valid species**
exmouthensis	Melvill	1888	W. Australia	**subsp. of *cribraria***
fallax	Smith	1881	SW Australia	**valid species**
fischeri	Vayssière	1910	Hawaiian Is.	syn. of *gaskoini*

APPENDIX 6.2 – continuation

Taxon	Author	Year	Distribution	Status
francescoi	Lorenz	2002	E. Africa	syn. of *esontropia*
ganteri	Lorenz	1997	Sri Lanka	**subsp. of *cribraria***
garciai	Lorenz and Raines	2001	Easter Island	**valid species**
gaskoinii	Reeve	1846	Hawaiian Is.	**valid species**
gaspardi	Biraghi and Nicolay	1993	Marshall Is.	**subsp. of *cribraria***
gravida	Moretzsohn	2002	NSW, Australia	**valid species**
lefaiti	Martin and Poppe	1989	Marquesas	syn. of *astaryi*
maculata	Anonymous	1810		syn. of *cribraria*
magnifica	Lorenz	2002	NW Australia	syn. of *exmouthensis*
melwardi	Iredale	1930	Queensland	**subsp. of *cribraria***
northi	Steadman and Cotton	1943	Melanesia	syn. of *cribraria*
occidentalis	Raybaudi	1987	W. Australia	syn. of *exmouthensis*
oceanica	Raybaudi	1993	Kwajalein	syn. of *gaspardi*
ocellata	Bolten (non Linnaeus, 1758)	1798		syn. of *gaskoini*
orientalis	Schilder and Schilder	1940		syn. of *cribraria*
peasei	Sowerby	1870		syn. of *gaskoini*
pellisserpentis	Lorenz	1999	Madagascar	**valid species**

Appendix 6.2 – continuation

Taxon	**Author**	**Year**	**Distribution**	**Status**
pellucida	Taylor	1916		syn. of *esontropia*
rottnestensis	Raybaudi	1987	W. Australia	syn. of *cribraria*
rottnestensis	Lorenz	2002	SW Australia	syn. of *exmouthensis*
taitae	Burgess	1993	Melanesia	**valid species**
zadela	Iredale	1939	Queensland	syn. of *cribraria*

Appendix 6.3. Dichotomous key to species of *Cribrarula* Strand, 1929

1 Shell with marginal spotting 4

1' Shell without marginal spotting, or rarely with faint marginal spots..... 2

2 Large shell (> 28 mm), slopping ribbed fossula with columellar teeth extending onto base, yellowish dorsal coat, indistinct dorsal spots (DS), from the Albany region (SW Australia)............................. *fallax*

2' Columellar teeth not extending onto base, brown (or white) dorsal coat 3

3 Large pyriform inflated shell (> 30 mm), slopping ribbed fossula, brown dorsal coat with large (> 2.8 mm diameter) elliptical indistinct DS, wide spire, from New South Wales, Australia................ *gravida*

3' Shell of variable size and color, but not as above .... *cribraria* (go to number 13 for subspecies of *C. cribraria*)

4 Marginal spots small or faint, in a single or few rows on labrum 5

4' Marginal spots black or brown, medium to large 7

5 Shell broad, ovate with blunt extremities, dorsal line distinct, dorsal margin of anterior canal not flared, from Melanesia............................. *catholicorum*

5' Columellar teeth coarse in anterior region of columella, fossula steep or inflected, dorsal bands visible 6

6 Marginal spots seen on base, dorsal line indistinct, shell ovate to rhomboidal, sometimes with heavy marginal calluses, dorsum densely spotted, from the Mascarene region and SE Africa .... *esontropia*

6' Shell cylindrical elongate, small (< 19 mm), 3-4 dorsal bands, from Mascarene Islands (Mauritius) .... *cribellum*

7 Several rows of marginal spots on labrum, ... 8

7' Single or few rows of marginal spots on labrum 9

8 Large black marginal spots, columellar teeth fine (> 23), broad ovate shell, blunt extremities, orange-brown dorsal coat, dark ring around sparse DS, from Easter Island or Marquesas .... *garciai*

8' Ovate elongated (< 18 mm) or inflated ovate shell, with rostrate extremities, orange-brown dorsal coat, many columellar marginal spots, from Hawaii .... *gaskoini*

9 Columellar teeth coarse in anterior region of columella, shell cylindrical elongate, small (< 19 mm), 3-4 dorsal bands, from Mascarene Islands (Mauritius) .... *cribellum*

9' Columellar teeth fine to very fine 10

10 Several rows of marginal spots on columellar margin, shell inflated, dorsal spots incomplete, from Madagascar .... *pellisserpentis*

10' Single or few rows of marginal spots, columellar teeth fine to very fine 11

11 Shell ovate rostrate, with very fine columellar and labral teeth, fossula finely denticulate, grooved, with callus, labrum flat, anteriorly declivous toward aperture, median labrum bent upward, from Polynesia .... *cumingii*

11’ Columellar teeth fine, shell not as rostrate as in previous species 12

12 Small shell (average 13 mm), fossula concave, labral teeth medium-fine, marginal spots brown, from Samoa or Marquesas .... *taitae*

12’ Shell larger than above (average 17 mm), fossula steep, grooved, columellar teeth fine than above, dark ring around DS, dorsal coat orange, marginal spots large, black, from the Marquesas Is. .... *astaryi*

13 Dorsal spots indistinct, dorsal coat dark brown 14

13’ Dorsal spots distinct, or completely or partially absent 15

14 Shell ovate pyriform, not rostrate, fossula abrupt, from East Africa ..... *comma*

14’ Shell pyriform to rhomboidal, sometimes inflated, fossula steep, from West Australia .... *exmouthensis*

15 Shell broad, marginally callous, thick labrum, shell completely white, or partially or fully covered with light brown dorsal coat, from Queensland, Australia .... *melwardi*

15’ Dorsal coat fully covers dorsum 16

16 Shell usually small, oval rostrate with relatively large and few dorsal spots, extremities finely margined, dorsal margin anterior canal flared, from the Marshall Islands .... *gaspardi*

16’ Shell ovate, densely covered with distinct DS, relatively smaller than as above 17

17 Brown or black marginal spots present, average 3 on each side, from Sri Lanka .... *ganteri*

17' Shell ranging from small to large (10 to 40 mm), columellar teeth usually fine, marginal spots absent, or rarely, a few faint spots, wide Indo-West Pacific distribution .... *crib. cribraria*

APPENDIX 6.4 - List of additional material examined not listed in the text. Note that the symbol "!" denotes "collector" in this study.

Cribrarula cribraria cribraria (Linnaeus, 1758)

Australia, Dampier Arch., King Exp.! (BPBM 209558, 1 specimen); Australia, Exmouth Gulf, 1 mi S. of S.S. Mildusa, N.W. Cape, W. Australia [other label: 1 mile S. of shipwreck, N.W. Cape] (AMS-C 86127, 1 specimen); Australia, Houtman-Abrolhos Is., 1/2 mi E. Little North Is., Houtman Abrolhos Is., Halpern Malacological Fund, ex Mr. and Mrs. C. Cate (# C.2943), ex A.R. Whitworth, A. Gilbertsen!, Jun. 1964 (AMNH 292287, 1 specimen); NW Australia, off Delambre Is., King Exp.! (BPBM 209539, 1 specimen); NW Australia, Long Is., King Exp.! (BPBM 209507, 6 specimens); Australia, Queensland, Albany Passage, Cape York Peninsula, 16-22 m, 010°45'S, 142°37'E, Mel Ward!, Sept. 1928 (AMS-C 58655, 1 specimen); Australia, Queensland, Great Barrier Reef, Whitsunday Ids., Hayman Is., 020°3.6'S, 148°53.5E, F.A. McNeill!, Dec. 1932 (AMS-C 81677, 1 specimen); Australia, Queensland, D. Pisor! (HBR R-141, 1 specimen); Australia, Queensland, Keppel Is., Coral Sea, ex W.E. Old Jr. coll., C. Coucom!, 1964 (AMNH 292280, 3 specimens); Australia, Queensland, Keppel Bay, ex Kienle coll. (DMNH 196201, 1 specimen); Australia, Queensland, Great Barrier Reef, Low Is., M.J. Flood! (BPBM 232303 Thaanum, 1 specimen); Australia, Queensland, Keppel Bay, V.I. Harris! (CAS 112319, 1 specimen); Australia, Queensland, Great Barrier Reef, Feather Reef. ex W.O. Cernohorsky # 47b, ex E. Wright coll., Fitzmaurice!, 1963 (USNM 773542, 2 specimens); Australia, Queensland, Camp Is., W. side of Abbott

Bay, Queensland, 19°50.50'S, 147°54.20'E, K.E. Stager!, 23 Oct. 1988 (LACM 1988-182.5, 2 specimens); Australia, Queensland, Great Barrier Reef, ex W.M. Ingram # 262. Blue dot on label, ex W.M. Ingram (DMNH 43219, 2 specimens); Australia, Shark Bay, AV Helm! (AMS-C 10548, 1 specimen); Australia, ex Stupakoff coll. (CM 62.23413, 1 specimen); Australia, ex Stupakoff coll. (CM 62.23704, 3 specimens); N. Borneo, Malawali Channel, Sabah, ex J. Donohue coll. (#380), 07°00'N, 117°51'E, M. Saul!, Jun. 1964 (ANSP 360141, 1 specimen); Comoros Is., Moroni Is., 011°41'S, 043°16'E, R. Laquay!, Jan. 1967 (AMS-C 364814, 1 specimen); Fiji, Bua, Gil Grau! (BPBM 246797, 1 specimen); Fiji, Lombassa, ex Kienle coll. (DMNH 196198, 1 specimen); Fiji, Mamanuca Group, ex E. Wright coll., W. Cernohorsky! under coral, shallow water (Cernohorsky # 97e), W. Cernohorsky!, 28 Jul. 1966 (USNM 773497, 4 specimens); Fiji, Nausori, behind Dilkusha, new road off Prince's Road, Nakasi Sandstone beds, fossil, Upper Pliocene, ca. 1.9 MYBP, 018°00'S, 178°30'E, K.J. Gilchrist!, pre-1988 (AMS-C 301907, 2 specimens); Fiji, N. Viti Levu, Vatia wharf, under coral, muddy sand location. ex E. Wright coll., W. Cernohorsky!, 1962 (USNM 773483, 3 specimens); Fiji, Viti Levu, West of Nadi, Malolo Lai Lai Id., 15 mi., N. side, Sta. 2, 4.6 ft snorkel, J. Bennett!, Aug. 1984 (DMNH 166744, 1 specimen); Guam, Apra Harbor, H. Conley!, 4 Feb. 1996 (FM 9, 1 specimen); Guam, Apra Harbor, Luminao Reef, ANSP Expedition, reef, 013°28'N, 144°39'E, A.J. + R. Ostheimer!, 1953 (ANSP 197543, 1 specimen); Guam, Apra Harbor, inside of breakwater, 013°22'N, 144°38'E, A.B. Bronson!, 1956 (ANSP 232419, 1 specimen); Guam, Apra Harbor, A. Sorensen coll. (#37287) (CAS 112333, 3 specimens); Guam, Asan Point, on coral heads, 013°28'N, 144°43'E, G.F. Herman!, pre-

1995 (AMS-C 363681, 1 specimen); Guam, Asan Point, 013°28'N, 144°43'E, C.L. Richardson! (ANSP 335316, 1 specimen); Guam, ex A.S. Koto coll., W. P. Cook, 1943 (FMNH 183057/1, 1 specimen); Guam, C.W. Yarrington! (FMNH 85796, 1 specimen); Guam, Mchangani Reef. ex J. Donohue coll. (# 467), 013°30'N, 144040'E, T. Montgomery!, Nov. 1964 (ANSP 359747, 2 specimens); Guam, ex Whitmore-Coats coll. (# 44687) (CAS 112328, 4 specimens); India, Koh Mapraoliam beach, H.M. Smith!, 24 Sept. 1923 (USNM 360987, 1 specimen); Indonesia, Irian Jaya, Sowek, Soepiori Is., Schouten Is., Ostheimer, Orr and Powel, NSF Expedition, Sta. 574, 00°48' 00S, 135°29' 54"E, natives!, 5 Mar. 1956 (ANSP 207887, 1 specimen); Indonesia, Irian Jaya, Irian Barat (ANSP 205127, 1 specimen); Indonesia, Irian Jaya, Irian Barat, Bouesaki Is. (ANSP 207757, 1 specimen); Indonesia, Java, Bantan, Keledjitan, Bryant and Palmer!, 1909-1910 (USNM 593616, 1 specimen); Indonesia, Java, Bantan, Bryant and Palmer!, 1909-1910 (USNM 260710, 2 specimens); Indonesia, Sumatra, Indonesia, Tukangbesi Is., 05°40'S, 123°50'E (CAS 112317, 1 specimen); Indonesia, Sumatra, Bakungan, 02°56'N, 97°30'E (ANSP 389645, 2 specimens); Indonesia, Sumatra, Sumatra, Palai Bai, Batu group, Te Vega "A" M°32, 0°18'S, 98°28'E (USNM 654501, 2 specimens); Japan, Chiba, 035°30'N, 140°20'E, ex A.R. Cahn coll (ANSP 240636, 1 specimen); Japan, Okinawa, Zampa Misaki, Crawford and Jean Cate coll., hypotype (illustrated by Cate), 026°26'N, 127°43'E, B. Albert!, 8 Jan. 1966 (AMNH 292284, 2 specimens); Japan, Okinawa, Miyako Is., 24°45'N, 125°20'E, RJ Rogers!, 1953-56 (FMNH 63306, 1 specimen); Japan, Okinawa, Kowan, Baron Sho Jun!, 1928 (BPBM 232306 Thaanum, 1 specimen); Japan, Okinawa, 26°30'N, 128°30'E, ex A.R. Cahn coll (ANSP 240657, 1 specimen); Japan, Okinawa, Ishigaki, Yuku-san reef, Thaanum!, 1932 (BPBM 232308 Thaanum, 1 specimen); Japan, Okinawa, ex Whitmore-Coats coll. (#44685) (CAS 112329, 2 specimens); Japan, Okinawa, Chishima, D.B.L. + Thaanum!, 1932 (BPBM 232307 Thaanum,4 specimens); Japan, Oshima (CAS 112321, 2 specimens); Japan, Tokyo Prefecture, Hachijo Id., 275 mi S. of Tokyo, ex A.R. Cahn coll., 033°05'N, 139°48'E, O. Omebayashi!, 1951 (ANSP 240283, 1 specimen); Japan, Wakayama, ex J. Donohue coll. (# 32), 034°00'N, 136°30'E, P.W. Clover!, May 1963 (ANSP 359732, 1 specimen); Japan, Wakayama, Kii Peninsula, 034°00'N, 136°30'E, ex A.R. Cahn coll (ANSP 240568, 2 specimens); Japan, Wakayama, 034°00'N, 136°30'E, P.W. Clover!, 20 May 1963 (BPBM 246787, 2 specimens); Japan, ex S. Vatikiotis coll., Dr. J.S. Schwengel!, 1945 (FMNH 77655, 1 specimen); Kenya, Kikambalo, Aug. 1958 (BPBM 246802, 1 specimen); Kiribati, Fanning Atoll, 03°52'N, 159°20'W, W.G. Anderson!, 1921 (BPBM 232309 Thaanum, 1 specimen); Line Ids., Washington Is. (Teraina Is.), 04°43'N, 160°24'W, Thaanum! (BPBM 232302 Thaanum, 2 specimens); Madagascar, Nosy Be, Nosy N'Tangain Is., 013°20'S, 48°15'E (ANSP 258761, 1 specimen); Madagascar (ANSP 260261, 1 specimen); Maldive Is., ex R. Summers coll., 03°15'N, 73°00'E, Rod Jonklaas!, Nov. 1960 (AMNH 292274, 1 specimen); Maldive Is., Male, 04°10'N, 73°30'E, J. Keval! (USNM 701998, 2 specimens); Marianas, Saipan, 015°12'N, 145°45'E, Wm. E. Old!, 1945 (USNM 637158, 4 specimens); Marshall Is., Enewatak, 011°30'N, 162°15'E, S. Johnson! (BPBM 251478, 1 specimen); Marshall Is., Kwajalein, 09°05'N, 167°20'E, ex Kienle coll. (DMNH 196200, 1 specimen); Mauritius, 20°11'S, 57°32'E, Johnson!, 1946 (DMNH 142, 1 specimen); Mauritius, 020°18'S, 057°36'E, Burch coll. (# 4656) (CAS 112320, 1 specimen); Mauritius, 020°18'S, 057°36'E, ex NW Lermond! (DMNH 170197, 1 specimen); Micronesia, Mortlock Is., 05°27'N, 153°40'E (BPBM 69260, 2 specimens); Micronesia, Ponape, 06°55'N, 158°15'E, Gil Grau! (BPBM 246793, 1 specimen); near Phoenix Is., Baker Is., Whippomill Exp., 00°12'N, 176°30'W, T. T. Dranga! (BPBM 67163, 1 specimen); near Phoenix Is., Baker Is., 00°12'N, 176°30'W (ANSP 196028, 1 specimen); New Caledonia, Huie Bay, ex Bledsoe coll. (USNM 876827, 1 specimen); New Caledonia, Nickel Bay, 3m, mud and sand, J. Bota!, Mar. 1980 (AMNH 279459, 1 specimen); New Caledonia, Noumea, Baie de Citron, 1-6 ft, rocks, sand and silt, NSF Expedition, 022°18'S, 166°26'E, G. and M. Kline!, 14 Dec. 1958 (ANSP 237541, 1 specimen); New Caledonia, Noumea, 5 fms., Scuba, 022°15' 24"S, 166°25' 44"E, Bota!, 1964 (DMNH 201203, 1 specimen); New Caledonia, Noumea, Ile Ste. Marie, NW and W side, 0-2 m, coral, rocks and algae, in sandy mud-floored bay, 22°18'S, 166°29'E, P.H. Colman!, Apr. 1971 (AMS-C 83608, 1 specimen); New Caledonia, Noumea, 022°15' 24"S, 166°25' 44"E, ex C. Heller (ANSP 389649, 1 specimen); New Caledonia, Noumea, 022°15' 24"S, 166°25' 44"E, ex Kienle coll. (DMNH 196960, 1 specimen); New Caledonia, Noumea, 022°15' 24"S, 166°25' 44"E (DMNH 196956, 1 specimen); New Caledonia, Noumea, 022°15' 24"S, 166°25' 44"E, ex Kienle coll. (DMNH 196956, 2 specimens); New Caledonia, Noumea, 022°15' 24"S, 166°25' 44"E, ex Kienle coll. (DMNH 196955, 3 specimens); New Caledonia, Nouville, J. E. du Pont!, Oct. 1976 (DMNH 117429, 1 specimen); New Caledonia, Oveu Is., ex Kienle coll., 1980 (DMNH 196925, 1 specimen); New Caledonia, Touho, Touho, By Ile Aiu, 2-5 ft, dead and live coral, sand, barrier reef, by Ile Ain, 3 mi. NSF Expedition, Kline and Orr!, 020°45' 12"S, 165°17' 00"E, 19 Jan. 1961 (ANSP 270282, 1 specimen); New Caledonia, ex Kay C. Vaught coll. (AMNH 292288, 1 specimen); New Caledonia, one specimen from N. Caledonia (melanic), one from Fiji (typical *cribraria*) [should be split into two lots], ex Craig Kauffman, 25 Apr. 1975 (DMNH 155312, 2 specimens); New Caledonia (CAS 112324, 1 specimen); New Caledonia (CAS 112318, 2 specimens); Palau, N. Auluptagel Is., Koror, coll by Ostheimer for ANSP, NSF Expedition, 07°20' 10"N, 134°27' 45"E, A.J. Ostheimer III!, 17 Aug. 1955 (ANSP 202029, 1 specimen); Palau, Babelthuap, coll for ANSP, NSF Expedition, 07°22' 45"N, 134°36' 45"E, A.J. Ostheimer III!, 13 Aug. 1955 (ANSP 203163, 2 specimens); Palau, Babelthuap Is., Reef 1 mi S. of Namelakl Passage, Babelthuap Is., NSF Expedition, 07°22' 45"N, 134°36' 45"E, A.J. Ostheimer III!, 13 Aug. 1955 (ANSP 203163, 2 specimens); Palau, Kayangel Is., N. sides of Ngariungs and Ngarapalas Is., coll. Ostheimer for ANSP, NSF Expedition, 08°03' 45"N, 134°43' 00"E, A.J. Ostheimer III!, 2 Aug. 1955 (ANSP 201433, 1 specimen); Palau, Koror, Reef S. of town, 07°15'N, 134°30'E, A.J. Ostheimer III!, 1954 (ANSP 266979, 1 specimen); Palmyra Is., ex Thaanum coll., 05°52'N, 162°06'W (USNM 348432, 1 specimen); Palmyra Is., ex W.M. Ingram # 151, old label on pencil says Kagoshima Bay in one side, and *Cypraea cribraria* Palmyra on the other side, 05°52'N, 162°06'W, ex W.M. Ingram (DMNH 43356, 1 specimen); Palmyra Is., 05°52'N, 162°06'W, Thaanum!, 1922 (BPBM 232305 Thaanum, 1 specimen); Palmyra Is., 05°52'N, 162°06'W, Thaanum!, 1922 (BPBM 232304 Thaanum, 1 specimen); Palmyra Is., 05°52'N, 162°06'W, L.A.T. and T.T.T.! (BPBM 197411, 2 specimens); Philippines, Bataan, Villa Carmen, western part of state, ex Norton, 29 Jun. 1966 (DMNH 183635, 1 specimen); Philippines, Bataan, Villa Carmen, western part of state, J. E. Norton!, 1962 (DMNH 183634, 1 specimen); Philippines, Bataan, ex J. Donohue coll. (#604), E. Liao!, Jan. 1966 (ANSP 359712, 2 specimens); Philippines, Bohol, Panglao, Hypotype, illustrated by Cate (*Veliger* 8(4), pl. 45, f. 72ab (1966)), Philippines Cowries. ex C. and J. Cate coll. (c.1252), F.G. Dayrit!, 1.iv.1966 (AMNH 292282, 1 specimen); Philippines, Bohol, Calituban, NW Bohol, fisherman!, Mar. 2001 (FM 997, 19 specimens); Philippines, Cebu Is., Malboal Is., H. Bradner!, Feb. 1987 (HBR, no catalog number, 2 specimens); Philippines, Cebu Is., ex R. Summers coll., 1970 (AMNH 292266, 3 specimens); Philippines, Cebu Is., Masbate Is., DAN, 1999 (FM 361, 1 specimen); Philippines, Cebu Is., ex J. Donohue coll. (# 340), 010°20'N, 123°45'E, D. Dan!, May 1964 (ANSP 359702, 1 specimen); Philippines, Cebu Is., ex J. Donohue coll (# 554), 010°20'N, 123°45'E, F. Dayrit!, Oct. 1965 (ANSP 359701, 1 specimen); Philippines, Cebu Is. (ANSP 395178, 1 specimen); Philippines, Cebu Is., Pyrema! (BPBM 246784, 9 specimens); Philippines, Masbate Is., Near Samar I., fisherman!, Mar. 2001 (FM 998, 22 specimens); Philippines, Mindanao, under coral, ex C. Kauffman (DMNH 155331, 2 specimens); Philippines, Mindoro, Cabra Is., ex P. Mesa coll. (BPBM 232310 Thaanum, 1 specimen); Philippines, Mindoro, Davao (BPBM 246798, 1 specimen); Philippines, Palawan, ex Norton!, 17 Dec. 1963 (DMNH 179024, 1 specimen); Philippines, Samar Is., ex R. Summers coll., 1968 (AMNH 292267, 2 specimens); Philippines, Samar Is., L. R. Fletcher coll. (#44195) (CAS 112327, 2 specimens); Philippines, Samar Is., Maqueda Bay, Samar Is. (BPBM 246786, 3 specimens); Philippines, Subic Bay (BPBM 246795, 2 specimens); Philippines, Sulu, Sulu Arch., Jolo Is. (ANSP 304053, 1 specimen);

Philippines, Sulu, S.W. Sanga Is., Bongao channel, 05°02'N, 119°45'E, du Pont-ANSP Expedition!, Jul. 1958 (ANSP 230695, 2 specimens); Philippines, Sulu Sea, S. DeMarco!, Nov. 1968 (AMNH 260776, 3 specimens); Philippines, W. Bohol, Mr. Zambo! (BPBM 246791, 3 specimens); Philippines, Zamboanga, ex Kienle coll. (DMNH 196205, 1 specimen); Philippines, ex J. Donohue coll (# 482), V. Dan!, Nov. 1964 (ANSP 359698, 1 specimen); Philippines (CAS 112315, 1 specimen); Philippines (FM 1014, 4 specimens); Papua New Guinea, Admiralty Is., Pitiylia I., N. of Papua New Guinea, part of Bismarck Archipelago, ex W.M. Ingram # 247, blue dot on label, 02°10S, 147°00E, K. Kenyon!, Sept. 1944 (DMNH 43218, 1 specimen); Papua New Guinea, Manus Is., Pere Village, reef, low tide, ex K.C. Vaught (AMNH 292283, 1 specimen); Papua New Guinea, New Ireland, Bismarck Archipelago, 03°20'S, 152°00'E, T.B. Wilson! (ANSP 39632, 5 specimens); Reunion Is., 021°06'S, 055°36'E, T. Gosliner! (CAS 76571, 1 specimen); Rotorua (Roturia?), H. St. John! (BPBM 201689, 2 specimens); S. Africa, Natal coast, 029°00'S, 032°00'E, J. E.du Pont!, Apr. 1954 (DMNH 11438, 5 specimens); Seychelles, Cap. Ternay, Seychelles, Cap. Ternay, 04°40'S, 055°28'E, Brother Frenette! (USNM 652449, 1 specimen); Seychelles, Mahe, 04°40'S, 055°28'E, Brother Norbert!, 1966 (ANSP 311704, 5 specimens); Seychelles, Les Mamillas Is., ex R. Summers coll., label reads: "should be *cribraria cribraria* but appears not! No lateral spots as in prodrome". Schilder wrote: "true *cribraria*, I possess similar shells from Mahé", G. Adam!, Mar. 1962 (AMNH 292277, 1 specimen); Seychelles, 04°35'S, 55°40'E, ex Univ. Miami, 1961 (ANSP 266247, 1 specimen); Solomon Is., Choiseul Is., 07°00'S, 157°00'E, P. Galo! (ANSP 302507, 1 specimen); Solomon Is., Guadalcanal, Marau Sound, Raphael!

(HBR, no catalog number, 2 specimens); Solomon Is., Guadalcanal, Marau Sound, I. Gower! (AMNH 292291, 2 specimens); Solomon Is., Guadalcanal, Marau Sound, 09°48'S, 160°51'E, ex C. Heller (ANSP 389648, 1 specimen); Solomon Is., Guadalcanal, Marau Sound, J. Donohue!, v.1967 (ANSP 359679, 2 specimens); Solomon Is., Malaita Is., Ata'a, Lau lagoon, ex R. Summers coll., Rev. J. van der Riet!, 1965 (AMNH 292278, 3 specimens); Solomon Is., Malaita Is., Ata'a District, 08°32'S, 160°55'E, Rev. J. van der Riet!, 1962 (ANSP 279458, 1 specimen); Solomon Is., Malaita Is., Ata'a, ex J. Donohue coll., 09°00'S, 161°00'E, Rev. J. van der Riet!, Jul. 1965 (ANSP 359687, 2 specimens); Solomon Is., Malaita Is., Ata'a, Rev. J. van der Riet! (CMB, 2 specimens); Solomon Is., Malaita Is., Ata'a, 08°32'S, 160°55'E, Rev. J. van der Riet!, 1967 (ANSP 312272, 3 specimens); Solomon Is., Malaita Is., Ata'a District. ex J. Donohue, 09°00'S, 161°00'E, Rev. J. van der Riet!, Jul. 1965 (ANSP 359686, 3 specimens); Solomon Is., New George Is., 08°30'S, 157°20'E, R.A. Deni!, 1965 (ANSP 302166, 1 specimen); Solomon Is., collected by natives after storm, ex Kienle coll., 1972 (DMNH 196957, 1 specimen); Solomon Is., ex Kienle coll. (DMNH 196204, 1 specimen); Somalia, Mogadishu (ANSP 295709, 1 specimen); Somalia, Mogadishu, D. Enrich! (USNM 673876, 5 specimens); Tanzania, Dar Es Salaam, Kedwa Is., 06°50'S, 39°02'E, 1956 (BPBM 246803, 1 specimen); Tanzania, Zanzibar, Chumbe I., NSF Expedition, sand, coral and rock. Ostheimer, Orr, and Thorington, 06°16'45"S, 039°11' 00"E, 31.I.1957 (ANSP 214893, 1 specimen); Tanzania, Zanzibar, ex Kienle coll. (DMNH 196192, 1 specimen); Thailand, Phuket Is., sand lagoon and coral reefs, 08°05' 45"N, 098°18' 00"E, R.T. Abbott and F.N. Crider!, 22 Feb. 1963 (ANSP A15647, 1 specimen); Thailand, Phuket Is. (BPBM

246783, 11 specimens); Tonga, Naiafu, shallow water on reef (HBR, no catalog number, 1 specimen); Tonga, Nuku'alofa, Tongatapu Is., 021°09'S, 175°14'W, H.C. Gay!, 1966 (ANSP 306716, 1 specimen); Tonga, Vavau, 10 ft., H. Bradner!, pre-Mar. 1984 (HBR M6, 1 specimen); Vanuatu, Efate Is., under rocks, 017°44'S, 168°37.5'E, 21 Jun. 1974 (USNM 787323, 1 specimen); Vanuatu, Efate Is., Erakor inner reef, ex E. Wright coll., 017°40'S, 168°25'E (USNM 773700, 2 specimens); China, Chamberlain!, Lea Coll. (USNM 611376, 1 specimen); "Hawaii" (BPBM 246790, 5 specimens); "Venezuela" [wrong locality], R. Swift! (ANSP 17398, 2 specimens); no locality, ex James Rogers coll. (CM 47508, 1 specimen); no locality (CM 62.9053, 1 specimen); no locality, Hartman coll. (CM 62.9121, 4 specimens); no locality (HBR, no catalog number, 1 specimen); no locality, ex R. Summers coll., label reads: "F.A. Schilder det. 1958 - *Cribraria cribraria cribraria* s.str. With rather numerous lateral spots, NOT from Mauritius". C.M. Burgess wrote on back of same label: "*esontropia* CMB" (AMNH 292303, 1 specimen); no locality, C.M. Wheatley coll. (ex Univ. Penn.) (ANSP 120058, 1 specimen); no locality (AMS-C 84793 (pt), 1 specimen); no locality (AMS-C 55929, 1 specimen); no locality, J. Brazier! (ANSP 39623, 3 specimens); no locality (AMS-C 55926, 3 specimens); no locality, ex Free Mus. Sci. Art U.P, Ms. G. Abbott and Ms. Matlock!, 1928 (ANSP 112617, 4 specimens); no locality, ex R. Swift (ANSP 17399, 4 specimens); Australia, NT, Yirkalla, Northern Territory, ex W.G. Buick Collection, 012° 15'S, 136o53'E, A. W. B. Mortimer, 1963 (WAM S14338, 1 specimen); Australia, Qld, Torres Strait, Meer Island, SW Reef, 09° 55'S, 144° 03'E, L. M. Marsh!, 3 May 77 (WAM S14339, 1 specimen).

Cribrarula cribraria comma (Perry, 1811)

Kenya, Ukunda, south coast, inside the lagoon, M. Blöcher! (HBR E4, 1 specimen); Kenya (BPBM 246800, 1 specimen); Madagascar, Antseranana Prov., Jan. 1971 (LACM 103611, 2 specimens); Madagascar, reef crest, intertidal, 23°5'S, 43°30'E, J. H. McLean!, 6 Apr. 1989 (LACM 1989-50.11, 1 specimen); Madagascar (USNM 608845, 1 specimen); Mauritius, 020°18'S, 057°36'E (CMB, 1 specimen); Mauritius, 020°18'S, 057°36'E, C. W. Yarrington! (FMNH 85810, 1 specimen); Mauritius, gift from J. E.du Pont, 020°18'S, 057°36'E, W.R. Over! (DMNH 6487, 4 specimens); Mozambique, Caducia Bay, 15 km N. Mozambique Is., ex. R. Summers' coll., labels read: "…unusual and beautiful", "rare - note lateral spots", 015°00'S, 040°50'E, K.J. Grosch!, 1959 (AMNH 292275, 7 specimens); Mozambique, Port (Amelia?), K.J. Grosch! (USNM 629126, 1 specimen); Mozambique, Port Amelia, J. E. du Pont!, Mar. 1958 (DMNH 11642, 2 specimens); Mozambique, ex J. E. Holeman (AMNH 292290, 1 specimen); Mozambique, v.1956 (BPBM 246799, 1 specimen); Mozambique, K. J. Grosch!, Oct. 1956 (BPBM 246801, 1 specimen); Mozambique, J. H. Ferriss! (FMNH 58929, 1 specimen); Mozambique, W. Cernohorsky! (USNM 773461, 1 specimen); Mozambique, ex Kienle coll. (DMNH 196191, 1 specimen); Mozambique, K.J. Grosch! (USNM 710482, 2 specimens); Mozambique, ex J. E. du Pont, 1963 (DMNH 11556, 4 specimens); Mozambique, J. C. Cox! (FMNH 295269, 1 specimen); S. Africa, Natal coast, 029°00'S, 032°00'E, F. Button! (FMNH 85811, 1 specimen); Somalia, Mogadishu, D. Enrich! (USNM 673861, 1 specimen); Tanzania, Tanga, ex Kienle coll. (DMNH

196203, 1 specimen); Tanzania, Zanzibar, Nuguri Reef, May-Jun. 1968 (AMNH 292289, 3 specimens); Tanzania, Zanzibar, Chumbe I., 06°15'S, 039°20'E, R.T. Dillon!, 22 Jul. 1992 (ANSP 240636, 1 specimen); Tanzania, Zanzibar, Ras Nungwe, 0-5 ft, reef, sand, coll for ANSP, NSF Expedition, Ostheimer, Orr and Thorington, 05°42' 36"S, 039°17' 36"E, 4 Mar. 1957 (ANSP 212829, 1 specimen); Tanzania, Zanzibar, Mchangani Reef, ex J. Donohue coll. (# 131), M. Virji!, Jul. 1963 (ANSP 359717, 1 specimen); Tanzania, Zanzibar, Blaiker (CMB, 1 specimen); Tanzania, Zanzibar, Fiumba (ANSP 389650, 1 specimen); Tanzania, Zanzibar, ex E. Wright coll. (USNM 773460, 1 specimen); Tanzania, Zanzibar, ex Kienle coll. (DMNH 196193, 1 specimen); Tanzania, Zanzibar, ex R. Summers coll., 1972 (AMNH 292273, 2 specimens); Tanzania, Zanzibar, coral rock reef, 0-10 ft, 5 mi S. of Paje, Jembiani Is., NSF Expedition, 06°18' 12"S, 039°34' 36'E, Ostheimer et al., 27 Feb. 1957 (ANSP 213175, 2 specimens); Tanzania, Zanzibar, D. Bahral! (USNM 635850, 2 specimens); Tanzania, Zanzibar, Pwani Mchangani (M'changani landing), coll for ANSP, 0-1.8m, sand, 05°58' 36"S, 039°24' 24"E, Ostheimer et al!, 10 Feb. 1957 (ANSP 212573, 2 specimens); Tanzania, Zanzibar, Kiwengwa, outer reef, NSF Expedition, 05°59' 36"S, 039°24' 00"E, Ostheimer et al.!, Feb. 1957 (ANSP 212441, 3 specimens); E. Africa, ex W.E. Old Jr. coll. (AMNH 292285, 8 specimens); E. Africa (AMS-C 364190, 1 specimen); Tanzania , Mafia Island , Pwani, Mafia Island, present from M. Blocher, Mar. 9, 1973 (WAM S 14347 , 1 specimen).

Cribrarula cribraria exmouthensis (Melvill, 1888)

Australia, Dampier, Delambre Beach, 9 Jun. 1960 (BPBM 250738, 1 specimen); Australia, Dampier, 40 mi S. of Dampier, W. Australia (AMS-C 86119, 2 specimens); Australia, Derby, ex E. Wright (USNM 773540, 1 specimen); Australia, Exmouth Gulf, 022°20'S, 114°09'E, ex C. Heller (ANSP 389646, 1 specimen); NW Australia, San Theaume Pt. (BPBM 246805, 1 specimen); NW Australia, Kuri Bay, on oyster bed at 60 ft. (DMNH 196196, 1 specimen); W. Australia, Pt. Gregory, Western Australia, 2.5 m reef and under stones, 20 May 1982, coll. and pres. N. Coleman (AMS-C no catalog number, 1 specimen); W. Australia (CAS 112330, 1 specimen); W. Australia, Broome, Light House Point, 017°58'S, 122°15'E, Gower!, iv.1959 (ANSP 239538, 2 specimens); W. Australia, Broome, ex R. Summers coll., 1963 (AMNH 292272, 3 specimens); W. Australia, Cervantes, Scuba at 90 ft (AMNH 239361, 1 specimen); W. Australia, ex Stein! (LACM 117512, 2 specimens); Western Australia, Broome, ex R. Summers coll., P. McDaniels!, 1958 (AMNH 292270, 1 specimen); Western Australia, Broome, ex G.G. Eddison coll., C.F. Kurtz!, 21 Mar. 1995 (AMNH 288658, 2 specimens); Western Australia, Broome, ex R. Summers coll. (AMNH 292271, 3 specimens); Western Australia, Broome, 80 ft, open sand in pearl beds, coll by pearl diver, Scuba, ex Fleischner, 1986 (AMNH 273366, 1 specimen); Western Australia, Broome, Rocks and pools, James Price Point, 35 mi N. of Broome, NSF Expedition, 017°29' 30"S, 122°07' 45"E, V. Orr!, 28 Sept. 1958 (ANSP 233610, 1 specimen); Western Australia, Broome, ex Bledsoe coll. (USNM 876826, 1 specimen); Western Australia, Broome, V.I. Harris! (CAS 112323, 1 specimen); Western Australia, Broome, W. Cernohorsky!, 1963 (USNM

773541, 2 specimens); Western Australia, Broome, Grantherine Pt., Broome, J. E.du Pont!, Sept. 1956 (DMNH 11559, 2 specimens); Western Australia, Broome, Ex. Minzak coll., Oct. 1969 (LACM 103591, 2 specimens); Western Australia, Broome (BPBM 246804, 2 specimens); Australia, WA, Dampier Archipelago, NW side of Delambre Island, WAM Dampier Archipelago Expedition 1961, 020° 26'S, 117° 04'E, G. W. Kendrick and B. R. Wilson!, Aug. 28, 1961 (WAM S14329, 1 specimen); Australia, WA, Kimberley, Cassini Island, W side, Bryce and Morrison's Kimberley Survey 1994, 18 m, 013° 57'S, 125° 38'E, C. W. Bryce and H. M. Morrison!, Sep. 23, 1994 (WAM S14335, 1 specimen); Australia, WA, Rottnest Island, Transit Reef. Beached shell, broken anterior canal, coral settled on columella, 031° 59'S, 115° 34'E, T. Gabelich!, pre-1971 (WAM S14315, 1 specimen); Australia, WA, Rottnest Island, Transit Reef, beached shell, repair scars on dorsum, 031° 59'S, 115° 34'E, ex F. Jones coll., Dec. 1975 (WAM S14317, 1 specimen); Australia, WA, Rottnest Island, Duck Rock, 031° 59'S, 115° 33'E, F. Wells, C. W. Bryce and N. Sinclair, Nov. 29, 1980 (WAM S14318, 1 specimen); Australia, WA, Off Cervantes, craypot, 6 fms, 030° 30'S, 115° 04'E, ex E.J. Harrold coll., Dec. 1965 (WAM S14320, 2 specimens); Australia, WA, 027° 42'S, 114° 10'E, F. Wells !, Jun. 10, 1980 (WAM S14321, 1 specimen); Australia, WA, Kalbarri, 027° 42'S, 114° 10'E, ex. E.H. Sedgwick, Jul. 1978 (WAM S14322, 2 specimens); Australia, WA, Bluff Point. Ex ANPWS Collection (seized Dec. 15, 1989 via Australian Customs), sponge trawled, 21 fms, 027° 51'S, 114° 06'E, (WAM S14323, 1 specimen); Australia, WA, Port Gregory, ex ANPWS Collection (Seized Dec. 15, 1989 via Australian Customs), 028° 11'S, 114° 14'E, (WAM S14324, 3 specimens); Australia, WA, Houtman Abrolhos Islands, SW of

Gun Island, outside outer reef, WAM Houtman Abrolhos Expedition 1976, 028° 53'S, 113° 51'E, F. Wells and C. W. Bryce!, Apr. 8, 1976 (WAM S14325, 1 specimen); Australia, WA, Shark Bay, Steep Point, 6 m, 026° 09'S, 113° 09'E, F.E. Wells, and C.W. Bryce!, 13 Mar 1986 (WAM S14326, 1 specimen); Australia, WA, Monte Bello Islands, reef flat, W side, station MB1/93/06, reef flat, 020° 26'S, 115° 30'E, F. Wells, C. W. Bryce and S. Slack-Smith!, Dec. 08, 1993 (WAM S14327, 3 specimens); Australia, WA, Dampier Archipelago, Kendrew Island, reef flat near Citadel Rock, Crown of Thorns Survey IV - May 1973, reef flat, 020° 28' 30"S, 116° 32'E, B. R. Wilson!, May 1973 (WAM S14328, 2 specimens); Australia, WA, Dampier Archipelago, Kendrew Island, Citadel Rock area, Crown of Thorns Survey 4 May 1973, reef crest + inner reef, 020° 28'30"S, 116° 32'E, Crown of Thorns Survey!, 4 May 1973 (WAM S14330, 2 specimens); Australia, WA, Dampier, ex ANPWS Collection (seized Dec. 15, 1989 via Australian Customs), 020° 40'S, 116° 43'E, (WAM S14331, 2 specimens); Australia, WA, Dampier Archipelago, Kendrew Island, N. of Citadel, reef coast, under rock. Crown of Thorns Survey IV - May 1973, under rock, 020° 28' 30"S, 116° 32'E, 5 May 1973 (WAM S14332, 2 specimens); Australia, WA, Dampier Archipelago, Rosemary Island, among coral heads, 3 m, 020° 29'S, 116° 35'E, B. R. Wilson!, Oct. 31, 1971 (WAM S14333, 1 specimen); Australia, WA, Broome, ex Herninjard Collection (presented Jan. 1960), 017° 58'S, 122° 14'E, pre-1960 (WAM S14334, 1 specimen); Australia, WA, NWA, Ashmore Reef, N. side of Middle Reef, "Bogorov" 1978, 012° 11'S, 122° 58'E, B. R. Wilson!, Oct. 19, 1978 (WAM S14336, 1 specimen); Australia, WA, Dampier, Regnard Bay, Nooreas Reef, pre-1978, 020° 49'S, 116° 26'E, ex E.J. Harold Coll., pre-

1978 (WAM S14337, 2 specimens); Australia, WA, 25 km N. of Ningaloo Homestead, Barrier Reef, under dead coral, 022° 29'S, 113° 40'E, F. Wells and L. M. Marsh!, Jul. 1977 (WAM S14344, 1 specimen).

Cribrarula cribraria melwardi (Iredale, 1930)

Australia, Queensland, albino specimen with eggs, fixed and preserved in formalin, under rocks, intertidal, 23°26'S, 151°57'E, A. Waren and C. Lamb!, 19 Aug. 1985 (AMS-C 364621, 1 specimen); Australia, Queensland, albino specimens preserved in formalin, on and under coral, intertidal, 23°18'S, 151°57'E, P. H. Colman!, 8 Sept. 1970 (AMS-C 364186, 2 specimens); Australia, Queensland, Yeppon, Keppel Is., Coral Sea, C. Coucom!, 1964 (AMNH 292281, 1 specimen); Australia, Queensland, Keppel Bay, North Keppel Is., 023°04'S, 150°54'E, T. A. Garrard!, pre-1970 (AMS-C 363560, 1 specimen); Australia, Queensland, Tryon Is., ex Glenn Goodfriend coll., under dead coral at low tide, "received from V. Harris on March 17, 1969 (albino)", V. Harris!, 17 Mar. 1969 (AMNH 260790, 1 specimen); Australia, Queensland, Great Barrier Reef, Capricorn Group, North West Is., 023°18'S, 151°42'E, Sept. 1954 (AMS-C 88600, 1 specimen); Australia, Queensland, Great Barrier Reef, Capricorn Group, North West Is., coll T. Iredale, M. Ward and G. P. Whitley, 023°18'S, 151°42'E, May 1931 (AMS-C 81687, 2 specimens); Australia, Queensland, Tryon Is., Coral Sea, ex R. Summers coll., A. Nash!, Oct. 1959 (AMNH 292269, 3 specimens); Australia, Queensland, NW Is., ex R. Summers coll., A. Nash!, Feb. 1958 (AMNH 292268, 4 specimens); Australia, Queensland, Northwest Is., albino, R. Summers!, 1958 (BPBM 246796, 1 specimen); Australia, Queensland, Keppel

Is., Conical Is., M. Bowman leg., ex C.N. Cate coll., M. Bowman!, 19 Jul. 1963 (AMNH 204047, 1 specimen); Australia, Queensland, Great Barrier Reef, North West Is., under rocks, coll extreme low tides, albino, ex Kienle coll., Jun. 1976 (DMNH 196951, 1 specimen); Australia, Queensland, albino, C. Heller! (ANSP 389647, 1 specimen); Australia, Queensland, Capricorn Group, ex E. Wright coll. (USNM 773567, 1 specimen); Australia, Queensland, Great Barrier Reef, Capricorn Is. Group, albino, ex Kienle coll. (DMNH 196194, 1 specimen); Australia, Queensland, T. and R. Burch! (BPBM 246794, 1 specimen); Australia, Queensland, Great Barrier Reef, Hinchinbrook Is., albino (ANSP 138682, 1 specimen); Australia, Queensland, albino (ANSP 349943, 1 specimen); Australia, Qld, Queensland, off Bowen, Gould Reef. Two labels: one says ex ANPWS, seized Dec. 15, 1989 via Australian Customs, and the other says ex. G.B.J. and D.V. Lawrence Collection., 019° 27'S, 148° 47'E, Jun. 12, 1972 (WAM S14340, 3 specimens); Australia, Qld, Northwest Island, ex. E. J. Harrold collection, 023° 18'S, 151° 42'E, pre-1978 (WAM S14341, 4 specimens); Australia, Qld, Keppel Bay, ex E.J. Harrold Collection, purchased 1978, 023° 25'S, 150° 52'E, pre-1978 (WAM S14342, 1 specimen); Australia, Qld, off Tryon Island, ex E. J. Harrold Collection, 023° 14'S, 151° 46'E, pre-1978 (WAM S14343, 2 specimens).

Cribrarula cribraria gaspardi Biraghi and Nicolay, 1993

Marshall Is., Enewatak Atoll, lagoon side, under dead coral, 3 m, 011°30'N, 162°15'E, S. Johnson! (BPBM 251486, 1 specimen); Marshall Is., Enewatak Atoll, Lagoon, 20 m, ex Woods Hole Oceanic Institution, coll by E. J. Kuenzler and L. R. Pomeroy!, 011°30'N, 162°15'E, 15 Jun. 1960 (ANSP 285243, 1 specimen); Marshall Is., Kwajalein, 09°05'N, 167°20'E, S. Johnson!, 1996 (FM 3, 1 specimen); Marshall Is., Kwajalein, Bustard reef, 09°05'N, 167°20'E, ex Kienle coll. (DMNH 196202, 2 specimens); Marshall Is., Kwajalein, 09°05'N, 167°20'E, 1947 (BPBM 246792, 4 specimens); Solomon Is., Malaita Is., Lau lagoon, coll. By Rev. J. van der Riet, 1965, ex R. Summers coll., Rev. J. van der Riet!, 1965 (AMNH 292278, 3 specimens).

Cribrarula cribraria ganteri Lorenz, 1997

Sri Lanka, Colombo, 08°45'N, 082°30'N, Dr. G.H.P. de Bruin! (BPBM 246785, 1 specimen); Sri Lanka, Colombo, Colombo Reef, in coral at 30 ft, 08°45'N, 082°30'N, ex. E. Wright coll. (# 237) (USNM 773744, 2 specimens); Sri Lanka, 08°45'N, 082°30'N, Dr. G.H.P. de Bruin! (BPBM 246788, 1 specimen); Sri Lanka, 08°45'N, 082°30'N, ex Stearns coll. (USNM 77665, 1 specimen); Sri Lanka, 08°45'N, 082°30'N (BPBM 246789, 1 specimen); Sri Lanka, 08°45'N, 082°30'N, Burch coll. SLF (#B-19) (CAS 112322, 2 specimens); Sri Lanka, 08°45'N, 082°30'N, Wesleyan Univ. (USNM 90547, 2 specimens); Sri Lanka, 08°45'N, 082°30'N, ex Whitmore-Coats coll. (#44686) (CAS 112331, 2 specimens); Sri Lanka, 08°45'N, 082°30'N, ex F. Stearn (FMNH 85812, 4 specimens); Sri Lanka, ex. S.R. Robert coll., 08°45'N, 082°30'N, ex Poulson! (ANSP 147224, 8 specimens); Sri Lanka, ex Rossell coll., pre-1965 (WAM S14346, 1 specimen).

Cribrarula cumingii (Sowerby II, 1832)

American Samoa, Manua Is., Ta'u Is., 014°15'S, 169°30'W (BPBM 201621, 4 specimens); South Cook Group, Atiu Is., W. Cernohorsky! (USNM 773728, 2 specimens); Cook Is., Danger Is., Whale Id., Pukapuka Atoll, W. Cernohorsky!, May 1966 (USNM 773824, 2 specimens); Cook Is., Danger Is., Pukupuka, ex Johnson (USNM 721529, 2 specimens); S. Cook Is., N. Rarotonga, Avarua, E. of hospital, R. Johnson!, 1962 (ANSP 279307, 1 specimen); Indonesia, Irian Jaya, Aoeri Is., 1 mi NE of Roemwakon Isle; Sta. 541, 20-25 fms, ex NSF Expedition!, 21 Feb. 1956 (ANSP 284739, 2 specimens); Kiribati, Flint Is., 011°26'S, 151°48'W, C.D. Voy!, 1901 (ANSP 80868, 1 specimen); Marquesas, Fatuhiva Is., under dead coral, 20-25 m, 09°00'S, 139°30'W, ex Fleischner (AMNH 273216, 1 specimen); Marquesas, Hiva Oa Id., 45 ft depth, 09°00'S, 139°30'W, ex K. Vaught, 1978 (AMNH 292295, 1 specimen); Marquesas, Nuku Hiva, Baie, Hatuatua, 08°56'S, 140°06'W, Pele Expedition!, Oct. 1967 (USNM 819907, 1 specimen); Marquesas, Nuku Hiva Is., 08°56'S, 140°06'W, C. Heller! (ANSP 389651, 1 specimen); Marquesas, Tahuata Is., off S.W. coast of Tahuata, 44 fms, 09°57'S, 139°05'W, Pele Expedition! (USNM 790717, 3 specimens); Marquesas, Ua Pou Is., 09°23'S, 140°03'W, C.D. Voy! (CMB 638-6, 1 specimen); Marquesas, Ua Pou Is., S. Of Baie de Vaieo, W. Coast, 09°23'S, 140°03'W, Pele Expedition!, 1967 (USNM 798427, 1 specimen); Marquesas, native diver! (CMB 638-4, 2 specimens); Marshall Is., Kwajalein, 09°05'N, 167°20'E, K. Jourdan!, 1990 (CMB 638-5, 2 specimens); Pitcairn Is., Henderson Id., NW beaches, G. Paulay!, v.1987 (USNM 878794, 1 specimen); Polynesia, Banaba Is., near Gilbert Is., Ocean Id. (Barraba I.), Lady Ellice!, 1939 (USNM

773696, 1 specimen); Society Is., Papeete, Fare Ute Pt., dredged lagoon, ex H.A. Rehder, Feb. 1963 (USNM 668883, 1 specimen); Society Is., Raiatea, 24 Aug. 1944 (BPBM 69259, 1 specimen); Society Is., Rauli, Rora, diver (DMNH 5441, 1 specimen); Society Is., Tahiti, Papeete, ex R. Summers coll., 1959 (AMNH 292293, 1 specimen); Society Is., Tahiti, Punaauia, ex R. Summer coll., 1974 (AMNH 292292, 1 specimen); Society Is., Tahiti, Off Punaauia, under coral slabs on reef in shallow water, ex Fleischner, Nov. 1983 (AMNH 273337, 1 specimen); Society Is., Tahiti, ex Dr. Pierson coll. (CMB 638, 1 specimen); Society Is., Tahiti, Hitia, East coast, coll. at 4.5 m, under dead coral, Scuba, ex Mrs. P.R. Fleischner coll. (AMNH 273338, 1 specimen); Society Is., Tahiti, Scuba 15-20 m, ex Mrs. P.R. Fleischner coll. (AMNH 273339, 1 specimen); Society Is., Tahiti, Papeete, 20 ft, collected on red sponge, J. D. Tobin!, 23 Jun. 1982 (AMNH 279462, 4 specimens); Society Is., Tahiti, ex Bledsoe coll., 1973 (USNM 886185, 1 specimen); Society Is., Tahiti, Patutoa, filled area, ex Sinberry (USNM 669651, 1 specimen); Society Is., Tahiti, Papeete, 17.32'S 149.34'W, J. Donohue! (ANSP 359752, 1 specimen); Society Is., Tahiti (DMNH 196207, 2 specimens); Society Is. (CMB 638, 1 specimen); Society Is., F. Button (FMNH 85792, 2 specimens); Society Is., R. Coats!, 1956 (BPBM 247852, 2 specimens); Society Is. (CMB 638-x, 2 specimens); Tuamotus, off Nuku Hiva, ex Kienle coll., Aug. 1984 (DMNH 196209, 1 specimen); Tuamotus, Paumotus Is., A. Garrett (BPBM 247851, 1 specimen); Tuamotus, Paumotus Is., Makatea (BPBM 67930, 1 specimen); Tuamotus, Paumotus Is., A. Garrett! (USNM 88196, 5 specimens); Tuamotus, Rangiroa, Avatoru Pass, outer reef, Pele Expedition!, 7 Jul. 1967 (USNM 782754, 1 specimen); Tuamotus, Raroia, SE Opakea Id., Pac. Sci. Bd.! (USNM 723087, 1 specimen); Tuamotus, Raroia, Ngarumaoa Is., outer side, Pac. Sci. Bd.! (USNM 697503, 1 specimen); Tuamotus, Raroia, Garumaoa Id., Pac. Sci. Bd.! (USNM 723323, 1 specimen); Tuamotus, Raroia, Garumaoa Id., Pac. Sci. Bd.! (USNM 723476, 1 specimen); Tuamotus, Raroia, Garumaoa Id., Pac. Sci. Bd.! (USNM 711704, 8 specimens); Tuamotus, Tikehoi (DMNH 196208, 1 specimen); Tuamotus, Vahi Tahi, F. Harescot!, 1973 (AMNH 292294, 1 specimen); Tuamotus, Vahi Tahi, D. Marshall! (USNM 613165, 5 specimens); Tuamotus (CMB 638-1, 1 specimen); Tuamotus (CMB 638-2, 1 specimen); Tuamotus, ex P. Dautzenberg (FMNH 63257, 3 specimens); Tuamotus, C. Kauffman! (DMNH 155440, 1 specimen); Tuamotus, ex E. Wright coll. (USNM 773494, 1 specimen); Tuamotus, ex USNM (ANSP 196021, 1 specimen); "Seychelles" [wrong locality], ex Univ. Miami, 1961 (ANSP 266251, 1 specimen); no locality, ex B.K. Fox coll., pre-1985 (AMS, no catalog number, 1 specimen); no locality (CMB 638-7, 2 specimens); no locality, C.R. Orcutt! (FMNH 8954, 4 specimens); no locality (FMNH 117640, 1 specimen).

Cribrarula esontropia (Duclos, 1833)

Mauritius, Flicenflacq, 020°17'S, 057°22'E, C. Heller! (ANSP 389683, 1 specimen); Mauritius, Port Louis, coral debris-mud, 36 m, 020°18'S, 057°36'E, ex Bledsoe coll. (USNM 876969, 1 specimen); Mauritius, S.W. coast, low tide, 20°11'S, 57°32'E, ex E. Wright (USNM 773468, 2 specimens); Mauritius, 20°11'S, 57°32'E, W. J. Ammen!, 1925 (FMNH 20764, 1 specimen); Mauritius, 20°11'S, 57°32'E, J.C. Cox!, pre-1912 (AMS C. 364812, 1 specimen); Mauritius, R. Summers wrote: "Can this be a giant *cribellum* or a slender *esontropia*?" Schilder underlined *esontropia* and noted "Schilder det [19]63", 20°11'S, 57°32'E, S. J. Dvorak!, Dec. 1962 (AMNH 292297, 1 specimen); Mauritius, 020°18'S, 057°36'E, ex Schilder coll. (#117) (BPBM 247839, 1 specimen); Mauritius, 020°18'S, 057°36'E, Thaanum! (BPBM 232474 Thaanum, 1 specimen); Mauritius, 020°18'S, 057°36'E (AMS C. 151, 1 specimen); Mauritius, 020°18'S, 057°36'E (CMB, 1 specimen); Mauritius, 020°18'S, 057°36'E (BPBM 240792, 1 specimen); Mauritius, 020°18'S, 057°36'E (CAS 112316, 1 specimen); Mauritius, 020°18'S, 057°36'E (AMS C. 275, 1 specimen); Mauritius, 020°18'S, 057°36'E (BPBM 247841, 1 specimen); Mauritius, 020°18'S, 057°36'E (AMS C. 313990, 1 specimen); Mauritius, 020°18'S, 057°36'E, A. Seale coll. (#28005) (CAS 112326, 1 specimen); Mauritius, 020°18'S, 057°36'E, ex H. Hemphill coll (# 1748) (CAS 112336, 2 specimens); Mauritius, 020°18'S, 057°36'E, ex H. Hemphill coll. (# 1749) (CAS 112335, 2 specimens); Mauritius, 020°18'S, 057°36'E, ex Whitmore-Coats coll. (# 44748) (CAS 112337, 2 specimens); Mauritius, 020°18'S, 057°36'E, J.C. Cox!, pre-1912 (AMS C. 84793, 3 specimens); Mauritius, ex F. Button coll., 20°11'S, 57°32'E, ex G.B. Sowerby (FMNH 85814, 3 specimens); Mauritius, 020°18'S, 057°36'E, J. E.du Pont!, 1965 (DMNH 11444, 1 specimen); Mauritius, 020°18'S, 057°36'E, J. E.du Pont!, Nov. 1956 (DMNH 11643, 1 specimen); Mauritius, 020°18'S, 057°36'E, ex E. Wright coll. (USNM 773478, 1 specimen); Mauritius, Port Louis Harbor, trawled, 020°18'S, 057°36'E, ex E. Wright coll. (USNM 773481, 1 specimen); Mauritius, Point d'Esnym, 020°18'S, 057°36'E, ex Bledsoe coll. (USNM 866188, 1 specimen); Mauritius, 020°18'S, 057°36'E, ex Kienle coll. (DMNH 196272, 1 specimen); Mauritius, 020°18'S, 057°36'E, J. Donohue! (ANSP

360220, 1 specimen); Mauritius, 020°18'S, 057°36'E, J.C. Bryant coll. (USNM 254037, 1 specimen); Mauritius, ex. USNM, 20°11'S, 57°32'E, N. Pike! (ANSP 196027, 1 specimen); Mauritius, 020°18'S, 057°36'E, ex W. H. Weeks coll (DMNH 8123, 1 specimen); Mauritius, 020°18'S, 057°36'E (DMNH 641, 1 specimen); Mauritius, 020°18'S, 057°36'E (DMNH 196271, 1 specimen); Mauritius, 020°18'S, 057°36'E, Higgins!, 1937 (DMNH 6113, 3 specimens); Mauritius, 020°18'S, 057°36'E, W. Cernohorsky!, 1961 (USNM 773479, 3 specimens); Mauritius, 020°18'S, 057°36'E (USNM 26799, 4 specimens); Reunion Is., Scuba 50-60 ft., 021°06'S, 055°36'E, ex Fleischner (AMNH 273365, 1 specimen); Reunion Is., 25-30 m, 021°06'S, 055°36'E, ex R. Cranmer (USNM 888401, 1 specimen); Madagascar, E.E. Hand! (FMNH 63256, 1 specimen); S. Africa, Natal coast, Umzumbi, 029°00'S, 032°00'E, E.L. Kessel coll. (#32238) (CAS 112325, 1 specimen); Tanzania, Dar-es-Salaam, Mboa Maji, 9 mi S. Dar-es-Salaam, R.T. Abbott!, 23.v.1953 (USNM 604651, 1 specimen); South Africa, Natal, Shelly Beach, 5 km N of Margate, 030° 51'S, 030° 22'E, G. W. Kendrick, and P. J. Vinnicombe!, 23 May 93 (WAM S14345, 1 specimen).

Cribrarula gaskoinii (Reeve, 1846)

Hawaii, Oahu, Barbers Point, ex Naide coll. (ANSP 400634, 1 specimen); Oahu, ex O. Schoenberg-Dole, 29 Apr. 1973 (FM 720, 2 specimens); Oahu, Haleiwa, rock, large coral on slope, W. Thorsson! 21 Nov. 1983 (BPBM 241409, 1 specimen); Oahu, Moanalua, Fantasy Reef, rock and coral, W. Thorsson!, 13 Sept. 1983 (BPBM 241410, 9 specimens); Oahu, Moanalua, hole, coral on slope, sand, 75 ft, W. Thorsson!, 17 Jun.

1985 (BPBM 241419, 1 specimen); Oahu, Haleiwa, large corals, 60-78 ft, W. Thorsson!, 1 Jul. 1986 (BPBM 241420, 1 specimen); Oahu, Haleiwa, Fir Trees, large corals, W. Thorsson!, 22 Jun. 1987 (BPBM 241423, 1 specimen); Oahu, Haleiwa, W. Thorsson! (BPBM 242421, 1 specimen); Oahu, Honolulu, reef flat at Waiameme St., D. Thaanum!, 1921-1936 (BPBM 231699 Thaanum, 3 specimens); Oahu, Honolulu Harbor, J. Trant!, 1930 (BPBM 231676 Thaanum, 7 specimens); Oahu, Honolulu Harbor, W.A. and E.L. Bryan!, 1915 (BPBM 62443, 8 specimens); Oahu, Honolulu Harbor, W.A. and E.L. Bryan!, 1917 (BPBM 62504, 1 specimen); Oahu, Honolulu Harbor, dredging (BPBM 197334, 4 specimens); Oahu, Honolulu Harbor, dredging, ex J. S. Emerson coll., 21 May 1930 (BPBM 69267, 4 specimens); Oahu, Honolulu Harbor, ex USNM, T.B. Hardy! (ANSP 196018, 1 specimen); Oahu, Honolulu, Barbers Point, 1967 (ANSP 313103, 1 specimen); Oahu, Makaha, Curt Fiedler!, 1996 (FM 57, 1 specimen); Oahu, Makaha, 50 ft., ex O. Schoenberg-Dole, ex Fred Radlein, F. Radlein!, Aug. 1984 (FM 722, 1 specimen); Oahu, Makua, coll. at 40 ft in cave at night, M. R. Hyett! (ANSP 349940, 1 specimen); Oahu, Moanalua, rock and coral, 45-55 ft, W. Thorsson!, 18 Mar. 1983 (BPBM 241400, 3 specimens); Oahu, Moanalua, rock on coral, W. Thorsson!, 22 Mar. 1983 (BPBM 241401, 7 specimens); Oahu, Moanalua, W. Thorsson! (BPBM 241402, 2 specimens); Oahu, Moanalua, Fantasy Reef, rock and coral, 78 ft, W. Thorsson!, 28 Mar. 1983 (BPBM 241403, 10 specimens); Oahu, Moanalua Bay, Fantasy Reef, rock and coral, 40-50 ft, W. Thorsson!, 1 Apr. 1984 (BPBM 241404, 3 specimens); Oahu, Moanalua, Fantasy Reef, rock and coral, 40-50 ft, W. Thorsson!, 1 Apr. 1983 (BPBM 241405, 1 specimen); Oahu, Moanalua, Fantasy Reef, coral and sand, 45-50 ft, W.

Thorsson!, 9 May 1983 (BPBM 241406, 2 specimens); Oahu, Moanalua Bay, Fantasy Reef, coral and sand, 45-50 ft, W. Thorsson!, 9 May 1983 (BPBM 241407, 1 specimen); Oahu, Moanalua Bay, Fantasy Reef, rock and coral, 45-50 ft, W. Thorsson!, 17 May 1983 (BPBM 241408, 2 specimens); Oahu, Moanalua Bay, "Fantasy reef", rock and coral on stratified rock mesas, W. Thorsson!, 9 Feb. 1984 (BPBM 241412, 1 specimen); Oahu, Moanalua, Fantasy Reef, stratified rock with coral, sand between islands, 50-55 ft, W. Thorsson!, 4 Apr. 1984 (BPBM 241413, 3 specimens); Oahu, Moanalua, Fantasy Reef, coral and sand on mesas, 35-40 ft, W. Thorsson!, 21 Jun. 1984 (BPBM 241415, 1 specimen); Oahu, Moanalua, Fantasy Island, coral and sand, 45-55 ft, W. Thorsson!, 28 Sept. 1984 (BPBM 241416, 2 specimens); Oahu, Moanalua, Fantasy Reef, coral on mesas, sand between, W. Thorsson!, 20 Oct. 1984 (BPBM 241417, 6 specimens); Oahu, Moanalua, Fantasy Reef, coral on mesas, sand between, W. Thorsson!, 29 Oct. 1984 (BPBM 241418, 5 specimens); Oahu, Haleiwa, Army Beach west, sandy bottom of cliff, corals on top, 45-70 ft, W. Thorsson!, 5 Nov. 1986 (BPBM 241422, 1 specimen); Oahu, Moanalua Bay, "Fantasy reef", coral on rock mesas, 40-45 ft, W. Thorsson!, 4 May 1983 (BPBM 248120, 1 specimen); Oahu, Mokapu, Pleistocene fossil, Polanski fossils, 1962-64 (BPBM 209066, 1 specimen); Oahu, Mokumanu I. (BPBM 62442, 4 specimens); Oahu, Nanakuli, M.E. Burgess!, Oct. 1956 (ANSP 216717, 1 specimen); Oahu, off Waikiki, 3 m, D. Thaanum! (BPBM 231700 Thaanum, 1 specimen); Oahu, off Diamond Head (BPBM 218082, 1 specimen); Oahu, Off Makua, 100 ft., D. Woodman! (CMB, 2 specimens); Oahu, out from Shark's Cove, Waimea, 70 ft., ex O. Schoenberg-Dole, D.B. Johnson!, Aug. 1973 (FM 721, 2 specimens); Oahu, Paumalu, A. J. Ostheimer III!, 1951

(ANSP 188624, 1 specimen); Oahu, Paumalu (BPBM 197330, 25 specimens); Oahu, Paumalu, D. Thaanum! (BPBM 231701 Thaanum, 1 specimen); Oahu, Paumalu, W.A. and E.L. Bryan!, 1915 (BPBM 62434, 1 specimen); Oahu, Paumalu (CMB 8-9, 4 specimens); Oahu, Pupukea, under dead coral, 50 ft., O. Schoenberg-Dole!, Sept. 1977 (FM 725, 1 specimen); Oahu, South Shore, Holocene (BPBM 218078, 1 specimen); Oahu, specimen illustrated in *Manual of Conchology*, ex S.R. Roberts coll (ANSP 147139, 1 specimen); Oahu, Sunset Beach (BPBM 205440, 2 specimens); Oahu, Sunset Beach (BPBM 205444, 2 specimens); Oahu, Waianae, under dead coral, 30 ft, O. Schoenberg-Dole!, Jun. 1977 (FM 726, 2 specimens); Oahu, Waianae, under dead coral, 30 ft., O. Schoenberg-Dole!, Sept. 1977 (FM 943, 1 specimen); Oahu, Waikiki, 12 ft in dead coral, Thaanum and Dranga!, 7 Sept. 1936 (ANSP 215536, 1 specimen); Oahu, Moanalua, Fantasy Reef, rock and coral, W. Thorsson!, 8 Nov. 1983 (BPBM 241411, 8 specimens); Oahu, ex S.R. Roberts coll (ANSP 147208, 5 specimens); Oahu, Brooklin Mus. Coll. (ANSP 182059, 2 specimens); Oahu (BPBM 197332, 3 specimens); Oahu (BPBM 197333, 1 specimen); Oahu (BPBM 202205, 1 specimen); Oahu, J.G. Malone!, 1922 (ANSP 215536, 1 specimen); Oahu, ex Niverns coll. (BPBM 247844, 2 specimens); Oahu (BPBM 247845, 1 specimen); Oahu (BPBM 247847, 6 specimens); Oahu, I. Spalding! (ANSP 329008, 1 specimen); Oahu, ex Pease (ANSP 39625, 2 specimens); Oahu (ANSP 39626, 1 specimen); Oahu, D. Woodman!, 1995 (FM 6, 1 specimen); Oahu, W.A. and E.L. Bryan!, 1917 (BPBM 65208, 12 specimens); Oahu, D. Woodman!, 1995 (FM 7, 1 specimen); Oahu, D. Woodman!, pre-1996 (CMB 8-37, 15 specimens); Oahu, D. Woodman!, pre-1994 (FM 942, 3 specimens); Oahu (CMB, 1 specimen); Oahu (CMB, 2 specimens); Oahu, D. Woodman! (CMB, 5 specimens); Big Island, Hilo, reef flat at Waiameme St., D. Thaanum!, Jan. 1921 (BPBM 231698 Thaanum, 16 specimens); Big Island, S. Kona, Kapua, beached shells, W.A. and E.L. Bryan!, 1 Jun. 1914 (BPBM 62439, 3 specimens); Big Island (BPBM 197331, 1 specimen); Kauai, Haena, W.A. and E.L. Bryan!, 1915 (BPBM 62438, 5 specimens); Kauai, Haena, W.A. and E.L. Bryan!, 1915 (BPBM 62437, 16 specimens); Kauai, Wainiha, W.A. and E.L. Bryan!, 1915 (BPBM 62436, 5 specimens); Kauai, Wainiha, W.A. and E.L. Bryan!, 1915 (BPBM 62435, 6 specimens); Kauai, ex I. H. Scott, 1894 (BPBM 231697 Thaanum, 2 specimens); Maui, Lahaina, small specimen, ex M.R. Hyett coll No. 2619, 020°52'N, 156°41'W, M.R. Hyett! (ANSP 349941, 1 specimen); Maui, Makena, C. Heller! (ANSP 389707, 1 specimen); Maui, J. Donohue! (ANSP 360248, 1 specimen); Laysan Is., Tanager Expedition, D. Thaanum!, iv.1923 (BPBM 66011, 10 specimens); Laysan Is., D. Thaanum!, 1938 (BPBM 231674 Thaanum, 2 specimens); Molokai, Popohaku, W.A. and E.L. Bryan!, 1914 (BPBM 62441, 1 specimen); Niihau, W.A. and E.L. Bryan!, Jun. 1914 (BPBM 62440, 2 specimens); Kahoolawe Is., "culture zone on top of Kahoolawe Is.", H.A. Pilsbry! (Holocene) (ANSP 116432, 1 specimen); (BPBM 201966, 1 specimen); (BPBM 201970, 3 specimens); (BPBM 201968, 12 specimens); Midway Is., 028°13'N, 177°22'W (BPBM 254028, 15 specimens); Midway Is., 028°13'N, 177°22'W, D. Lee!, Sept. 1959 (BPBM 254029, 18 specimens); Hawaiian Is., A.F. Judd!, 1924 (BPBM 67590, 4 specimens); Hawaiian Is., ex Whitney coll., 1860 (BPBM 67607, 20 specimens); Marshall Is., Ralik Chain, dead coral, 24-28 m, K. Jourdan!, 1984 (FM 938,

2 specimens); Philippines, ex SR Robertson coll. (ANSP 147201, 1 specimen); Philippines!, Cebu, L. D. Foucher!, 1939 (BPBM 247848, 1 specimen).

Cribrarula cribellum (Gaskoin, 1849)

Mauritius, 020°18'S, 057°36'E, W.S. Vaux! (ANSP 17400, 1 specimen); Mauritius, 020°18'S, 057°36'E, V. Robillard! (ANSP 39624, 1 specimen); Mauritius, ex F. Button coll., ex G. B. Sowerby coll., 020°18'S, 057°36'E (FMNH 85813, 4 specimens); Mauritius, 020°18'S, 057°36'E, D.D. Baldwin coll. (# 25365) (CAS 112338, 2 specimens); Mauritius, ex S.R. Roberts coll., figured Pl, 17, figs 66, 67 (illustration on label), ex Poulson coll., 020°18'S, 057°36'E (ANSP 147225, 1 specimen); Mauritius, 020°18'S, 057°36'E, ex Schilder coll (# 116) (BPBM 247835, 1 specimen); Mauritius, 020°18'S, 057°36'E, J. Couacaud! (BPBM 247836, 1 specimen); Mauritius, 020°18'S, 057°36'E, J. Couacaud! (BPBM 247837, 1 specimen); Mauritius, 020°18'S, 057°36'E, Robillard! (BPBM 247838, 1 specimen); Mauritius, 020°18'S, 057°36'E, V. Orr!, Oct. 1960 (ANSP 273758, 1 specimen); Mauritius, ex H. Boswell coll., 20°11'S, 57°32'E, G.G. Eddison coll. (AMNH 288656, 1 specimen); Mauritius, 20°11'S, 57°32'E, ex Haines (AMNH 292302, 5 specimens); Mauritius, Port Louis, 020°10'S, 057°30'E, C. Heller! (ANSP 389644, 1 specimen); Mauritius, Chamberlain! (USNM 128408, 2 specimens); Mauritius, 020°18'S, 057°36'E, J. Parker! (DMNH 133563, 3 specimens); Mauritius, 020°18'S, 057°36'E, H. C. Fulton!, 1927 (BPBM 232301 Thaanum, 1 specimen); Mauritius, 020°18'S, 057°36'E, ex White coll. (USNM 253390, 1 specimen); Mauritius, 020°18'S, 057°36'E, Pike! (USNM 26809, 1 specimen); Mauritius, 020°18'S, 057°36'E, ex R. Summers coll., c. 1926 (AMNH 292296, 1 specimen); Mauritius, 20°11'S, 57°32'E, F. A. Constable! (AMNH 292304, 2 specimens); Mauritius, on coral in 20 ft water, 20°11'S, 57°32'E, G. F. Herman!, pre-1996 (AMS C. 364816, 1 specimen); Mauritius, Rianbel (S. Mauritius), Rianbel Reef, 3 ft, night collected, ex Maurice Maurel coll., 20°11'S, 57°32'E, M. Maurel!, 18 Feb. 1971 (DMNH 45422, 1 specimen); Mauritius, ex Waterhouse coll., 20°11'S, 57°32'E, ex M. J. Waterhouse, pre-1929 (AMS C. 55925, 3 specimens); Mauritius, ex S. H. Stupakoff coll. (CM 62.23646, 1 specimen); Mauritius, 020°18'S, 057°36'E, ex E. Wright coll. (USNM 773477, 1 specimen); Mauritius, 020°18'S, 057°36'E (AMS C. 84788 (pt), 1 specimen); Mauritius, 020°18'S, 057°36'E (AMS C. no cat. #, 1 specimen); Madagascar, Nosy Be, 013°20'S, 48°15'E, J.E du Pont!, 1.v.1967 (DMNH 12222, 1 specimen); Reunion Is., St. Paul, 021°06'S, 055°36'E, M. Jay!, 1965 (ANSP 301723, 4 specimens); Reunion Is., 021°06'S, 055°36'E, J. Donohue! (ANSP 360172, 1 specimen); [label has very detailed collection data, but wrong locality: "Brampston Reef, Bowen, Queensland, completely sheltered, shore based reef, under edge of table coral on the extreme edge of reef, extreme low water, Coll. and pres: Frank Plant., Aug. 1966"] (AMS-C 85912, 1 specimen).

Cribrarula fallax (Smith, 1881)

Western Australia, Canal Rocks, S. of Yallingup, 33°40.2'S, 114°30'E, R. Hancey, 7 Aug. 1972 (AMS-C 364829, 1 specimen); Western Australia, Denmark, near Albany. ex R. Summers coll., 35°01'S, 117°09'E, F. Haddrill!, 1977 (AMNH 292300, 1 specimen); Western Australia, Denmark, Parry's Beach, collected by Misses Knight and Haddrill,

1973. ex R. Summers coll., 35°01'S, 117°09'E (AMNH 292298, 1 specimen); Western Australia, Denmark, Parry's Beach, Fran Haddrill!, 1974, ex Waverley H. Harmon coll., ex C.M. Burgess coll # 232-3 (illustrated in Burgess 1985: 255), 35°01'S, 117°09'E (AMNH 272879, 1 specimen); Western Australia, Denmark, Parry's Beach. ex R. Summers coll., 35°01'S, 117°09'E, Fran Haddrill!, 1978 (AMNH 292299, 1 specimen); Western Australia, Denmark, coll. Fran Haddrill, Feb 27, 1976. ex R. Summers coll., 35°01'S, 117°09'E (AMNH 292301, 1 specimen); Western Australia, ex James D. Jobin coll., F. Haddrill!, Jan. 1975 (AMNH 279472, 1 specimen); Western Australia, Parry's beach, 35°01'S, 117°09'E, Fran Haddrill!, 30.v.1974 (BPBM 247913, 1 specimen); Western Australia, Parry's beach, 35°01'S, 117°09'E, Knight and Haddrill! (CAS 112332, 1 specimen).

Cribrarula catholicorum (Schilder and Schilder, 1938)

Solomon Is., Guadalcanal, Marau Sound, 09°31'S, 160°11'E, ex Bledsoe coll. (USNM 876894, 2 specimens); Solomon Is., Guadalcanal, Marau Sound, 09°31'S, 160°11'E, Gower!, 1968 (ANSP 400653, 1 specimen); Solomon Is., Guadalcanal, Marau Sound, 09°31'S, 160°11'E, R. Crammer!, 23 Feb. 1972 (USNM 888123, 1 specimen); Solomon Is., Guadalcanal, Marau Sound, 09°31'S, 160°11'E, Aslakson! (USNM 778159, 1 specimen); Solomon Is., Guadalcanal, 09°31'S, 160°11'E, C Kauffman! (DMNH 155435, 1 specimen); Solomon Is., Guadalcanal, 09°31'S, 160°11'E, ex Kienle coll. (DMNH 196109, 1 specimen); Solomon Is., Guadalcanal, ex Katsaras coll., blue dot on label, 09°31'S, 160°11'E (DMNH 25806, 2 specimens); Solomon Is., Guadalcanal, 09°31'S, 160°11'E, J. Donohue! (ANSP 359678, 1 specimen); Solomon Is., Ata'a, Malaita, 09°00'S, 161°00'E, ex Schilder coll. (# 118) (BPBM 247843, 1 specimen); Solomon Is., Ata'a, Malaita, Coll. Rev. van der Riet, on reef under coral at low tide, ex Clifton Weaver, 09°00'S, 161°00'E, Rev. J. van der Riet!, 1965 (DMNH 10033, 1 specimen); Solomon Is., Ata'a, Malaita, 09°00'S, 161°00'E, Rev. J. van der Riet!, 1967 (ANSP 312264, 2 specimens); Solomon Is., Ata'a, Malaita, 09°00'S, 161°00'E, J. Donohue! (ANSP 359685, 2 specimens); Solomon Is., Ata'a, Malaita, 09°00'S, 161°00'E, J. Donohue! (ANSP 359684, 1 specimen); Solomon Is., San Cristobal Is., Kirakira, 010°30'S, 161°55'E, C. Heller! (ANSP 389615, 2 specimens); New Caledonia, Loyalty Is., Lifou, 020°53'S, 167°13'E, J. Brazier! (ANSP 17402, 1 specimen); Vanuatu, Efate Is., Pago Point, Efate Is., near lighthouse, 017°40'S, 168°25'E, W. Cernohorsky!, 5 Sept. 1970 (USNM 773759, 8 specimens); Vanuatu, Lifu, 020°53'S, 167°13'E, Mar. 1973 (CMB, 1 specimen); Vanuatu, 017°40'S, 168°25'E, T. Male!, Jul. 1997 (EAK, no cat. #, 1 specimen); no locality (AMS C. 88604, 1 specimen).

CHAPTER 7

CONCLUSIONS AND FUTURE DIRECTIONS

Introduction

The Mollusca is the second largest phylum, with 50,000 to 100,000 Recent species, and some 35,000 fossil species described. Mollusks have a long fossil history, going back as far as the Cambrian. Fedonkin and Waggoner (1997) suggest that mollusks may have appeared in the Late Precambrian. With such a long evolutionary history, and the great diversity seen today, mollusks can be considered one of the most successful animals, having colonized nearly all habitats.

Included in the phylum are animals with different body plans such as bivalves, gastropods and cephalopods. Because most mollusks have shells and a radula, these characters have been the most used in molluscan taxonomy. However, mollusks in the class Aplacophora, many Cephalopoda, and some Gastropoda (e.g. Nudibranchia) either lack or have internal or reduced shells, and all Bivalvia lack a radula, therefore, these taxonomic characters do not apply to the whole phylum.

Taxonomic characters

This dissertation reviews the traditional characters used in gastropod taxonomy (shell and radular characters), and uses cowries, a well-known and diverse gastropod family to explore non-traditional and novel characters, such as dorsal spots (DS) and allied characters, and the odontophore.

As reviewed in Chapter 2, DS and related characters can be useful in separating cowries. Although about 45% of the cowries have some spotting, ocelli, lacunae, and other spots (personal observation), not all are formed the same way as those in the *Cribrarula* complex. Although of relatively limited taxonomic range, DS and related characters are interesting because unlike most traditional taxonomic characters, DS and allied characters may provide information about the soft parts (papillae and the mantle) previously only available from the study of life or preserved material.

Chapter 3 introduces a new taxonomic character, the odontophore cartilage. The role of the odontophore in feeding has been studied in detail in some gastropods (e.g. Graham, 1973; Fretter, 1983; Fretter and Graham, 1994), and a few studies have used the number of odontophore cartilages as a phylogenetic character (e.g. Ponder and Lindberg, 1997; Haszprunar, 2000). Although known since at least the 1800's and intimately connected with the radula, the odontophore has been neglected as a taxonomic character. The study of cowrie odontophores reported in Chapter 3 suggests that the odontophore can be useful as a source of taxonomic characters. Because most mollusks have odontophores, the structure can potentially be as taxonomically useful as the radula, and become another standard character in the Mollusca.

The radula is widely used as a taxonomic character, and most recent studies illustrate the radula in SEM micrographs for comparative taxonomic purposes (e.g. Kool, 1993; Bradner and Kay, 1996). There are several methods for preparing the radula (e.g. Morris and Hickman, 1981; Mikkelsen, 1985, Bradner and Kay, 1995), but a new, simpler method of mounting radulae for SEM was developed during the study of cowrie radulae to allow a longer time to arrange the radula before it dries and settles on an SEM stub (Chapter 4). Although only tested with cowrie radulae (which are relatively simple and large, compared to other gastropods), the method potentially can be useful for other mollusks as well.

A taxonomic review of the genus *Cribrarula* Strand, 1929 (Cypraeidae) (*cribraria* complex) was carried out using the traditional and non-traditional taxonomic characters described above (Chapter 6). A large number of specimens (1298) was studied in several large museums in the USA and Australia, and additional material was borrowed from other museums and private collections. During the study of the *cribraria* complex, an undescribed species was discovered in the Australian Museum collection, and it was described as *Cribrarula gravida* Moretzsohn, 2002 (Chapter 5). The review of *Cribrarula* consists of the main part of this dissertation, but the other chapters are important in explaining the taxonomic characters used in the dissertation.

When I started my PhD program at the University of Hawaii, I planned to travel to the different islands in the Indo-Pacific to collect fresh cowries in the *cribraria* complex for a molecular, anatomical and morphological study. I managed to travel to Micronesia and Palau, but the difficulty in finding specimens started to appear as a logistic problem. Requests were made to biologists collecting in other locations, but because most species are uncommon or rare, few specimens were obtained. Then, I decided to visit museums to look for specimens, but few preserved specimens were located, and among them, some were preserved in formalin, which nearly precludes molecular studies. The solution I found was to use museum specimens with dried tissue to extract DNA and the radula (Moretzsohn, 2002c). However, using dried tissue as the DNA source brought new problems: the inhibition of polymerase chain reaction (PCR) amplification of a 313 bp fragment of the mitochondrial DNA (mtDNA) cytochrome oxidase unit 1 (CO1), and the typical low yield and high degradation of DNA. After many frustrated attempts, eventually few samples were sequenced, but still only single or few sequences per taxon, and the molecular dataset was still incomplete. Therefore, the molecular dataset was not included in the dissertation, but I plan to add more data as samples become available.

Molecular characters are potentially the most universal characters not only among mollusks, but also for all living organisms (Avise, 1994). As the whole genome of more organisms become available, molecular systematics will be continue to grow in importance. However, it is unlikely that the whole genome of any mollusk will be sequenced in the near future, until other organisms with higher economic interest than mollusks in general (such as many microorganisms) have been sequenced, or the process becomes more affordable. Meanwhile, malacologists have lagged far behind many other groups in the molecular field (Davis, 1994). It is not necessary to sequence the whole genome of an organism to be able to do molecular systematics. In fact, as a strategy it is best to sample multiple genes or regions, such as certain mtDNA regions (Avise, 1994; Hillis et al, 1996).

There has been a long debate over which characters are best: molecular or morphological (reviewed by Hillis, 1987; Hillis and Wiens, 2000), and there are good arguments for both types of characters. To name a couple, advantages of molecular data include: 1) the large number of observable characters available, and 2) the genetic basis of molecular data is usually known. Advantages of morphological data include: 1) wide taxonomic sampling usually easier (and cheaper) than in molecular data, and 2) morphology is the only way most fossil taxa can be analyzed phylogenetically -- and fossils are important in polarizing character states. However, both datasets also have problems and limitations, and the best approach is to include all available characters in the analysis – although there are different ways to integrate datasets (e.g., Hillis and Wiens, 2000; Schander and Sundberg, 2001).

There is a wealth of anatomical characters in mollusks, which are usually informative, and can be used for comparative analysis. Kay (1957a, 1960b) pioneered the comparative anatomical analysis in the cowries, studying in detail many species of cowries. Other examples of comprehensive anatomical studies include Frètter and Graham (1962, 1994), Ponder and Lindberg (1997), and Simone (in press). Anatomical characters, other than the radula and odontophore, were not used in this dissertation because fresh or preserved specimens were not available for most species in the *cribraria* complex. The study of live specimens could yield other types of data, such as behavioral, physiological and ecological, that could be of taxonomic importance.

Future of taxonomy

The future of taxonomy is often debated in discussion groups such as Taxacom (www.usobi.org/archives/taxacom.html), as it is usually believed to be bleak because of: 1) decreasing funding for traditional (morphological) taxonomy; 2) lack of taxonomic training in most universities; 3) many taxonomists retiring without being replaced by young taxonomists and the lack of transmission of the knowledge only acquired by experience; and 4) biodiversity is being lost faster than we can document and study it (Gaston and May, 1992; Moretzsohn, 2002d).

Dissemination of taxonomic information is generally perceived as crucial. One advantage that molecular data have over morphological data is that the former are stored and shared online via large databases such as GenBank, while morphological data are still disseminated slowly via the literature.

My own experience and frustration with the difficulties of locating type specimens and taxonomic literature, and having to visit museums to study type specimens prompted me to propose (at the Species 2000 Workshop, Tsukuba, Japan, July 1999) an online database for taxonomic research, TaxonBank (Moretzsohn, 2002d). Like GenBank, the successful online molecular database maintained by the National Center for Biotechnological Information, the idea behind TaxonBank is to make taxonomic data on type specimens available online. TaxonBank's core consists of data on primary type specimens such as taxonomic ranks, species author, depository collection and catalog number, basic measurements, etc., as well as photographs or illustrations, facsimiles of the original description and related articles in PDF (Portable Document Format), and links to other databases such as GenBank, and websites of depository museums, taxonomic experts, field biologists, etc. The goals of TaxonBank are to expedite taxonomy by helping the location of type specimens and literature fast. Also, the use of digital imaging reduces or eliminates most of the need for a taxonomist to visit a museum just to study type specimens.

Other similar ideas have been proposed to increase funding for taxonomy (Godfray, 2002), to register species in an universal name registry (Bouchet, 1999), and other more complex and radical proposals to make the review process of taxonomic manuscripts open to the whole taxonomic community (Yanega, 2003). A group of taxonomists who believe that the future of taxonomy will be digital started the discussion group Digitaxa (http://linnaeus.all-species.org/pipermail/digitaxa/), which was active for a short while, but produced some good ideas. Hopefully some of these ideas will be implemented in the near future.

One step in the right direction is a recent journal, Zootaxa (www.mapress.com/zootaxa/), which publishes peer-reviewed papers on zoological taxonomy fast, simultaneously both on paper and online. The journal takes advantage of modern electronic publication technology to print each article as an issue, so that the printer does not have to wait for other articles to complete and print an issue. The journal also offers free color illustrations in the online version, no page limit, and manuscript submission e revision by email. The whole process can be much faster than traditional journals, while maintaining the same high standards expected from scientific journals.

While traditional, morphology-based taxonomy is in crisis, molecular systematics is on the rise. Currently it is difficult to obtain funding for a taxonomic project that does not include a molecular component. A rare exception seems to be the National Science Foundation's PEET program – Partnerships for Enhancing Expertise in Taxonomy.

Large, multi-year projects are funded every year, and require: 1) the partnership between universities and museums (or herbaria), 2) training of students in taxonomy; and 3) electronic dissemination of the results. The use of molecular data is not required, but its use is certainly welcome. Again, it is hoped that more initiatives like PEET will become available soon.

Recommendations

Having gone through the enriching experience of a graduate program in Zoology, and learned from others and my own experience, I would like to offer some recommendations to future students who are interested n taxonomy:

1) Choose a group of organisms that is readily available for collection, or that has a good collection of recently preserved specimens available, and avoid groups that are uncommon or difficult to collect;

2) Consider logistic problems such as field work in the design of the project. The easier to collect your specimens, the faster you can get your results;

3) Familiarize yourself with the techniques and methods to be used, and practice them with common species;

4) Molecular data: secure funding before starting a large molecular project to avoid having to continuously apply for grants. Design specific primers using closely related species. Although it is possible to extract DNA from dried tissue, it is better if you can only use fresh or preserved tissues;

5) Start writing your thesis or dissertation early -- that will save you a lot of time at the end. Publish as much as you can along the way. Good luck!

Conclusions

This dissertation explores non-traditional and novel taxonomic characters in the Mollusca, and uses them in conjunction with traditional characters to review a genus of marine gastropods, *Cribrarula* Strand, 1929. One of the conclusions of this study is that cowrie shells may be more informative than previously believed.

Besides the review of *Cribrarula*, I believe that the main contribution of this dissertation to the field of molluscan taxonomy is the use of odontophores as taxonomic characters. I plan to continue to study the odontophore and its taxonomic utility in other molluscan groups. I also would like to pursue the implementation of an online database such as TaxonBank, because of the potential benefits it could bring to the field of taxonomy.

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