A Revision of the genus *Cryptospira* Hinds, 1844 (Caenogastropoda: Marginellidae)

Andrew WAKEFIELD
14 Forest Side, Buckhurst Hill, Essex, IG9 5SL, U.K.
e-mail: bmw.awake@btinternet.com

KEY WORDS. Marginellidae, *Marginella*, *Cryptospira*, species groups, new species, type specimens, taxonomy, biogeography, evolution, Pliocene and Pleistocene fossils, Sunda Shelf, Wallace line, South China Sea, Java Sea, Andaman Sea.

ABSTRACT. The marginellid genus *Cryptospira* Hinds, 1844 is revised on the basis of characteristic shell morphologies. Three species groups within the genus are proposed; the *Cryptospira tricincta* group, the *Cryptospira ventricosa* group and the *Cryptospira elegans* group. The recent species and the fossil species are presented and discussed separately.

In the first section, all of the taxa in the *Cryptospira tricincta* group are revised and updated. Of the nine published taxa, six (*Marginella tricincta* Hinds, 1844; *M. onychina* A. Adams & Reeve, 1848; *C. quadrilineata* Gaskoin, 1849; *M. immersa* Reeve, 1865; *M. fischeri* Bavay, 1902; *C. sabelli* Cossignani, 2006) are considered to be valid species, and three are considered to be synonyms (*M. ovalis* Marrat, 1881 and *C. quiquandoni* Cossignani, 2006 are junior synonyms of *M. tricincta* Hinds, 1844, and *M. quadrilineata* Reeve, 1864 is a junior synonym of *C. quadrilineata* Gaskoin, 1849). From an argument based upon regional differences in shell morphology, the phenotypes currently accepted as *C. tricincta* are assumed to be a complex of species and/or subspecies. Further division of the *C. tricincta* group into three sub-groups is also proposed on the basis of morphologic features, and three new species are described: *C. wallacei* n. sp. from the Makassar Strait, Eastern Kalimantan, *C. cloveriana* n. sp. from Taiwan to Singapore, and *C. mccleeryi* n. sp. from the Gulf of Thailand.

The *Cryptospira ventricosa* group comprises six published taxa, three of which are valid species, namely *M. ventricosa* G. Fischer von Waldheim, 1807, *M. dactylus* Lamarck, 1822 and *M. trailii* Reeve, 1865. Three further taxa are considered to be junior synonyms of *M. ventricosa* (*M. quinqueplicata* Lamarck, 1822; *M. vermiculata* Redfield, 1851; *M. hainesii* Petit, 1851) and one dubious name, *Voluta porcellana* Perry, 1811 is also discussed.

The *Cryptospira elegans* group comprises thirteen published taxa of which seven are considered valid species; *Voluta elegans* Gmelin, 1791; *V. strigata* Dillwyn, 1817 (synonym *M. undulata* Deshayes, 1844, with *M. Bernardii* Largilliert, 1845 introduced as a new synonym); *C. marchii* Jousseaume, 1875 (removed from the synonymy of *V. strigata* Dillwyn, 1817 and elevated to valid species status. *M. Burchardi* Reeve, 1864 is transferred from the synonymy of *V. strigata* Dillwyn, 1817 to the synonymy of *C. marchii*); *M. praecallosa* Higgins, 1876 (previously considered by authors to be a synonym of *V. strigata* Dillwyn, 1817, with *M. loebbeckeana* Weinkauff, 1878 introduced as a new synonym); *C. glauca* Jousseaume, 1875; *Persicula grisea* Jousseaume, 1875 (senior synonym *M. obtusa* Sowerby, 1870 and junior synonym *M. sexplicata* Weinkauff, 1879); and *M. scripta* Hinds, 1844.

The holotype of *M. loebbeckeana* Weinkauff, 1878 is rediscovered, and this taxon is considered not to be a variety of *C. glauca* Jousseaume, 1875 as commonly accepted, but rather a junior synonym of the valid *M. praecallosa* Higgins, 1876, here considered as a valid species. *C. bridgettae* n. sp. from the Andaman Sea is described as a new species in the *Cryptospira elegans* group.

Three taxa occurring exclusively as fossils from the Indonesian Pleistocene have been published (*C. sangiranensis* Martin, 1906; *C. dactylus var. inflata* Martin 1895; *M. birmanica* Vredenburg, 1923), and all are considered to be extinct. Eight further fossil phena comprising three forms of *M. tricincta* Hinds, 1844 (one a synonym named *C. quinqueplicata var. minor* Martin, 1931), *M. ventricosa* Fischer von Waldheim, 1807, *M. dactylus* Lamarck, 1822 (synonym *M. dactylus var. minor* Pannekoek, 1936), *V. elegans* Gmelin, 1791 (synonym *M. (C.) ex aff. elegans* Oostinghe, 1938), *V. strigata* Dillwyn, 1917 (synonym *M. (C.) aff. loebbeckeana* Oostinghe, 1938) and *M. trailii* Reeve, 1865 are considered to match recent species. Two new fossil species of *Cryptospira* from the late Pliocene of Sangiran, central Java, are described; *C. bundharmai* n. sp. from Sambang Macan, and *C. kemukusi* n. sp. from Kemukus. Both are considered to be extinct.

In examining the phylogenic relationships of the genus, evidence from the fossil record and comparative analysis of the radula of recent species point towards a relatively recent evolution of the genus as an adaptive radiation from the main *Prunum / Volvarina* stock into the region of the Sunda Shelf, probably during the last 3-5 million years. The current biogeographic distribution of the genus is examined and three species group radiations from a central evolutionary zone, where species diversity is at its greatest are proposed.

INTRODUCTION

The compact and very distinctive Asian marginellid genus *Cryptospira* is arguably the most widely recognised and collected of this large family of carnivorous gastropods. This is largely due to the above average shell size, attractive patterns and colours, and ready availability of specimens. It has a turbulent taxonomic history which plays host to far too many synonyms and dubious names on account of high variability and an apparently confusing array of superficially similar morphologies. Even the name of the genus is confusing as the majority of its species do not have concealed spires. Several papers, limited in their scope, have made the principal contributions to our knowledge to date (Coomans, 1969; Clover, 1979 & 1981; Dharma & Dunlap, 1994), but the genus has never been the subject of a general revision, despite being distinct and confined to a well-defined geographical area. There is a low number of recognized species probably because the absence of clear specific distinction in the literature causes great difficulty in sorting out the distinct species from morphological varieties. A lack of scientifically organized prospecting in the field and the difficulty in obtaining reliable data with specimen lots when they are collected also contributes to the uncertainty, with the result that a historic tendency to lump species together has lingered on to the present day. This has occurred most noticeably in the type species *Cryptospira tricincta* Hinds, 1844 which has been used as the default name for several closely related but in fact different species. Not surprisingly, therefore, there is general confusion about the identity of many specimens and they are often labelled inappropriately with their names simply guessed at. A comprehensive revision of the genus and its constituent taxa is therefore well overdue.

Genus Taxonomy

The genus received extensive coverage in the 19th Century monographs, catalogues and iconographies of Lamarck (1822), Reeve (1864-65), Sowerby (1870), Redfield (1870), Jousseaume (1875) and Weinkauff (1879), wherein lie many of the original descriptions. However, in the absence of a suitably established generic arrangement, the species featuring in these monographs and catalogues were often listed under the all-encompassing family name *Marginella*. Hinds (1844a) reviewed *Marginella*, splitting it into two sections; *Cryptospira* for species with hidden spires, and *Phaenospira* for species with exposed spires. Hinds' usage of division here is valid as a generic level name according to the International code of Zoological Nomenclature (Article 10e). Subsequent reviewers oscillated between generic division, and the use of the family name alone. *Cryptospira* was one of fourteen genera adopted by Jousseaume (1875) although not all of the species we now consider to be *Cryptospira* made it into his definition of the genus. For example, he placed *C. grisea* (Jousseaume, 1875) in *Persicula*, and *C. scripta* (Hinds, 1844) and others in *Egouena*, a new genus he created for many species we now consider to be in the *Prunum / Volvarina* complex, and a generic name not currently in popular use. Tomlin (1917) separately listed the genera without attempting to use them in his list of species. In his proposed reclassification of the family Marginellidae, Coan (1965) listed *Cryptospira* (along with the genus *Closia* Gray, 1857) as a subgenus of *Bullata* Jousseaume, 1875. *Bullata* is a genus restricted to the western Atlantic (northeast South America) and with *Closia* and *Cryptospira* having restricted ranges and evolutionary origins in the north-western Indian Ocean and south-east Asia respectively, a close link to *Bullata* seems unlikely. Coan's classification has been superseded by that of Coovert & Coovert (1995) and is now rarely used.

So what are the main morphologic criteria enabling separation of *Cryptospira* from other genera in the *Prunum / Volvarina* complex? Coovert & Coovert (1995) separated it from the *Volvarina* and *Prunum* phyletic lineages on the basis of the extra columellar plications (from the four in *Prunum / Volvarina*, up to six plications plus a parietal denticle in *Cryptospira*) which they considered to be a major specialization. However the increased plication count is not in itself diagnostic; one *Prunum* group (*Prunum fulminatum* and associated species which will be mentioned later) has five, and the the *Serrata* lineage also has a fifth plication, albeit a discontinuous one, apparent in the aperture. Therefore some other homogenous character needs to be identified to define the genus.

In the *Prunum / Volvarina* complex generally, and including *Cryptospira*, there is no resorption of internal whorls and the plications spiral up the columella gradually reducing in size but otherwise remaining unmodified (Fig. 1a). Further heterogenous characters are general shell shape and size, spire elevation, presence of a thick labial margin, parietal callus deposits and labial denticulation. The only homogenous shell characters for the genus *Cryptospira* are the unique morphology of the columella plications, their angle of orientation on the columella, and the percentage of apertural length they

occupy. The plications in *Cryptospira* occupy from over ½ to almost the whole of the aperture if the remote 6th plication or lira is included, and their orientation becomes progressively more horizontal. This is demonstrated in the cutaway sections of *C. elegans* (Fig. 1b), *C. tricincta* (Fig. 1c), and *C. ventricosa* (Fig. 1d). Even the 6th plication, thinner and finer than the preceeding ones is continuous all the way up the columella (Fi. 1e). In comparison, the 4 or 5 plications of *Prunum / Volvarina* only occupy up to half of the apertural length and their orientation remains relatively oblique (e.g. *Prunum pergrandis* Clover, 1974, Fig. 1h). In *Closia*, the four thin, sharp plications are even more uniform and concentrated at the anterior third of the aperture (e.g. *Closia giadae* Cossignani, 2001, Fig. 1i). In *Serrata* the plications occupy less than half of the aperture and if a fifth plication is present it becomes discontinuous within the aperture after only half a revolution, unlike the comparable continuous 6th plication in *Cryptospira*.

Alhough the first two plications are similar to those encountered in the *Prunum / Volvarina* complex, the third, fourth and fifth plications, especially in the *Cryptospira elegans* and *Cryptospira tricincta* groups, have square topped plications in cross - section (Fig. 1g). These are strongly emergent from the aperture, and in some species cross almost the entire ventral surface. These plications are wider at the crest, and bear a double beading along it, resulting in an apparent bifurcation at the distal terminus of each plication (Fig. 1f). The thin and remote sixth plication, where present, often terminates further out of the aperture than earlier ones, and forms a distincly 'club – shaped' distal end which often points posteriorly.

The presence of the three divergent *Cryptospira* groups comprising species which share common ancestral lineages is revealed from further morphologic trends and geographic distribution patterns. It is the exploration of these species groups, presented herein for the first time, which forms the main thrust of this paper.

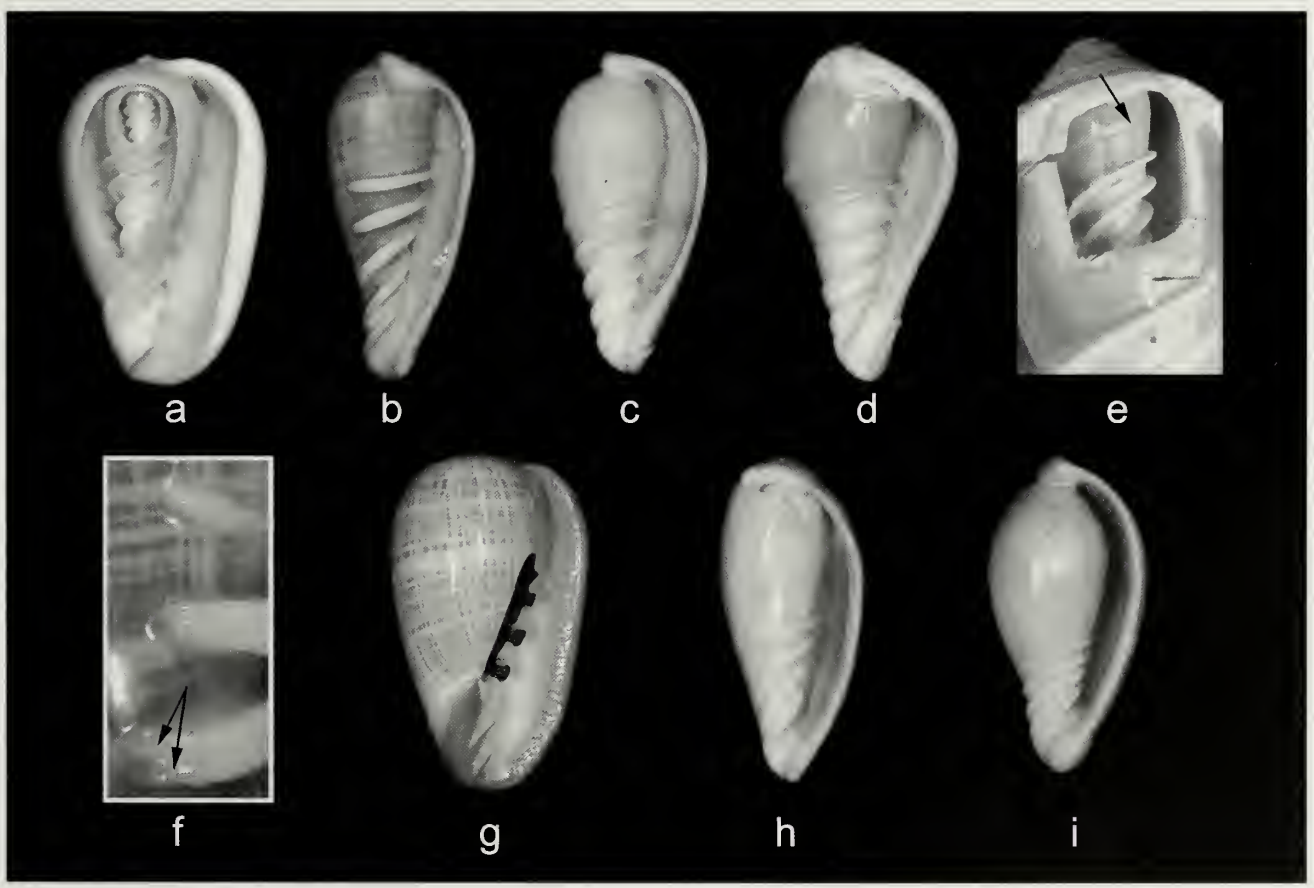


Figure 1. Shell sections revealing Columella morphologies of *Cryptospira* and related genera.
a. Unmodified internal whorls and plications in *C. marchii.*; **b.** ½ adult whorl section of *C. elegans*; **c.** ½ adult whorl section of *C. tricincta*; **d.** ½ adult whorl section of *C. ventricosa*; **e.** Continuous 6th plication in early whorl of *C. ventricosa*; **f.** Terminal bifurcation of plications of *C. elegans*; **g.** Cross section of plications 3 - 5 and parietal lira in *C. elegans*; **h.** ½ adult whorl section of *Prunum pergrandis* Clover, 1974; **i.** ½ adult whorl section of *Closia giadae* Cossignani, 2001

Specific Taxonomy

Until recently, the majority of the described species were known only from their type material, which was often confined to single specimens discovered on the major 19th Century collecting expeditions to the Far East. Consequently there are a number of old, poorly known taxa lying dormant in the literature, their names having fallen out of popular use because further specimens were unavailable. This was, and continues to be, mainly a reflection of the fact that the entire invertebrate fauna (including the Mollusca) of the whole region is very poorly prospected, with no concerted effort made to record and accumulate accurate locality and other data. However, the recent discovery and naming of several new species (see fig. 2) is both a reflection of the fact that there has been an increase in the prospecting for specimens for study, many of which come with more reliable data, and also due to a more analytical approach to their taxonomy. What is clear is that this apparently small genus is naturally more diverse than was first thought, with probably even more new species to be discovered in the future.

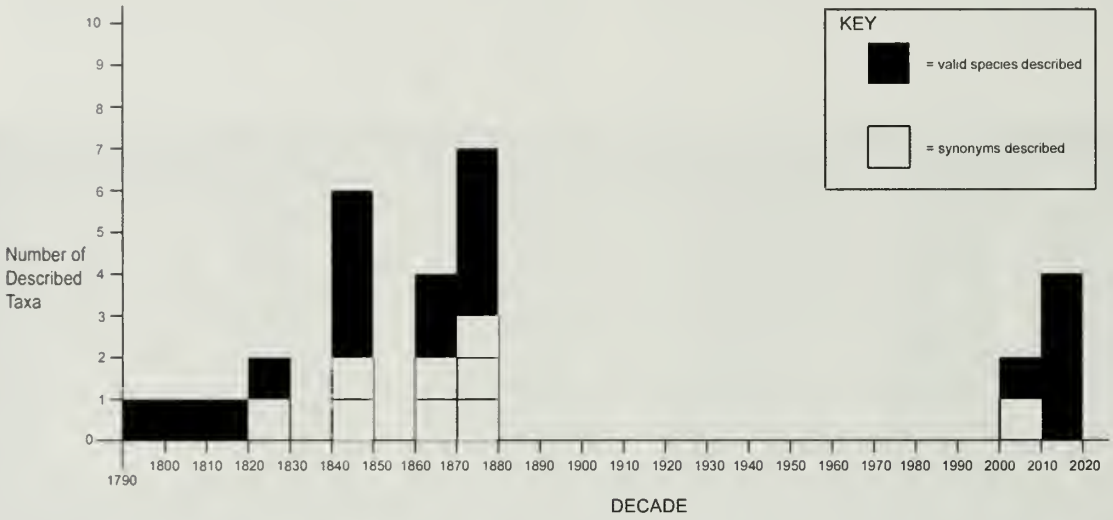


Figure 2. Bar chart indicating the number of *Cryptospira* taxa described, decade by decade, since 1790.

Apart from a few extracted radulae, patchy anatomical descriptions, and a few photographs and drawings, we know little about the living animals of *Cryptospira*, and population studies and DNA analyses are non-existent. So, through necessity, our species definitions are limited to morphologic studies of their shells. Throughout the current paper therefore I will be naming and describing morphospecies and will be assuming, rightly or wrongly, that these translate to biological species.

Natural Diversity

The genus is at its most diverse in the warm, shallow waters of the continental shelf (Sunda Shelf) region of Indonesia, where it completely dominates the large marginellid fauna (Fig. 5). The greatest concentration of species occur in the Java Sea off Java, Sumatra and Kalimantan (Borneo) and along the South China Sea-facing coast of Kalimantan and including the Straits of Malacca, the Karimata Strait, the Sunda Strait and the Makassar Strait (12 species). This continues northeast into Palawan (5 species) and the Sulu Sea up to the western central Philippine Islands (1 species) and on to southwestern Taiwan (2 species). The genus has also dispersed west to the Nicobar and Andaman Islands (2 species). Continental distribution extends westwards from Peninsular Malaysia (3 species) along the coasts of Thailand (6 species) and Myanmar (Burma) (2 species), to eastern India and Sri Lanka (1 species). From peninsular Malaysia it extends into the Gulf of Thailand (3 species) along the coasts of Cambodia and Vietnam (2 species) and the entire length of the Chinese coastline (3 species) up to the Taiwan Strait.

Incorrect generic assignments

Marginella mabellae Melvill & Standen, 1901 from Sri Lanka, and *M. angustata* Sowerby, 1846, two west-central Indian Ocean species often regarded as being *Cryptospira* in modern texts, do not belong in the genus. They have been confused with *Cryptospira* because their spires are covered by an apical callus extending from the posterior end of the lip and parietal surface. Adult shells of *M. mabellae* have an extensive opaque white parietal callus covering all of the ventral surface and columella, an external varix which is very wide anteriorly, a strongly inflexed lip and four very short stocky plications. Its morphology has more in common with that of northeast African and western Atlantic *Prunum* species such as *Prunum oblonga* (Swainson, 1829). *M. angustata* on the other hand, has a very wide labial varix which is only weakly externally thickened and completely lacks a varix groove. It too has a strongly inflexed lip and four oblique anteriorly situated plications. These typically *Volvarina*-like characters immediately rule out any direct association with *Cryptospira*. Furthermore, the distribution of these two non-labially denticulate species on the extreme western end of the range of the extremely dissimilar, labially denticulate *Cryptospira elegans* group species, provides biogeographic evidence that they are to be distinguished from *Cryptospira*.

Morphological species groups

Coovert & Cooovert (1995) took their reclassification to genus level. Yet it is obvious, when one views specimens of *Cryptospira* species in any quantity, that certain species bear morphological affinities with each other, and that the genus should be able to support a further taxonomic tier based upon natural groupings with shared characteristics. Such subdivision has in fact already been intimated by Gary Coovert (p. 93, 1995) who noted that 'One species group within the genus has distinctively gray-coloured shells'. It is difficult to know to which species he was referring, and as far as I am aware he did not publish his ideas further.

When the morphological characters of all of the species in the genus are assessed, it becomes apparent that three distinct diverging lineages branch off from the evolutionary *Cryptospira* 'tree'. They are introduced and defined herein as the *Cryptospira tricincta* group, the *Cryptospira ventricosa* group and the *Cryptospira elegans* group. The *Cryptospira tricincta* group can be divided further into three sub-groups. The differences between these groups and sub-groups are summarised in figure 3. It can be seen that analysis of a set of four primary shell characters shown in light grey (the angulation of the anterior canal, the shape of the anterior end, the number of plications with which callus is associated, and the total number of plications) will permit placement of the species in its correct group.

The angle that the siphonal canal makes with the long (columella) axis of the shell when viewed laterally, is a new and exceedingly important character that has not been previously utilised as a diagnostic tool. It is to be differentiated from, though it is associated with, truncation of the posterior end of the lip which is a character best observed from the ventral aspect of the shell.

Perhaps surprisingly for a genus whose name means 'hidden spire', this character does not actually define the genus. In fact, of the 20 valid species in the genus (including the new species described herein), only 5 have submerged spires. Neither is this character useful in the assignment of a species to one of the three groups. For example, the gracefully curving posterior end to the lip of *C. dactylus* and its submerged spire might suggest that the species was closely related to *C. tricincta* which also has a submerged spire and a similarly shaped posterior end to the lip. In fact the columella morphology and the profile of the anterior end of *C. dactylus* are quite diagnostic, outweigh the secondary character of the spire morphology, and positively place the species in the *Cryptospira ventricosa* group. Along with morphology of the lip and columella plications, the spire morphology is only of use in the assignment to sub-groups of the *Cryptospira tricincta* group species.

Other characters such as colour are also useful, but generally more so for identification of individual species. For example, the shells of *C. cloveriana*, *C. ventricosa*, and *C. glauca* are all of a similar, even grey colour, yet all three species are in fact in different morphological groups. As in other families, pattern styles (when present) tend to be much more reliable taxonomic indicators than the colours themselves.

Such morphological grouping has another, very valuable taxonomic function in that it is a useful aid in the separation and subsequent identification of some species which are often confused with one another, such as *C. glauca* and *C.ventricosa* (see p. 26). A good understanding of the morphological characters of the three *Cryptospira* groups can therefore make a significant contribution to nomenclatural stability.

It is likely that anatomical characteristics of the animal and its chromatism are also group specific characters but this remains to be confirmed.

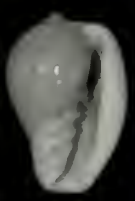
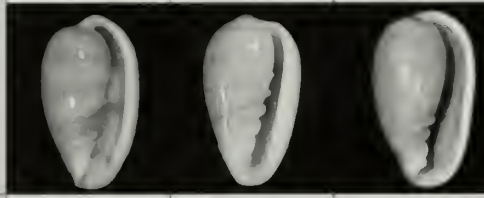
Shell Character		*Cryptospira tricincta* Group			*Cryptospira elegans* Group	*Cryptospira ventricosa* Group
		'Cryptospira tricincta sub-group'	*'Cryptospira fischeri* sub-group'	*'Cryptospira quadrilineata* sub-group'		
						
Angulation of anterior canal From lateral viewpoint	In line with columella axis	No	No	No	No	Yes
	Angled downwards by 30°	Yes	Yes	Yes	Yes	No
Shape of anterior end	Smoothly rounded	Yes	Yes	Yes	Yes	No
	Truncated	No	No	No	No	Yes
Extent of callus formation at distal ends of plications	From 1st to 3rd plication	Yes	Yes	Yes	No	No
	From 1st to between 3rd and 4th plication	No	No	No	Yes	No
	From 1st to 4th plication	No	No	No	No	Yes
Number of plications (not incl. denticles)	4	No	No	Yes	No	No
	5	No	No	No	Yes	Yes
	6	Yes	Yes	No	Yes	No
Labial Morphology	Denticles Present	No	No	No	Yes	No
	Denticles Absent	Yes	Yes	Yes	Yes	Yes
	Relatively curved	Yes	No	Yes	No	No
	Relatively straight	No	Yes	No	Yes	Yes
Spire morphology	immersed and callused	Yes	No	Yes	Yes	Yes
	Exposed/elevated	No	Yes	No	Yes	Yes
Morphology of plications	Strongly cross ventral surface	Yes	No	No	Yes	Yes
	Weakly cross ventral surface	Yes	Yes	Yes	Yes	Yes
	Later ones tend towards horizontal	Yes	Yes	No	Yes	Yes
	Later ones tend towards remaining oblique	No	No	Yes	Yes	Yes
	Thick and square crested	Yes	Yes	No	Yes	Yes
	Remaining thin	Yes	Yes	Yes	Yes	Yes
Pattern style	Axial	Yes	Yes	No	Yes	No
	Spiral	Yes	Yes	Yes	Yes	No
	unpatterned	Yes	Yes	No	Yes	Yes

Figure 3. Comparison of species groups and sub-groups in *Cryptospira*.

Materials and Methods

Type material was examined at the Natural History Museum (BM(NH)) and the Liverpool Museum (MCM). Observations were supported by additional material present in the BM(NH), MNHN (CORINDON expedition material), and the Cambridge University Museum of Zoology (CMZ), the authors collection and in several other private European and Indonesian collections. Type material in the Paris, Geneva, Dusseldorf, and Cupra Maritima (Italy) museums was studied from digital photographs. Photographs taken by the author were taken with a Nikon D70 digital SLR camera with 60 mm macro lens and ring flash. On any one plate, whole shells are shown at the same magnification. Dimensions given are maximum shell length followed by maximum shell width, or maximum shell length only, and are of adult shells unless specified otherwise.

Abbreviations and symbols

MNHN: Muséum national d'Histoire naturelle, Paris
MHNG:Muséum d'Histoire Naturelle de Genève
LMD: Loebbecke Museum, Dusseldorf, Germany
BM(NH): Natural History Museum, London
NMW: National Museum of Wales, Cardiff
MGB: Museum Geologi Bandung, Bandung, Indonesia
MZB: Museum Zoologicum Bogoriense, Bogor, Indonesia
MMP: Museo Malacologia Piceno, Cupra Maritima, Italy
MZUB: Museo di Zoologiá dell'Università di Bologna, Italy
ZMUM: Zoological Museum of the University of Moscow
CMZ: Cambridge University Museum of Zoology, England
MCM: Merseyside County Museum, Liverpool, England
ANSP: Academy of Natural Sciences, Philadelphia, USA
ZMA: Zoological Museum of Amsterdam
MMM: Malacologia Mostra Mondiale, Cupra Maritima, Italy
AWC: Andrew Wakefield Collection, United Kingdom
TMC: Tony McCleery Collection, United Kingdom
BDC: Bunjamin Dharma Collection, Indonesia
SPC: Somwang Patamakanthin Collection, Thailand
FBC: Franck Boyer Collection, France
ATC: Andrew Tournier Collection, France
TCC: Tiziano Cossignani Collection, Italy
ICZN: International Code of Zoological Nomenclature
juv.: juvenile
sh.: dead collected shell
n. sp.: new species
†: fossil

SYSTEMATICS

Family **MARGINELLIDAE** Fleming, 1828
Subfamily **MARGINELLINAE** Fleming, 1828
Genus ***Cryptospira*** Hinds, 1844

Cryptospira Hinds, 1844: 76. Type species (by subsequent designation, Gray 1847: 142), *Marginella tricincta* Hinds, 1844.

Diagnosis

Shell small to moderately large (7 to 50 mm in length), cylindrical, elongate to elliptic, obovate, pyriform or subtriangular, thick, opaque, occasionally heavily but incompletely callused ventrally, uniformly coloured or with spiral bands and/or axial pattern; spire immersed, low or slightly elevated; lip thickened, internally smooth or denticulate; single external varix present, clearly demarcated by a groove; posterior notch absent or weak, siphonal notch absent or weak; columella with 4 to 6 plications occupying over half to two thirds of the apertural length. Sixth plication often remote, distinct callus often involving anterior 3 plications; first two plications very close to distally fused, occasionally an elongated parietal denticle present between fifth and sixth plications. Type 2 marginellid animal (Coovert & Coovert, 1995); siphon long; mantle smooth, extending over external shell surface (Figs 136, 148). Radula uniserial, relatively short, composed of relatively few (up to 48), overlapping, wide (0.06-0.158 mm), flat, multicusped (9-21 cusps) rachidian plates. Each oblong plate has a flat side and a cusped working side giving a 'comb-like' appearance (Fig. 4). The cusps increase in size up to the central cusp (statistics from Coovert, 1989(b)).

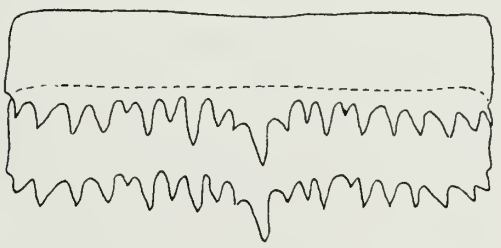


Fig. 4. Radula of *Cryptospira fischeri* (Bavay, 1902), from Coovert (1990) pl. 4, fig. 5.

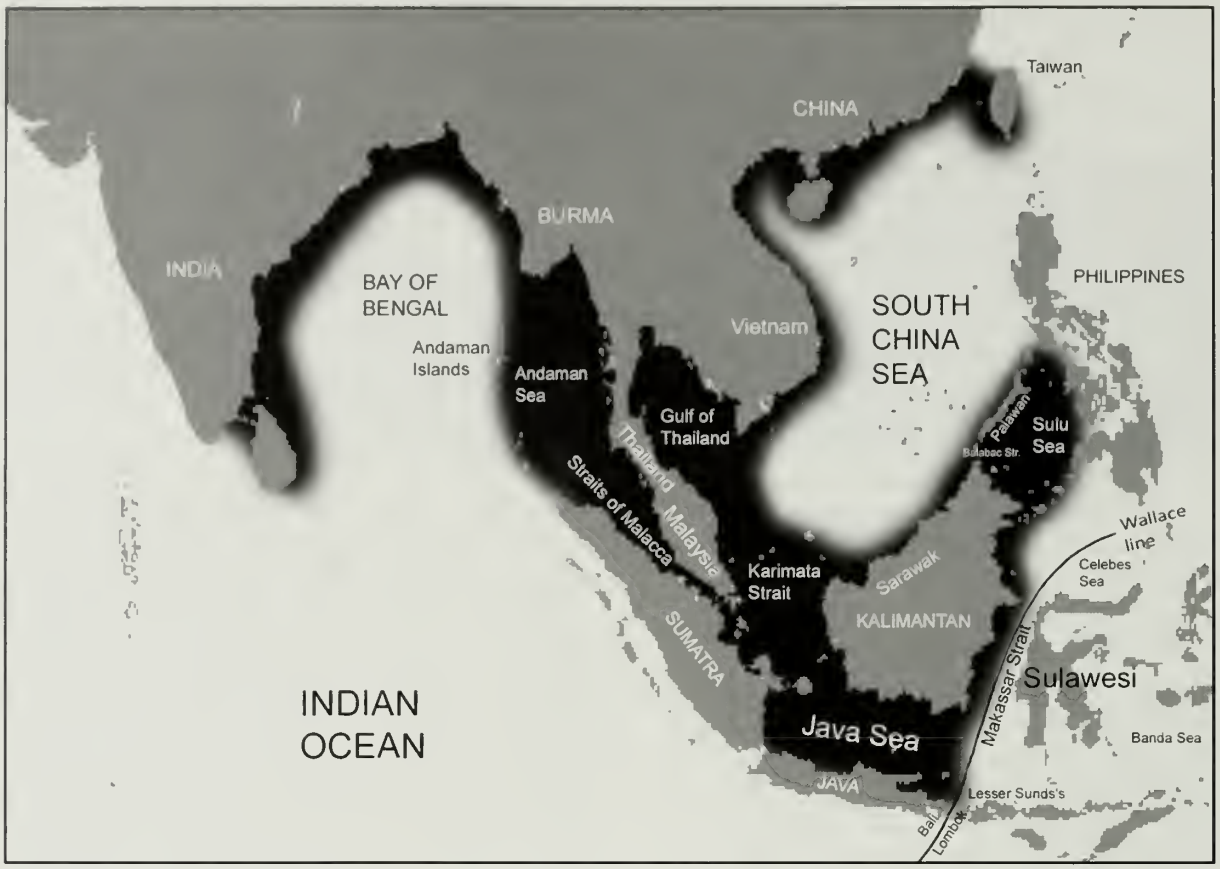


Figure 5. Distribution range of the genus *Cryptospira*

(A) *CRYPTOSPIRA TRICINCTA* GROUP

This is the largest of the three groups, comprising at least nine species, and up to six more forms, some of which may also eventually reach recognition as distinct species. The principal characteristics of the *Cryptospira tricincta* group are:

- ovate, ob-ovate to elongate shape
- 7-30 mm adult length for recent and fossil shells
- columella with 5-7 plications occupying 2/3 of the aperture
  Note: exception is *C. quadrilineata* at 1/3
- Anterior ventral callus, where present, only extends to the end of the third columella plication
- uniform light grey, pale brown, pale greenish brown, or pale pinkish brown colour, often with dark and light alternating axial growth zone markings which never form a zig-zag pattern
- 3-4 narrow red-brown spiral lines or wider bands visible internally and/or externally, or absent, depending upon species
- Lip without denticles, central section straight to slightly convex, inserting to side or top of spire, opaque white, pale orange or light brown
- immersed to slightly elevated spire
- weak to very weak anterior and posterior ventral callus

The currently accepted species concept of *C. tricincta* (Hinds, 1844) is all inclusive of its widely ranging forms (see figs 9-38), yet the morphologies of these forms are so disparate and discontinuous that they are difficult to explain away as a single species. Many of these bear little relation to the syntype, original description and first figures of *C. tricincta* (Figs. 15, 16, 77, 78). Lumping together all of these forms under a single species name would therefore seem to be an extreme oversimplification, and it is likely that potential new species are buried within the taxon. In the light of this, and following the convention that the definition of *C. tricincta* has to be provided by the original description and figure, supported by the morphology of the type, it is proposed to review this situation of singularity. Of the forms which do not fit well with this definition, those that deserve full separation from it are;

1. The grey, heavy opaque form from Taiwan which appears to extend in its range southwest to Vietnam and possibly further on to Singapore. It

is herein considered to be a distinct species. It certainly overlaps in its geographical distribution with typical *C. tricincta*, but seems not to intergrade with it. It has incorrectly been referred to as *Marginella (Cryptospira) Bernardii* Largilliert, 1845 by Reeve (1864/5), Redfield (1870), Tomlin (1917) & Clover (1979). Abundant material is available for study and it is described herein as *C. cloveriana* n. sp. (Figs. 30-33).

2. A new species from the Makassar Strait with a totally distinctive pattern, colouration and morphology. It is described herein as *Cryptospira wallacei* n. sp. (Figs. 34-37) from limited material.
3. A new species with a thin, light and slender shell with a curved siphonal canal and a peak at the posterior labial insertion. This impressive and wholly original morph is found on the Gulf coast of Thailand. It is described herein as *Cryptospira mccleeryi* n. sp., from limited material (Figs 23-26).

Those that may be deserving of full species recognition, but which require further studies before formally being named are;

4. A bulbous, oval form from the Taiwan Strait, given the reference *Cryptospira cf. C. tricincta* form '*ovalis*' (Figs 27, 28), after Marratt, 1881.
5. A large, thin, inflated form with an axial lined pattern and only five thin and weak plications, from the Karimata Strait, western Kalimantan. Given the reference *Cryptospira cf. C. tricincta* form A. Known from only a single specimen in BDC (Fig. 18).
6. A small squat form with wide spiral bands found in southern Kalimantan. Given the reference *Cryptospira cf. C. tricincta* form B (Figs 13, 14).
7. A narrow elongated dwarf form with spiral bands found in deep water in the Makassar Strait and at shallower depths in southern Kalimantan. Given the reference *Cryptospira cf. C. tricincta* form C (Figs 19-22).
8. An inflated giant form found in deep water in the Makassar Strait. Given the reference *Cryptospira cf. C. tricincta* form D (Fig. 17). Found sympatrically with form C.
9. An olive green to brown form with no external banding and a white lip, from Kalimantan. Given the reference *Cryptospira cf. C. tricincta* form E (Fig. 12).

The evidence presented by these diverse living forms, supported by similar diversity in the fossil record (Figs 223-236, 241-253), provides the evidence that it is the multiple species concept of *C. tricincta* (of authors) which looks the most likely, rather than the currently held view of singularity.

Within the *Cryptospira tricincta* group, three further sub-groups can be recognized;

The *C. tricincta* sub-group

In the *C. tricincta* sub-group species and forms, the posterior end of the lip arches gracefully over the posterior end of the shell and inserts almost directly on top of the depressed and buried spire (Figs. 9-38). This imparts a curved profile to the aperture. The species included in this sub-group are C. *tricincta* (Hinds, 1844), (TS), (Including forms A-E. Possible syn; *Marginella ovalis* Marrat, 1881 [MS name]), *Cryptospira cloveriana* n. sp., *Cryptospira wallacei* n. sp. and *Cryptospira mccleeryi* n. sp.

The *C. fischeri* sub-group

In the *C. fischeri* sub-group species, the posterior end of the lip inserts nearer to or at the shoulder (Figs. 39-61) the effect of which is to reveal the spire and to straighten up the aperture. The species included are *C. fischeri* (Bavay, 1902), *C. sabelli* Cossignani, 2006, *C. immersa* (Reeve, 1865), (Syn; *C. quiquandoni* Cossingnani, 2006) and *C. onychina* (A. Adams & Reeve, 1848), and they gradually increase in size in the order *C. fischeri/sabelli* < *C. immersa* < *C. onychina*.

The *C. quadrilineata* sub-group

This mono-specific sub-group is represented by *Cryptospira quadrilineata* Gaskoin, 1849.

C. quadrilineata could be considered the 'odd-one out' of the *Cryptospira tricincta* group as a result of its unusual columella morphology, which is at considerable variance with all other members of the group. It has been retained in it because all of its other morphologic characters are correct for the group. It is acknowledged that the erection of a fourth, mono-specific *Cryptospira* group to house this species would be an alternative classificatory option.

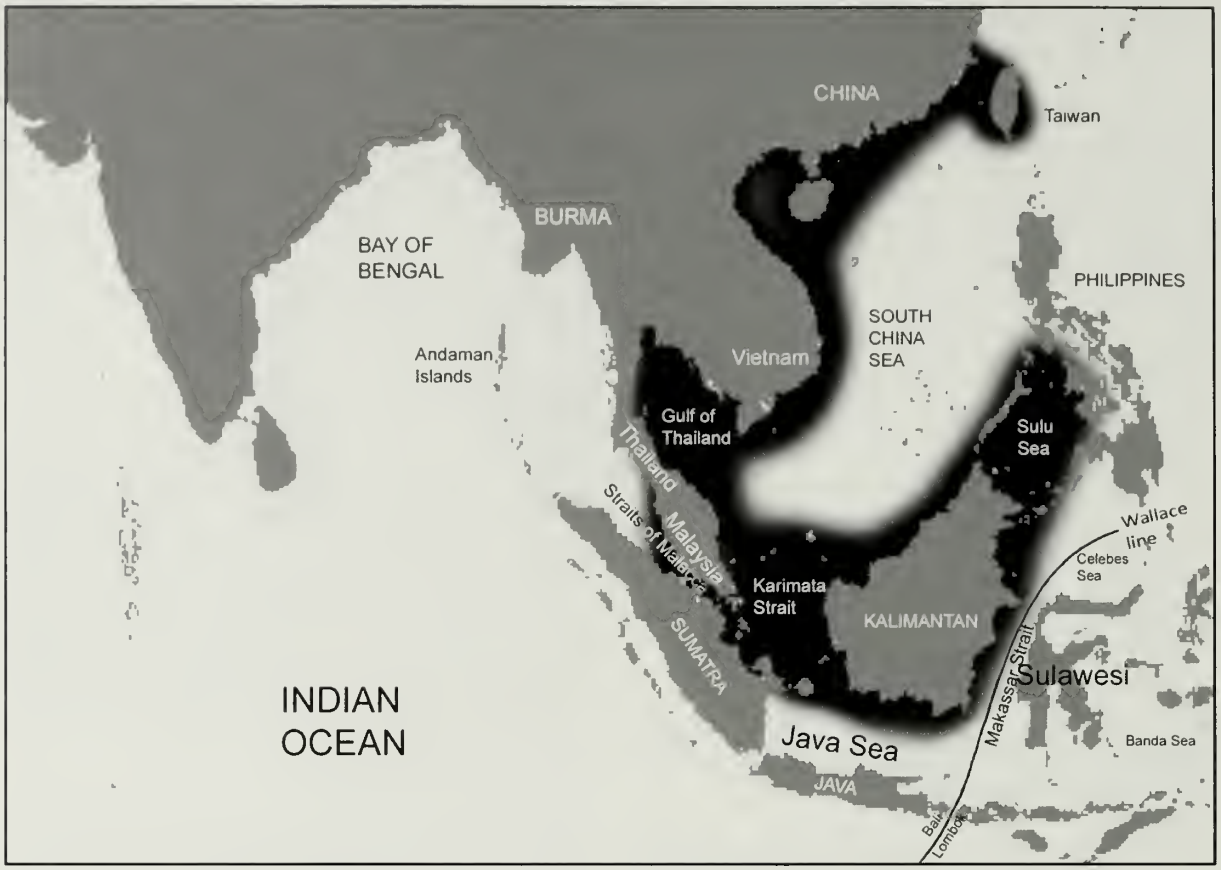


Figure 6. Distribution range of the *Cryptospira tricincta* group

(i) *Cryptospira tricincta* sub-group species.

Cryptospira tricincta (Hinds, 1844)
Figs 9-22, 27-29, 38, 73, 77, 78, 233-236, 241-253

Marginella (Cryptospira) tricincta Hinds, 1844(a) [Sept.] p. 76 & Hinds, 1844(b) [Oct] p. 46, pl. 13., figs. 12, 13.
Marginella (Cryptospira) ovalis Marratt, 1881 [MS name].
† *Cryptospira quinqueplicata* var. *minor* Martin, 1931

Type material. 2 spm, syntypes, Strait of Makassar, 11 fathoms, ex. Capt. Sir E. Belcher; 19.5 x 11.4 mm, Reg. No. 1844.6.7.38 (Figs 15, 16) & 25.5 x 15.7 mm, BM(NH) Reg. No. 1844.6.7.39 (Fig. 17).

The syntypes are light, inflated, pyriform, faded straw-coloured shells and one has three narrow reddish brown spiral lines on the body whorl, visible externally and internally. Tomlin (1917) recorded that the BM(NH) had two series, mounted on tablets: one of two specimens labelled 'Straits of Macassar, 11f., Sir E. Belcher, C.B.' and beneath the tablet '*tricincta*, Hds.' in Hinds' own handwriting: the other of three specimens labelled 'M.C., 11f., coarse mud, Str. Macassar, R. B. Hinds esq.'. A search only revealed the first series, and the tablet from which they had become detached. The smaller of the two syntypes (Figs 15, 16) most closely matches the description and original figure (Figs 77, 78), whereas the larger one (Fig. 17) is a specimen of *C. cf. C. tricincta* form D (see below).

Other material.

<u>*C. tricincta* typical;</u>
Mersing, East Coast Malaya, presented by R.D. Purchon, trawled, 1 spm, BM(NH).
North Borneo, Ex. A. Everett coll., 1 spm, BM(NH).
North Borneo, Brunei, Ex. P. W. Barrett-Smith coll., 1 spm, BM(NH).
Northwest Borneo, Natuna Is, net at 30 fathoms, 2 spm, 17.5 x 10.9 mm, 15.9 x 9.8 mm, AWC.
West Borneo, Karimata Strait, net at 20 fathoms, 2 spm, 18.9 x 11.4 mm, 15.6 x 9.6 mm, AWC.
East Borneo, Samarinda, 20 fthms, 1 spm, 28.6 x 15.9 mm, AWC.
East Borneo, Makassar Str., 5 spm, BM(NH).
East Borneo, Makassar Str., Pulau Balabalangan, 1 spm, 25.2 x 14.5 mm, (Fig. 38), AWC.
South Sumatra, Tulang Bawang, trawled 10-15m, 1 spm, 20.0 x 11.5 mm, (Figs 9, 10), AWC.
South Sumatra, Tanjung Menjangan, trawled in 10-15 metres, 2 spm, 21.1 x 12.7 mm, 17.8 x 11.0 mm, AWC.
East Sumatra, Syap Is., near Singkep Is., net 20 fathoms, 5 spm, 23.1 x 13.6 mm, 20.7 x 12.7 mm, 25.2 x 14.7 mm, 19.3 x 11. 8 mm, 20.0 x 12.0 mm, AWC.

East Sumatra, Bangka Is., trawled 10-15 metres , 2 spm, 22.4 x 13.5 mm, 17.5 x 11.0 mm, AWC.
East Sumatra, Tanjung Pinang, net in 20 fathoms, 2 spm, 17.0 x 10.5 mm, 15.4 x 9.2 mm, AWC.
Southeast Sumatra, Dua Is., Mesuji, trawled 10-15 metres, 2 spm, 20.5 x 12.9 mm, 22.2 x 13.3 mm, AWC.
Philippines, Palawan, Balabac Strait, 25 spm, 23 – 26.5 mm, (Fig. 11), AWC.
Vietnam, Nha Trang, 1 spm, 23.2 x 13.3 mm, (Fig. 29), AWC.
Vietnam, Nha Trang, 4 spm, MMM.
Hong Kong, 5 fathoms, B. Smith coll. Admiralty, 1 spm, BM(NH).
Southern China, 1 spm, 19.5 x 10.7 mm, trawled May 2007, AWC.

C. cf. C. tricincta form *ovalis*;
Taiwan Strait, trawled on gravel/sand in 40 metres, February 2010, 1 ad. spm., 21.9 x 15.1 mm, (Figs 27, 28), AWC.

C. cf. C. tricincta form A;
Western Borneo, Karimata Strait, in 20 fathoms, 30.0 x 17.0 mm, (Fig. 18), BDC.

C. cf. C. tricincta form B;
South Borneo, South Banjarmasin, net 20 fathoms, 3 spm, 9.3 x 6.0 mm (juv), 12.9 x 8.7 mm, 13.0 x 8.8 mm, 15.0 x 10.0 mm (Figs 13, 14), AWC.

C. cf. C. tricincta form C;
South Borneo, Sampit, net at 20 fathoms, 2 spm, 13.6 x 7.8 mm, 13.3 x 7.5 mm, (Figs 19, 20), AWC.
East Borneo, Makassar Str., 01° 08'S 117°18'E, trawled 49 metres, CORINDON Exp., st. CH205, 1 juv. spm, 12.2 x 6.3 mm, 1 spm, 13.0 x 6.9 mm (Figs 21, 22), MNHN.
East Borneo, Makassar Str., 00°40'N 117°51'E, dredged 96 metres, CORINDON Exp., st. DR216, 2 spm, 15.5 x 8.8 mm, & 15.5 x 9.5 mm, MNHN.

C. cf. C. tricincta form D;
East Borneo, Makassar Str., 00°40'N 117°51'E, dredged 96 metres, CORINDON Exp., st. DR216, 1 spm, 28 mm, MNHN.

C. cf. C. tricincta form E;
Northeast Borneo, Pula Sapangar, 2 spm, 19.0 x 11.45 mm, 18.6 x 11.5 mm, AWC.
Brunei, Jenudong Beach, from dredger pumping onto beach, 2 ad. spm., 22.4 x 13.1mm (Fig. 12), 24.1 x 13.6mm, AWC.

Type locality. Strait of Makassar, Indonesia.

Distribution. Widespread in the Sunda Shoal area (Java Sea and the Straits of Karimata and Makassar); from the north coast of Kalimantan southwest to the lower end of the Strait of Malacca (Malaysian Peninsula), and northeast to Palawan in the Philippines. It also extends along the northern coastline of the South China Sea, from Vietnam to the Taiwan Straits (Fig. 6).

Habitat. Soft muddy sand and gravel in 10 to 100 metres.

Descriptive notes. Shell small to medium sized (L= 12.5-30 mm, W:L ratio 55-69%), moderately thin, ovoid to sub-pyriform, inflated posteriorly, tapering smoothly to base. Colour light tan, creamy, pinkish, or pale greenish with or without axial growth line markings. Lip cream to opaque white. Four red-brown narrow spiral lines on body whorl; first at level of or just posterior to fourth plication, second at the level of the sixth plication, third halfway between the second spiral line and posterior labial insertion, and the fourth, often almost completely obscured, at the suture. Spire involute, immersed in callus. Shoulder smooth, rounded. Posteriorly, aperture as wide as labial varix, widening anteriorly. Lip thickened externally as a single varix with a smooth rolled edge. External varix groove present. Siphonal notch absent, posterior notch weak to absent. Lip extending beyond apex, curving round to insert into callus fractionally to labial side of spire. Columella with six plications (rarely only five) occupying anterior 2/3 of apertural length; first moderately strong, long, rounded in cross section, at 45° to axis; second very strong, long, close to first plication, edge flattenned, also at 45° to axis; third very strong, long, square in cross section, at 60° to axis; fourth slightly less strong, long, square in cross section, 80° to axis; fifth moderately strong, short, square in cross section; sixth often remote from fifth, short, often with a denticle at its distal end. Columella excavated between 2nd and 3rd plications. Anterior ventral callus merging laterally with the external varix and medially with the distal ends of the first four plications. Anterior end rounded. Parietal surface posterior to plications is smooth, callus absent to weak.

Remarks. The original description of *C. tricincta* in the Proceedings of the Zoological Society, September 1844 was confined to text only as follows:
'*Mar. testa obeso-ovata, cinereo-caerulescente, fusco trifasciata, labro incrassato, luteo, intùs laevi; columella sexplicata, ad basin alba; plicis tribus superioribus transverses, suprema paululùm obsoleta.*'
This translates as 'ob-ovate shell, greenish-ash coloured, with three darker bands, lip thick, golden yellow, inside on the left; columella six-plicate, white towards the base, first three superior plications transverse, the highest somewhat obsolete'.
The first illustrations (Figs 77, 78) appeared in October that same year in Hinds' account of the molluscs found on the voyage of the Sulphur (1844b). It was subsequently illustrated by Sowerby (1846), Chenu (1849), and Reeve (1864).

Marginella (Cryptospira) ovalis is considered here to be a regional form of *C. tricincta*. It was 'described' in one of F. P. Marrat's conchological leaflets, which were printed in small numbers and circulated for the benefit of his close acquaintances. *M. (C.) ovalis* is thus considered to be a manuscript name only. It was recorded as coming from Swatow, China (now known as Shantou, situated 300km northeast of Hong Kong at the entrance to the Taiwan Strait), which is at the northern end of the range of *C. tricincta*. Marrat described it as being a pale straw colour, with three spiral lines on the body whorl and having an orange labrum and columellar base. A search for this shell in the Marrat collection in the Liverpool Museum (Merseyside County Museums, England) was undertaken by the author but proved fruitless. Its original figures (Figs 79, 80) and description appears to be accurate enough to confirm its identity as *C. tricincta*, and this is confirmed by the acquisition of a fresh specimen from the Taiwan Strait by the author (Figs 27, 28). The remaining forms A-E of *C. tricincta* were discussed earlier.

Although Reeve (1864) referred to *C. tricincta* as the 'three-girt marginella', each patterned species in this group potentially has four spiral lines. In *C. tricincta*, the sub-sutural spiral line tends to be obliterated by the insertion zone of the posterior labial callus.

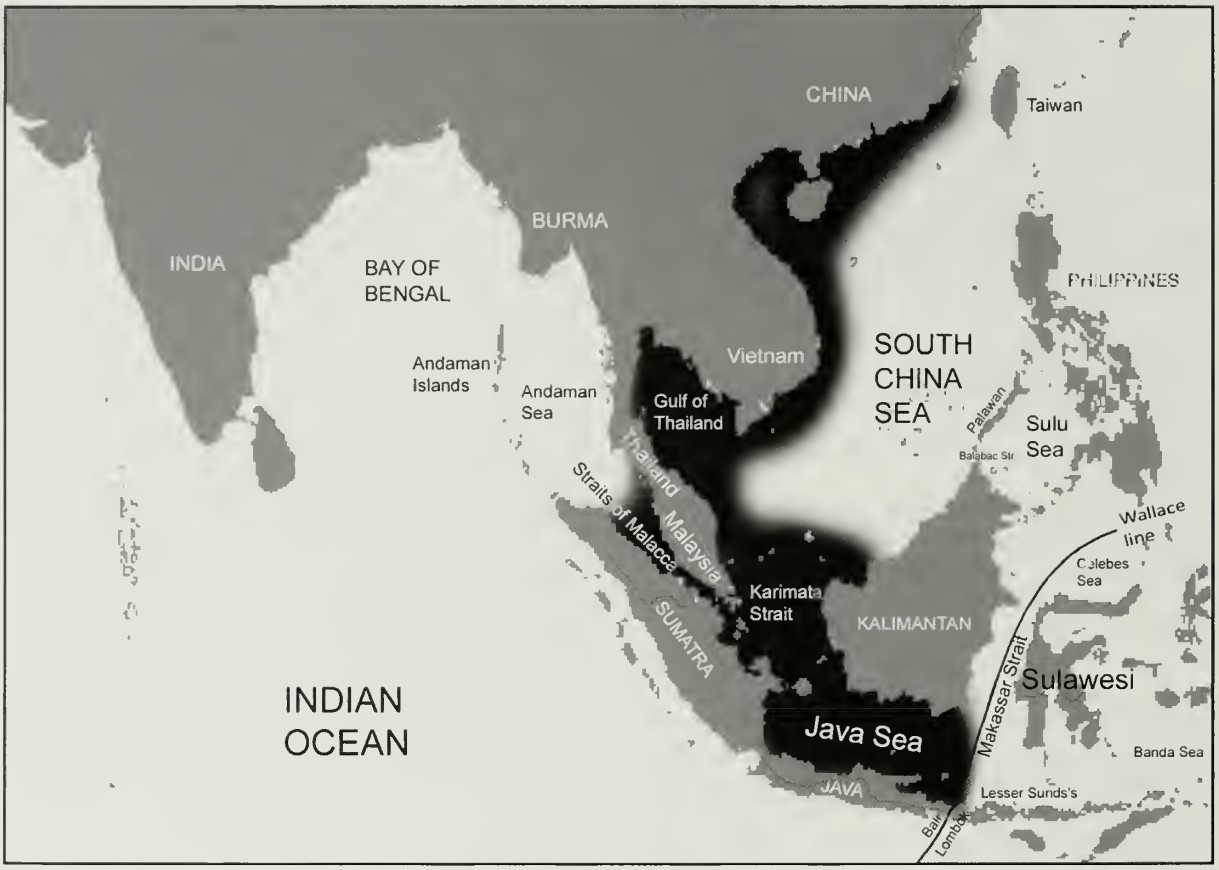


Figure 7. Distribution range of the *Cryptospira ventricosa* group

***Cryptospira cloveriana* n. sp.**
Figs 30 - 33, 65

Type Material. Taiwan, Southeast of Kaohsuing, 20 fathoms, ex. P. Clover, 5 spm;
Holotype, 20.3 x 12.9 mm, BM(NH) Reg. No. 20100331 (Figs 32, 33); Paratype 1, 21.3 x 13.5 mm; Paratype 2, 19.6 x 12.2 mm; Paratype 3, 19.6 x 11.8 mm; Paratype 4, 19.6 x 12.9 mm, BM(NH) Reg. Nos. 201000332/1 - 4.

Other Material Examined. Taiwan, An Ping, 2 spm, 22.5 mm, 23.2 mm, 23.3 mm, FBC.
Taiwan (southwest), 20 – 40 fathoms, 7 spm, 20.5 - 29.3 mm, ATC.
Taiwan, Chii Lung, 1 ad. spm., 22.5 x 13.5 mm, AWC.
Taiwan Straits, trawled, 1 ad. spm., 19.5 x 12.4 mm, AWC.
Vietnam, Nha Trang, 2 spm, 25.7 x 16.1 mm (Fig. 30), 25.5 x 15.3 mm (Fig. 31) , AWC.
Vietnam, Nha Trang, 3 spm, 24.6 - 27.9 mm, MMM.
Singapore, 2 spm, 23.9 x 14.9 mm, 23.5 x 14.0 mm, AWC.

Distribution. Taiwan, along the Chinese coast to Vietnam, and on to Singapore.

Habitat. On sand and gravel to 40 m.

Description. Shell medium sized (L = 19-26 mm, W:L = 62-63 %), thick, heavy, barrel-shaped. Colour even pale to mid grey with darker and lighter axial growth line markings. Lip edge opaque white, darkening to dark grey at marginal groove. Spiral pattern absent externally and internally, or three very faint internal spiral lines. Spire submerged, callus over apex joining with labial insertion. Shoulder smooth, rounded. Aperture as wide as labial varix, only slight widening anteriorly. Lip thickened, with single varix, denticles absent. External varix groove present. Siphonal notch absent, posterior notch weak to moderately strong. Posterior end of shell extending beyond apical level. Lip curves sharply to insert into apical callus cap fractionally to labial side of apex. Columella with six very strong, flat-crested plications, occupying 2/3 of aperture, extending markedly across parietal surface and terminating abruptly. First two plications close together, oblique, remaining plications becoming more perpendicular to long axis. First three plications merge with anterior ventral callus. Second to fifth plications equidistant. Sixth plication remote. Ventral callus pad present opposite labial insertion deepens posterior notch. Anterior end rounded.

Type Locality. Kaohsuing, Taiwan.

Remarks. When compared with the typical form of *C. tricincta,* specimens of *C. cloveriana* have solid, heavy, barrel-shaped shells with stronger, more emergent plications, usually have no sign at all of the three spiral bands internally, never show the spiral bands externally, are a bluish-grey colour, often with fine, alternating light and dark axial growth lines, and have an opaque white lip turning darkish grey at the marginal groove. They are often imperfect and scarred.

In 1970, Phillip W. Clover deposited five voucher specimens of this species from Kaohsuing, Taiwan, in the BM(NH) collection, and it is these which have been selected as the type lot (holotype and four paratypes). Notes accompanying this lot state '*these shells identified and widely sold as bernardii (Habes#2 book pl. 35, no 1). However, these are not typical of the types. They seem to be tricincta without bands. I have seen a few with very faint bands within the aperture*'. From the context of this note it would seem that Clover was comparing them to the types of *C. onychina* (which were annotated later with the name *M. bernardii*), a good species. *C. cloveriana* n. sp. is indeed often labelled *C. Bernardii* Largilliert, 1845 (Clover, 1979; Cossignani, 2006) but the assignation of this name demands closer scrutiny. *M. (C) Bernardii* was described by Largilliert as having five columella plications, with the internal aspect of the labial shoulder bearing denticles, and brown zig-zag axial lines decorating the last whorl. Contrast this with C. *cloveriana* n. sp. which has six plications, a smooth lip, and if any axial streaks are present they occur along growth lines and do not describe a zig-zag pathway. The holotype of *M. Bernardii* is missing from the MNHN in Paris but the original description and accompanying illustration (Figs 91, 92) clearly reveal it to be a small, narrow variety of *C. strigata* (Dillwyn, 1817). The length of the shell is given as 22 mm, which although small for *C. strigata*, still lies within its size range, which has specimens as small as 12 mm at its lower end (AWC & BDC). Therefore, the name *M. (C.) Bernardii* should only be used when referring to the synonymy of *C. strigata*, a member of the *Cryptospira elegans* group. Its application to any taxon from the *Cryptospira tricincta* group should be discontinued.

A series of shells from off Nha Trang, Vietnam (MMM, pictured in Cossignani, 2006: pp. 321-322, all designated *C. tricincta* by the author of that book) are clearly separable into specimens possessing the characteristics of typical *C. tricincta*, namely finer, thinner shells with three internal *and* external spiral lines and a yellowish lip and a greenish or brownish body whorl and others which are more robust, pale to dark grey, having a narrower aperture, a white lip becoming grey at the marginal groove, stronger and longer plications, very faint or no internal banding and completely absent external banding, all of which are characters of *C. cloveriana*. No intergrades are shown, and it is not known if any such specimens were selected out. To check this, an independent search of specimens sourced from Nha Trang was undertaken and it was possible to easily locate examples of both of these forms (Figs 29-31) but no progressively intergrading series of shells between the two forms could be found or assembled. It would seem that, at least in Nha Trang, both *C. tricincta* and *C. cloveriana* occur sympatrically. In the authors collection are two specimens from Singapore which also exhibit the characteristics of *C. cloveriana*, and it is likely that this represents the southern end of the range of this species.

Both *C. tricincta* and *C. cloveriana* also occur northeast along the Chinese coast. *C. tricincta* becomes rare in Taiwanese waters, where *C. cloveriana* takes over as the dominant morph, but it has been found recently in sand and gravel in 40 metres in the Taiwan Strait (Figs 27, 28), comparing well with the description of Marrat's *C. ovalis*. Interestingly, the oval profile of the shell and strong plications match those of many Taiwanese specimens of *C. cloveriana*, yet the thinner body whorl and presence of clear internal and external banding and a rich yellowish coloured labial margin clearly place it as a form of *C. tricincta* as defined here.

Examples of *C. cloveriana* from Vietnam are not quite as thick and callused as their Taiwanese counterparts. The extremely thickened, heavy, grey, totally non-banded and often scarred shells from this extreme northern end of the range are probably ecophenotypic effects resulting from the adaptation of the animal to

harsher environmental conditions and heavier predation.

In some parts of northern Kalimantan, solid greenish-grey specimens with the pyriform profile of typical *C. tricincta* are found. These too completely lack external spiral lines and their internal ones are either very weak or absent altogether (Fig. 12). These have been referred to here as *Cryptospira cf. C. tricincta* form E. They are not regarded as *C. cloveriana* because they have relatively weak plications, their overall shape is closer to *C. tricincta* and the colour is greenish rather than grey.

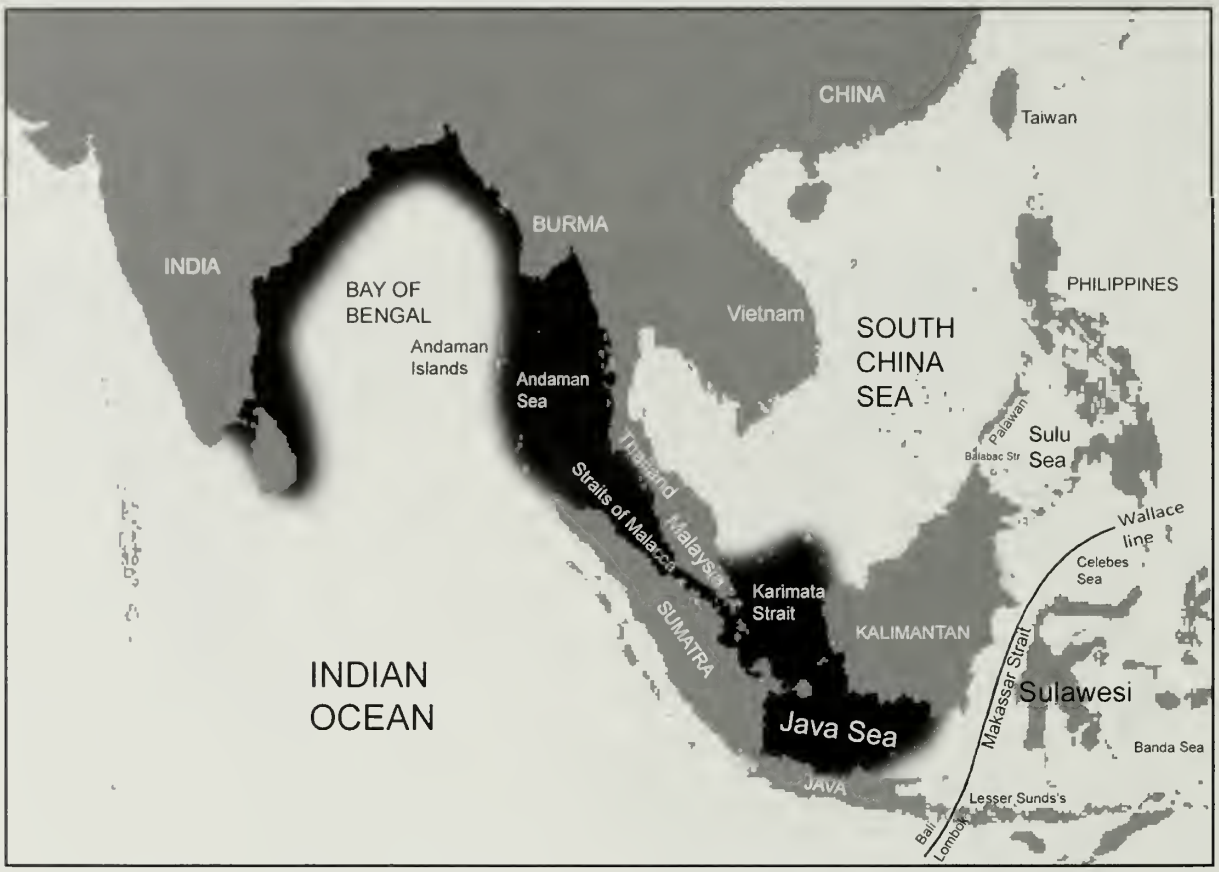


Figure 8. Distribution range of the *Cryptospira elegans* group

Cryptospira wallacei n. sp.
Figs 34 - 37, 133

non-*Marginella (Egonena) wallacei* Jousseaume, 1875 (= *Primum rostrata* Redfield, 1870).

Type material. Pulau Balabalangan, 02° 26.3' S 117° 25.3' E., East Kalimantan (Makassar Strait), 3 ad. and 1 juv. spms:
Holotype, 22.0 x 12.6 mm, BM(NH) Reg. No. 20100328 (Figs 34, 35).
Paratype 1, 21.9 x 12.3 mm, AWC (Figs 36, 37)
Paratype 2, 22.0 x 12.5 mm, BDC.
Paratype 3, juv., 12.0 x 7.5 mm, BM(NH) Reg. No. 20100326.

Type locality. East Kalimantan, Makassar Str., Pulau Balabalangan, 02° 26.3' S 117°25.3' E.

Distribution. Only known from the type locality.

Habitat. In sand patches amongst coral in 5-10 m.

Description. Shell medium sized (L = 22 mm, W:L = 57 %), heavy, smooth, shiny, elongate pyriform, pale creamy yellow with four wide pale purplish brown bands, first band originating at level of fourth plication, second & widest band between fifth and sixth plication, third band halfway between sixth plication and posterior labial insertion, fourth band on top of spire. Pale purplish brown axial streaks, following growth lines, irregular in density of colour and frequency. Lip white ventrally, strong yellow orange external varix, varix groove more deeply coloured. Lip straight for most part, angling over at level of third spiral band to insert posteriorly on top of spire. Aperture narrow, flaring very slightly anteriorly. Columella straight, with six placations occupying 2/3 of apertural length; first moderately strong, long, rounded in cross section, at 45° to axis; second very strong, long, close to first plication, flat topped, also at 45° to axis; third very strong, long, square in cross section, at 60° to axis; fourth slightly less strong, long, square in cross section, 80° to axis; fifth moderately strong, short, square in cross section; sixth often

remote from fifth, short, often with a denticle at its distal end. A very strong elongated denticle present between fifth and sixth plications. Anterior ventral callus merging laterally with the external varix and medially with the distal ends of the first four plications. Parietal surface posterior to plications is smooth. Strong anterior ventral callus from distal end of first to third plications, fusing with external varix anteriorly, creating a wide columella base. Strong posterior ventral callus from the denticle between fifth and sixth plications to posterior labial insertion, ending in a raised pad of opaque white callus forming a false posterior notch.
Animal not observed.

Remarks. This beautiful new species is currently known from limited material collected in shallow sediments off eastern Kalimantan on the biogeographic boundary known as the 'Wallace Line', at the leading edge of the Sunda Shelf. In a comparison with *C. tricincta*, C. *wallacei* has a different colour pattern (wide spiral bands and alternating light and dark axial streaks), a different shape (elongated narrow shell with wide columella base) and an elongated denticle between the 5th and 6th plication. The discovery of a specimen of *C. tricincta* (Fig. 38) sympatrically with *C. wallacei* serves to reinforce the fact that *C. wallacei* is not a local form of *C. tricincta* but is a distinct species.
The small narrow form (Figs 21, 22) collected by the CORINDON Expedition (MNHN) from deep water in the strait, lacks the wide spiral bands, heavy callus and extra parietal denticle of *C. wallacei*, and is listed here as *Cryptospira cf. C. tricincta* form C.

Etymology. *C. wallacei* n. sp. is named in honour of Alfred Russel Wallace (1823 - 1913), English naturalist, explorer, anthropologist and biologist, who explored the geological and geographical pattern of species divergence, and in so doing became the founder of modern biogeography.

***Cryptospira mccleeryi* n. sp.**
Figs 23-26

Type material. Thailand, Gulf of Thailand, Pattani Province, from prawn trawlers, 2 ad. spm.;
Holotype, 29.8 x 15.6 mm, (Figs 25, 26), BM(NH) Reg. No. 20100329; Paratype, 31.2 x 16.5 mm, (Figs 23, 24), SPC.

Type locality. Pattani Province, Gulf of Thailand.

Distribution. Only known from the type locality.

Description. Shell large (L= 29.8 mm, W:L = 52 %), thin, light, elongate-ovate to sub-pyriform, tapering to base. Colour pale cream, including lip. Three narrow spiral lines, first at level of fourth plication, second at level of sixth plication, third halfway between sixth plication and labial insertion. Spire submerged, covered with callus from labial insertion which is directly on top of apex. Shoulder gently rounded, smooth. Aperture as wide as labial varix to level of the sixth plication gradually widening to twice as wide. Lip thickened externally as a single varix with a smooth, pale, rolled edge. External varix groove present. Siphonal notch absent, posterior notch deep. Lip extends to a peak beyond apex, curving round to insert into callus directly over apex. Columella with six plications occupying 2/3 of apertural length; first two close together, fine edged, and oblique. Plications three to five flat crested, gradually becoming perpendicular to axis. Very weak sixth plication remote from fifth. Columella slightly concave between second and third plications. Anterior ventral callus merging with first three plications. Anterior end rounded. Parietal surface posterior to plications smooth, callus absent.

Remarks. This morph has been named as a distinct species on the basis of its distinctive, elongated form and very pronounced extension of the posterior end of the lip. It appears to be rare and only known by its type material.

Etymology. *Cryptospira mccleeryi* n. sp. is named in honour of Tony McCleery who has done so much to advance the scientific understanding and species diversity of the Marginellidae and Cystiscidae.

(ii) *Cryptospira fischeri* sub-group species.

Cryptospira fischeri (Bavay, 1902)
Figs 42 - 52, 69, 81

Marginella fischeri Bavay, 1902, I, 407, pl. viii, figs 10, 11.

Type material. 1 spm, syntype, 10.3 x 6.0 mm (Fig. 47), no loc., Collection du Journal de Conchyliologie, MNHN.

Other material. Northwest Borneo, Subi Is., 4 spm, 8.0 - 9.2 mm, in fisherman's net, 70 m, AWC, (Fig. 43).
Thailand, Ranong, 1 spm, 8.0 mm, AWC, (Fig. 42).
Philippines, Palawan, 100 spm, Length 10 - 13.0 mm, AWC, (Figs 44-46, 48-52)
Philippines, South Palawan, 10 spm, ATC.
Philippines, Davao, 1 spm, 11.8 mm, FBC.
Philippines, Palawan, Balabac, 10 spm, FBC.
Philippines, Sulu Archipelago, Tawi Tawi Island, 1 spm, 12.0 mm, AWC.

Type locality. Unknown.

Distribution. From southern Thailand, along the northern coast of Kalimantan into Palawan and the central Philippines (Sulu Sea).

Habitat. In muddy sand in approximately 15 - 20 m.

Descriptive notes. Shells are small (L = 10 - 13 mm, W:L = 58-69 %), pale straw to greenish-grey. Four red-brown narrow spiral lines encircle the body whorl; the first line emerges at the level of, or just above the fourth plication; the second emerges just beneath the sixth plication; the third emerges halfway between the sixth plication and the posterior labial insertion and the fourth lies just below the suture. The shoulder smoothly curves or is slightly angular. The lip is straight and inserts posteriorly at the shoulder below the apical level. Six columella plications, occupying 2/3 of the aperture; first two close, oblique. Third to fifth becoming more perpendicular to the axis. Sixth plication finer, thin edged, more emergent than the fifth plication and remote from it. Aperture evenly narrow along entire length, as wide as labial varix, and straight. Labial insertion at shoulder, lip thinning to a fine edge at the posterior notch. Parietal surface posterior to the plications smooth and lacking callus deposit.

Remarks. The insertion of the lip in *C. fischeri* is always at the shoulder. This leaves the entire spire morphology and pattern fully visible (Fig. 69) and creates a relatively straight aperture when compared with, say, *C. tricincta*. There are four spiral lines in total, three on the body whorl and one subsuturally, visible on the spire in clearly marked specimens (Figs 48-50). It is interesting to note that on the type specimen (Fig. 47) the centrally placed spiral line is absent. The absence of this particular line is a phenomenon commonly seen in this species and it has also been noted by the author in a specimen of *C. quadrilineata*. Four spiral lines are also present in the closely related *C. immersa*, but they are always less distinct and that species is larger. The spire of *C. fischeri* is usually more elevated than that of *C. immersa* and will always separate it from the very flat or depressed spire of *C. onychina*. The thicker shell, stronger and longer plications and lack of colour and pattern of *C. sabellii* appear to be reliable characters with which to distinguish it from *C. fischeri*.

Specimens of *C. fischeri* west of the Balabac passage are small and thin, with weak columellar plications and very faint or absent spiral lines (< 10 mm in length, W:L ratio 59 - 60 %, Figs 42, 43) compared with specimens from Palawan and the central Philippines, which are often more substantial shells tending towards a more intense colour and pattern (Figs 48-52). At 10 - 14 mm in length, they are often much larger, and can be elongated (Fig. 49), subtriangular (Figs 50, 52), or rather ovoid (Fig. 48), giving a wide W:L ratio of 59.5%-66.9%. A mixture of all of these morphologies was found in a large unselected sample of 100+ specimens from Palawan and there is no evidence as yet to separate them into different species.

Coovert (1990) examined the radula of this species (Fig. 4). The radula has 48 plates, each with a straight basal edge, and 21 cusps per plate along the cutting edge. The central cusp is strongest and is flanked on either side by a subordinate cusp, with the remaining cusps being irregular.

There are many shells in recent circulation incorrectly identified as *C. fischeri* (Figs 60, 61). These Palawan specimens are much larger (16 - 20 mm in length) and the lip extends posteriorly beyond the immersed spire. These are in fact examples of *C. onychina* (A. Adams & Reeve, 1848).

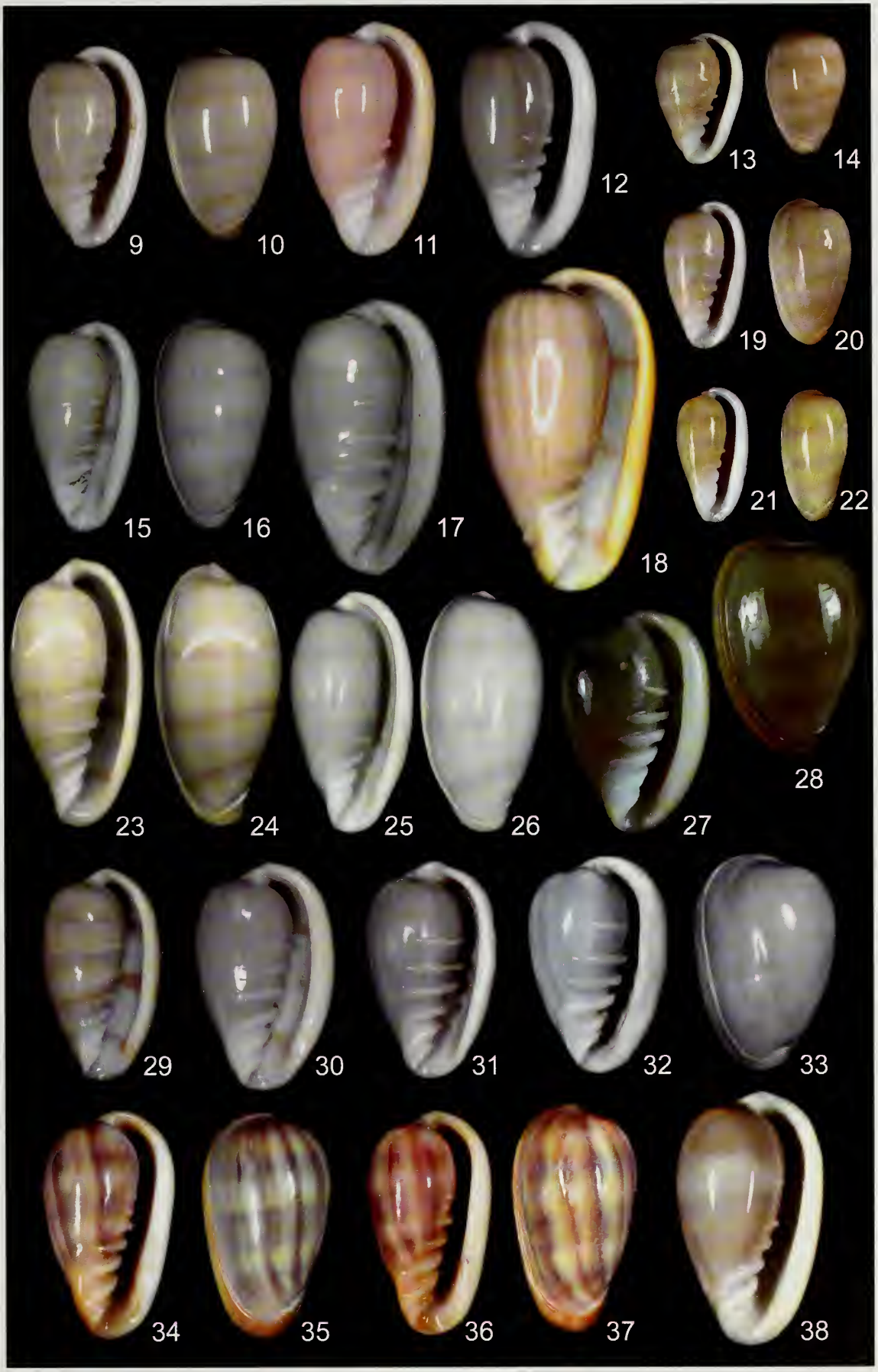
Figures 9-38. *Cryptospira tricincta* group.

9-22, 27-29, 38. *Cryptospira tricincta* Hinds, 1844
9-10. Sumatra, Tulang Bawang, 20.0 x 11.5 mm, AWC. ; **11.** Palawan, Balabac, L = 23.5 mm, AWC; **12.** Brunei, Jenudong Beach, 22.4 x 13.1 mm, AWC; **13-14.** South Borneo, Banjarmasin, in 60 m, 15.0 x 10.0 mm, AWC; **15-16.** 19.5 x 11.4 mm, Syntype, BM(NH) Reg. no. 1844.6.7.38; **17.** 25.5 x 15.7 mm, Syntype, BM(NH) reg. no. 1844.6.7.39; **18.** Western Borneo, Karimata Strait, in 60 m, 30.0 x 17.0 mm, BDC; **19-20.** South Borneo, Sampit, 60 m, 13.3 x 7.5 mm, AWC; **21-22.** Makassar Strait, CORINDON Expedition, 01° 08' S 117°18' E, 13.0 x 6.9 mm, MNHN; **27-28.** Taiwan Strait, 21.9 x 15.1 mm, AWC; **29.** Vietnam, Nha Trang, 23.2 x 13.3 mm, AWC; **38.** Makassar Strait, Pulau Balabalangan, 02°2.3' S 117°25.3' E, 25.2 x 14.5 mm, AWC.

23-26. *Cryptospira mccleeryi* n. sp. Thailand, Gulf of Thailand, Pattani Province;
23-24. Paratype, 31.2 x 16.5 mm, SPC; **25-26.** Holotype, 29.8 x 15.6 mm, BM(NH) Reg. no. 20100329.

30-33. *Cryptospira cloveriana* n. sp.
30. Vietnam, Nha Trang, 25.7 x 16.1 mm, AWC; **31.** Vietnam, Nha Trang, 25.5 x 15.3 mm, AWC; **32-33.** Southeast of Kaohsuing, Taiwan, holotype, 20.3 x 12.9 mm, BM(NH) Reg. no. 20100331.

34-37. *Cryptospira wallacei* n. sp. Makassar Strait, Pulau Balabalangan Group, 02° 26.3' S 117° 25.3 E.
34-35. Holotype 22 x 12.6 mm, BM(NH) Reg. no. 2010032; **36-37.** Paratype 1, 21.9. x 12.3 mm, AWC.


9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38

***Cryptospira sabellii* Cossignani, 2006**
Figs 39 - 41, 70

Cryptospira sabellii Cossignani, 2006. (April), 51: 5, 6.

Type material. Borneo, 1° 42.44'N 108° 22.92'E: holotype, 9.72 mm (Fig. 39), MMP; Paratype 1, 9.97 mm (Fig.40), TCC; Paratypes 2 & 3, 9.09 mm & 9.30 mm, MMM; Paratype 4, 8.50 mm, MZUB; Paratypes 5 - 18, unmeasured, MMM.

Other material. Natuna, Northwest Borneo, 1 spm, Length 9.5 mm, in fisherman's net, 120 m, AWC.
Pejantan, West Borneo, 4 spm, 9-10.5 mm, in fishermans net, 60 m, (Fig. 41), AWC.

Type locality. North Borneo, 1° 42.44' N 108° 22.92' E.

Distribution. Restricted to the northern coast of Borneo.

Habitat. Type material dredged at 48 m. The species is a deep water one.

Descriptive notes. The shell is identical to that of *C. fischeri* except that the columella plications are much stronger and continue across the parietal surface. The shell is pure creamy white and lacks any spiral ornamentation, and is small at 9 - 10 mm in length.

Remarks. Cossignani (2006) separated *C. sabellii* from the closely related *C. fischeri* on the grounds of its consistently smaller size (he was comparing it with Palawan specimens of *C. fischeri*), the lack of any colour pattern, the strength of the columella plications, and the limited range. Despite these differences, these two species bear a strong resemblance to each other.
Bunjamin Dharma kindly provided several lots of small *Cryptospira* from northern Borneo localities for study. These were separable into typical *C. sabellii* (W:L ratio 62 - 63 %) and a very small, pale and thin morph bearing spiral lines, which are herein regarded as the Borneo form of *C. fischeri* (W:L ratio 59 - 60 %) [see remarks under that species]. As they appear to be distinct in the material studied, I cautiously regard *C. sabelli* and *C. fischeri* to be separate species.

Cryptospira immersa (Reeve, 1865)
Figs 53 - 57, 66, 67, 82

Marginella immersa Reeve, 1865 (Jan.) xv, pl. xxi, fig. 109.
Cryptospira quiquandoni Cossignani, 2006. (April), 51: 5, 6.

Type material. Locality not given, 1 spm, 13.4 x 8.2 mm, holotype, ex - Mrs. J. Lombe-Taylor coll., (Figs 53, 82), BM(NH) Reg. No. 1874.12.11.87.

Other material. On the tablet which bears the holotype of *M. onychina*, the right hand one of the three shells present is a specimen which compares extremely closely with the holotype of *C. immersa* and measures 12.9 x 8.1 mm.
Balabac Is., south Palawan, Philippines, 11 spm, 14.3 x 9.1 mm, 14.4 x 8.9 mm, 14.5 x 8.9 mm, 14.5 x 8.9 mm (Fig. 57), 14.9 x 9.0 mm (Fig. 56), 15.0 x 9.0 mm, 15.0 x 9.0 mm, 15.0 x 9.0 mm, 15.0 x 9.1 mm, 15.0 x 9.2 mm, 15.3 x 9.4 mm, AWC.
Philippines, Palawan, Balabac Is: Holotype of *C. quiquandoni,* 15.18 mm (Fig. 54), MMP; Paratype 1 of *C. quiquandoni,* 14.97 mm (Fig. 55), TCC.
Philippines, Palawan, South Balabac. Three specimens dived in 10-30m, 14.6 x 8.9 mm, 14.2 x 8.6 mm, 14.0 x 9.0 mm, deposited as voucher material. BM(NH) Reg. no. 20100325.

Type locality. Not given.

Distribution. Currently only known from Balabac Is., South Palawan.

Descriptive notes. Shell small (L = 13-15 mm, W:L = 61-64%), thin, rounded sub-triangilar, inflated posteriorly, tapering smoothly to base of columella. Colour pale cream to pale pinkish, with weakly evident axial growth line markings. Lip white. Four very weak narrow spiral lines of darker colour evident, absent in very pale specimens; first at level of or just posterior to fourth plication, second at the level of the sixth plication, third halfway between the second spiral line and posterior labial insertion, and the fourth, often almost completely obscured, at the suture. Spire of 3.5 whorls including protoconch, flat or weakly elevated, protoconch raised, suture glazed over. Shoulder smooth, rounded. Aperture straight, evenly narrow, as wide as labial varix, flaring slightly anteriorly. Lip thickened externallyas a single varix with a smooth rolled edge. Denticles absent, external varix groove present. Siphonal notch absent, posterior notch moderately strong. Lip extending to level of highest point of spireand inserting just onto the spire, causing the posterior end of the lip to kink over at a sharp angle before its insertion point, thinning out as it does so. Columella with six strong evenly placed plications occupying 2/3 of the aperture; the first two close together and oblique, the third to fifth more horizontal, strongest and flat edged, the sixth weaker and finer but not remote from the fifth. Anterior ventral callus merging laterally with the external varix and medially with the distal ends of the first four plications. Anterior end rounded. Parietal surface posterior to plications is smooth, callus absent to weak.

Remarks. The short original description of this species is as follows; 'Shell somewhat pyriformly-ovate, bluish white, spire small, immersed, whorls timidly rounded at the upper part, lip callusly

reflected, columella strongly five-plaited.' Rather unhelpfully, Reeve also comments that '*it is difficult to convey an accurate notion of this species, either by figure or description, but it is clearly distinct to the eye.*' The challenge therefore is to be more objective in our observations in order to establish the true identity of this species.

'New Caledonia' has been annotated in an unknown hand to the board to which the holotype was attached, but at a later time than it was mounted and described. This Pacific island locality is remote from the Sunda Shelf distribution of all of the other members of the genus. As it is not possible for the same genus to evolve independently in two geographic locations (Wallace, 1855) and since numerous MNHN expeditions have been performed in New Caledonia at both deep and shallow levels without finding this species, I regard this annotation as erroneous.

The data with the holotype also states that a second specimen from the tablet has been removed to the general collection at the NHM. There are two specimens labelled *C. immersa* in the main collection at the NHM, but neither appears to be this 'second' specimen. The first is the right hand shell on the tablet to which is mounted the type specimen of *C. onychina* and the second is a specimen from the Sykes collection, not previously mounted to a tablet, and is clearly a specimen of *C. tricincta*.

Despite the rarity of antiquarian records of the species, examples of *C. immersa* are now widely available. Cossignani (2006) brought it to the attention of collectors when he described it as a new species, *C. quiquandoni*, and again it is one of the exciting finds from the Balabac Strait between Borneo and Palawan. The size and morphology of most fresh specimens of *C. quiquandoni* (W:L ratio 60 - 63 %) match the holotype of *C. immersa* (W:L ratio 61.1 %) very well indeed. They also share the same wide, flattened and closely spaced columella plications, and the slightly elevated protoconch (note; the original figure and holotype are at odds with the description and the name given to the species in that the spire has a raised protoconch and is therefore not immersed!). The pattern of axial striations is present in both, and the spiral lines faintly present in *C. quiquandoni* would have originally been present in the now faded specimens of *C. immersa*. I am of the opinion that *C. quiquandoni* Cossignani, 2006 is conspecific with *C. immersa* (Reeve, 1865) and therefore the latter should be adopted as the correct specific name.

The close relationship between *C. onychina* and *C. immersa* is obvious to the eye. The latter however, is a consistently smaller species and there is no size overlap. *C. onychina* has a more elongate and more smoothly tapering shell (W:L ratio 55.2%-61%), the posterior end of the lip is more pronounced and the spire, including the protoconch, is flat or immersed, unlike the slightly raised spire of *C. immersa*. Its colour is also greenish-grey compared to the pale pinkish *C. immersa*.

Cryptospira onychina (A. Adams & Reeve, 1848)
Figs 58 - 61, 80, 82, 83

Marginella onychina A. Adams & Reeve, 1848. Voy. Samarang. Moll., p. 29, pl. x, fig. 25

Type material. Three shells mounted to a tablet are collectively the syntypes, BM(NH) Reg. No. 20100333. The figured syntype is the specimen on the left, 21.05 x 13.1 mm (Fig. 58). Labels: on reverse, original label states '*M. onychina* Adams & Reeve, Types, China Seas'. On front, '*bernardii*, Largilliert' as an annotation. [Note; Middle specimen is a juv. *C. onychina* 18.5 x 10.9mm, right specimen is *C. immersa* 12.9 x 8.1mm].

Other material. South China Sea, 1 spm, 22.9 x 13.1 mm (Fig. 59), BM(NH).

Balabac Is., south Palawan, Philippines, 6 spm., 16 x 9.5 mm, 16 x 9.5 mm, 16.5 x 9.7 mm, 16.5 x 10 mm, 17.1 x 10.2 mm, 17.7 x 10.3 mm, AWC.

Balabac Is., south Palawan, Philippines, dived in 15 - 20 m, 7 spm, 18.0 x 10.0 mm, 18.0 x 10.5 mm, 18.5 x 10.9 mm, 18.8 x 10.9 mm, 19.0 x 11.0 mm (Fig. 61), 20.0 x 10.75 mm (Fig. 60), 20.0 x 11.5 mm, AWC.

Balabac, south Palawan, Philippines, 3 ad spm, 16.2 x 9.8 mm, 16.0 x 9.4 mm, 16.6 x 9.7 mm, deposited as voucher material, BM(NH) Reg. No. 20100330.

Type locality. 'South China Sea', without further precision.

Distribution. Currently only known from the Balabac Strait and the Sulu Sea coast of Palawan Is.

Habitat. Muddy sand in 15-20 m.

Descriptive notes. Shell medium sized (L = 18-23 mm, W:L ratio 55.2% - 61%), cylindrical-ovate, pale cream to greyish-brown. Purplish-brown axial lines weakly decorate the body whorl along growth lines. The spire is flat to involute, the shoulder smooth and rounded. The lip is straight for the most part, extending beyond apical level but with a sudden arch posteriorly to insert to callus at the side of the spire. The aperture is narrow, flaring only slightly anteriorly. The columella has six plications morphologically comparable with *C. tricincta*, occupying the anterior 2/3 of the aperture. All are flat topped and moderately strong with the exception of the sixth plication which is weak and fine. Three spiral lines are visible on the body whorl – very faint in the holotype but easily distinguished in live taken specimens; first just posterior to the fourth plication, the second just anterior to the sixth plication, and the third mid way between the second spiral line and the labial insertion. Anterior ventral callus merges laterally with the external varix and medially with the distal ends of the first four plications. Anterior end is rounded. Parietal

surface posterior to plications is smooth, callus absent to weak.

Remarks. The original description makes note of the elongated aperture and depressed, almost hidden spire which are important features of this species. The figure of *Marginella onychina* (Fig. 84) in the original description by A. Adams & Reeve (1848) is accurate and unambiguously depicts the type specimen (Fig. 58). However, sixteen years later in the Marginella Monograph in Conchologia Iconica (1864/5), Reeve presented less accurate illustrations (made by G.B. Sowerby) of this type specimen (Figs 86, 87), and chose to name it *Marginella Bernardii* Largilliert, 1845, listing his own *M. onychina* as a synonym. In fact, on the tablet to which the type of *M. onychina* is mounted, '*bernardii*, Larg. China Seas, M.C.' is annotated in Reeve's own handwriting. The name M. (or C.) *Bernardii* continued to be used for this species by subsequent reviewers such as Redfield (1870), Tomlin (1917), & Clover (1979), but only Jousseaume (1875) noticed the error. He drew attention to the fact that Largilliert's original description and figure of *M. Bernardii* are very different from those of *M. onychina*. He observed that the spire of *M. onychina* was depressed and hidden whereas that of *M. Bernardii* was prominent and visible and that the issue was so clear-cut for him that other differences did not need to be pointed out! For the sake of clarity, I will expand further. The original figure of *M. Bernardii* (Figs 91, 92) are accurate drawings which clearly show the khaki coloured shell to have a finely zig-zagging axial pattern, relatively oblique columellar plications and a morphology highly suggestive of a small specimen of the *C. elegans* group species *C. strigata* (Dillwyn, 1817). The description is also detailed and mentions the denticulate inner labial border – a character entirely restricted to the *Cryptospira elegans* group. Although the type specimen of *M. Bernardii* has not been traced, photographs of specimens matching the description can be seen in Dharma (2005, p. 150, figs. 15a & c) which illustrate the point perfectly.

In their description of *Marginella onychina*, Adams and Reeve commented that '*this species might be readily confounded with Marginella tricincta, but it differs materially in form, being more depressed and rounded at the hinder extremity, with the spire buried as in the cowries, and less swollen in the middle. The streaky character of the painting is also characteristic.*' With regard to this last comment, the material of this species present in the BM(NH) is dead collected and worn. It is well known that erosion of the surface nacre in some species enhances the underlying pattern, and *C. onychina* is no exception. The axial lines are much less obvious in live specimens, but are visible nevertheless.

Until recently there were only four specimens of *C. onychina* available for study; the holotype, one adult and one juvenile specimen in the BM(NH) collection and the specimen depicted by Clover (1979, fig. 3) which he referred to as *C. bernardii*. All are worn, dead collected shells labelled 'South China Sea'.

Figures 39-64. *Cryptospira fischeri* group.

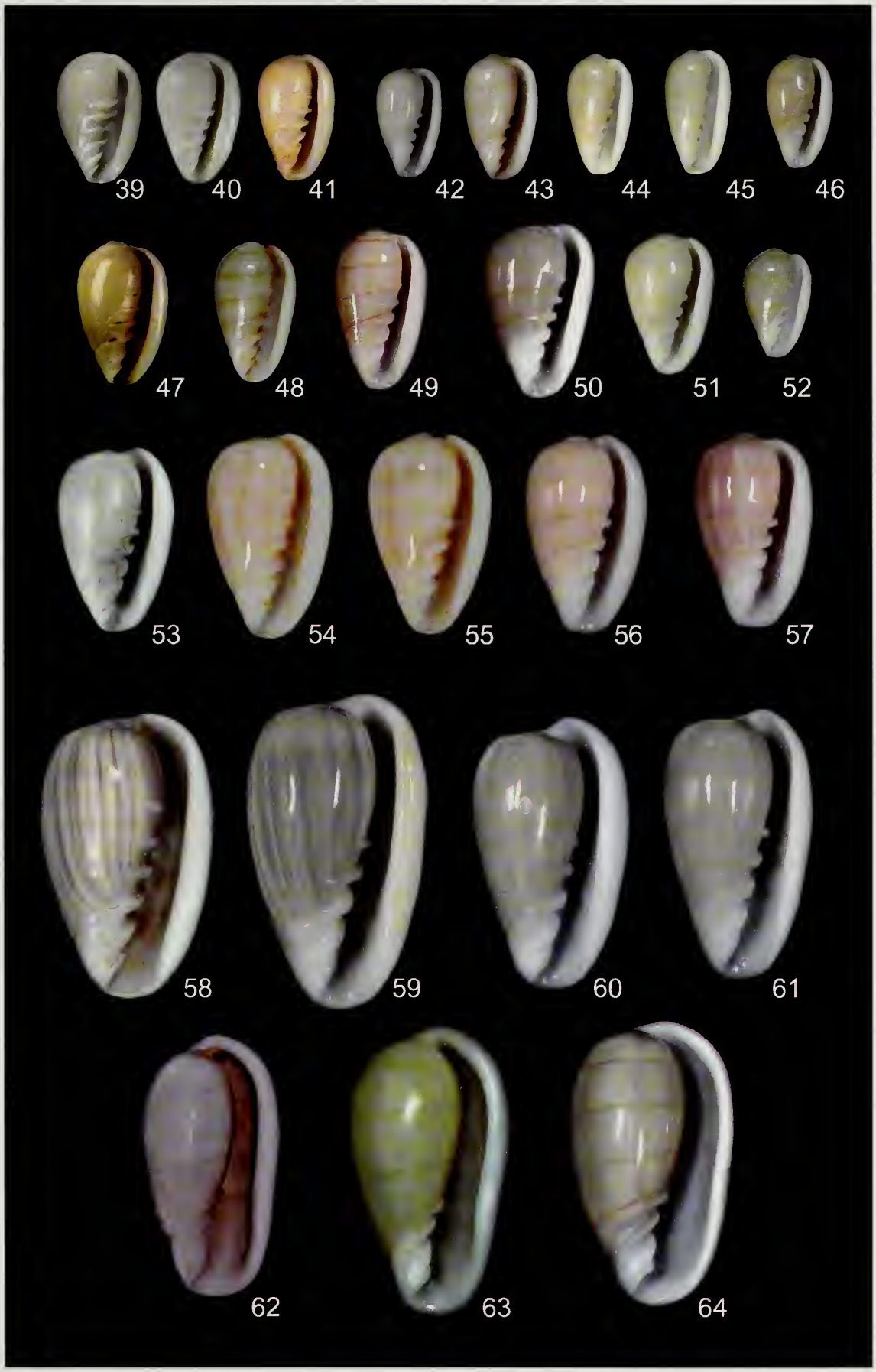
39-41. *Cryptospira sabellii* Cossignani, 2006
39. Holotype, 9.72 mm, Borneo, 01° 42.44' N 108° 22.92' E, 48 m , MMP; **40.** Paratype 1, 9.97 mm, Borneo, 01° 42.44' N 108° 22.92' E, 48 m, TCC; **41.** Pejantan, north Borneo, 9.0 mm, AWC.

42-52. *Cryptospira fischeri* Bavay, 1902
42. Thailand. Ranong. 8.0 mm, AWC; **43.** Northern Borneo, Subi Is., 9.0 mm, AWC; **44.** Palawan, 11.08 x 5.87 mm, AWC; **45.** Palawan, 10.1 x 5.92 mm, AWC; **46.** Palawan, 9.85 x 5.85 mm, AWC; **47.** Syntype, MNHN, 10.3 x 6.0 mm, locality unknown; **48.** 10.29 x 5.89 mm
49. Philippines, 11.8 mm (photo courtesy Marcus Coltro); **50.** Palawan, 12.78 x 7.98 mm, AWC; **51.** Palawan, 10.9 x 6.75 mm, AWC; **52.** Palawan, 9.86 x 6.18 mm, AWC.

53-57. *Cryptospira inuersa* Reeve, 1865
53. Holotype, 13.4 x 8.2 mm, BM(NH) Reg. No. 1874.12.11.87; **54.** Holotype of *C. quiquandoni* Cossignani, 2006, Philippines, Palawan, Balabac Is., 15.1 mm, MMM ; **55.** Paratype 1 of *C. quiquandoni* Cossignani, 2006, 14.9 mm, Philippines, south Palawan, Balabac Is., TCC; **56.** Philippines, south Palawan, Balabac Is., 14.9 x 9.0 mm, AWC; **57.** Philippines, south Palawan, Balabac Is., 14.5 x 8.9 mm, AWC.

58-61. *Cryptospira onychina* A. Adams & Reeve, 1848
58. Holotype, BM(NH) Reg. no. 20100333, 21.05 x 13.1 mm, 'China Seas'; **59.** South China Sea, 22.9 x 13.1 mm, BM(NH); **60.** Philippines, south Palawan, Balabac Is., 20.0 x 11.5 mm, AWC; **61.** Philippines, south Palawan, Balabac Is., 19.0 x 11.5 mm, AWC.

62-64. *Cryptospira quadrilineata* Gaskoin, 1849
62. Holotype of *M. quadrilineata* Reeve, 1864, 18.8 x 10.3 mm, BM(NH) Reg. no. 1874.12.11.76; **63.** Philippines, Palawan, 21.0 mm (photo courtesy Alistair Moncur); **64.** Philippines, Palawan, 21.0 mm, AWC.


39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64

Recently though, many fresh specimens of this species have been discovered in Balabac, Palawan. The main character differences from *C. tricincta* are that although the posterior end of the lip extends beyond the apex of the shell, it inserts well to the side of the spire, rather than directly on top of it. This creates a more cylindrical body whorl and shoulder which is more tightly rounded compared to the sweeping posterior end of the lip of *C. tricincta*. Specimens currently in circulation are often labelled incorrectly as *C. fischeri*, presumably due to the colour and the spiral lines which are common to both. *C. fischeri*, however, has an elevated spire, not an immersed one and it does not attain such a large size. The old museum specimens are a little larger than the new records and have a stronger axial pattern, though this is considerably enhanced by erosion. They are therefore probably from a different population, but nevertheless appear to be conspecific.

(iii) *Cryptospira quadrilineata* sub-group.

Cryptospira quadrilineata Gaskoin, 1849
Figs 62 - 64, 72, 130

Cryptospira quadrilineata Gaskoin, 1849 (Dec. 14), p. 17
Marginella quadrilineata Reeve, 1864

Type material. No locality (ex. voyage Samarang, J. Lombe-Taylor coll.), 1 spm, 18.8 x 10.3 mm, holotype of *Marginella quadrilineata* Reeve, 1864, BM(NH) Reg. No. 1874.12.11.76, (Fig. 62).

Other material examined. No locality, 2 juv. spms, 17.3 mm & 14.4 mm, & 1 spm, 24.4 x 14.9 mm, all on a tablet, ex. Mus. Cuming, BM(NH).
No Locality, 1 spm, 23.7 x 14.7 mm, AWC.
Balabac, Palawan, Philippines, 5 ad. spm, 21.0 - 23.0 mm, (Fig. 63, 64), AWC.

Type locality. Unknown.

Distribution. Clover (1979), states that it is trawled in 80 m off southern Palawan and on into Borneo.

Habitat. 20 - 80 m on muddy sand.

Descriptive notes. Shell medium sized (L = 18 - 24 mm, W:L = 55 %), thin, light, oval to sub-pyriform, inflated. Colour pale greyish to light brown with occasional growth lines. Lip white. Four very narrow, sharply defined red-brown spiral lines on body whorl; All four evenly spaced across parietal surface from just below the labial insertion to just above the fourth plication. Spire involute, buried directly under callus cap at the labial insertion. Shoulder smooth, very rounded. Posteriorly, aperture slightly wider than labial varix, flaring noticeably anteriorly to 3-4 times the width of the varix. Lip thickened externally as a single varix with a smooth rolled edge. Internal aspect of lip smooth, lacking denticles. External varix groove present. Anterior and posterior notches absent. Lip extending beyond apex, curving round to insert into callus pad directly over apex of spire. Columella with four moderately strong, thin-edged plications, set in the anterior 1/3 of the aperture; First two oblique, close together then fusing distally, columella deeply excavated between second and third plications. Third and fourth plications oblique. Parietal surface smooth from fourth plication to labial insertion, and anterior ventral callus wash merges medially with the distal ends of the first three plications.

Remarks. Until relatively recently this species was known only from material in old collections, and possibly exclusively from examples brought back to England on H.M.S. Samarang. It is now relatively easy to source fresh specimens of this species from southern Palawan. Gaskoin's original description is very thorough and requires little additional comment for this instantly recognizable species, apart from the variability in the profile of the shell, which has become apparent from studying non-type material and the illustration in Clover (1979). Apparently Reeve was unaware that this species had been described by Gaskoin, because in *Conchologica Iconica* he described it as a new species whilst coincidentally using the same specific epithet as Gaskoin!
With a W:L ratio of 60 - 60.4%, the shell morphology varies from inflated (Fig. 64), to slightly pyriform (Fig. 63), to narrow and sub-cylindrical (Fig. 62). The four fine spiral lines, wide aperture, light shell, immersed spire and smooth labrum would seem to place this species firmly in the *Cryptospira tricincta* group. However, the columella is very concave and the first and second plications are distally fused. These characters represent such a significant departure from the normal columella morphology of the group, that the presence of a mono-specific sub-group within it is a distinct possiblility.

(B) *CRYPTOSPIRA VENTRICOSA* GROUP

The *Cryptospira ventricosa* group is the smallest of the three species groups within the genus. It comprises three extant and one fossil species; *C. ventricosa* (G. Fischer, 1807), C. *dactylus* (Lamarck, 1822), *C. trailii* (Reeve, 1865) and the now extinct *C. sangiranensis* Martin, 1906. The principal characteristics of the *Cryptospira ventricosa* group are :

- A truncated columella base and anterior end of the lip.
- In lateral view, the entrance to the anterior (siphonal) canal is in-line with the columella axis (Figs 122-124). In the *elegans* and *tricincta* groups it is oriented downwards by 30° (Figs 119-121).

- Lip strongly thickened internally except at the posterior end where it thins and appears to flare forming a deep and wide posterior notch and a strong shoulder. Labial denticles absent, although both the inner lip and external margin are often irregularly callused giving a non-uniform surface.
- Five columellar plications. First plication thin, close to second, long, angled at base to form truncation and shallow anterior notch. Second to fifth plications strong, equidistant. Weak to very strong elongated parietal lira posterior to fifth plication. This begins just within the aperture, and extends across the parietal surface. It is always much longer than the plications. A short denticle between fourth and fifth plications is uncommonly seen (Fig. 114). Plications + lira + denticle occupying 2/3 of apertural length.
- Wide and callused columella base extending to ends of of first four plications, often extending as a pad onto side of shell. Pad of callus on parietal surface opposite posterior labial insertion serves to further define and deepen the posterior notch.
- spire usually moderately elevated, occasionally high or nearly flat.
- size 7-45 mm.
- solid grey or tan colour with no banding pattern. Axial ornamentation restricted to parallel growth lines, and surface defects caused by mantle injury during shell formation.

Distribution. The geographical distribution of the group is essentially the distribution of the nominate species and it occupies a central position in the overall range of the genus. The group is recorded from Vietnam down to Singapore and the Strait's of Malacca, north and east Sumatra, the north coast of Java, to Lombok and eastern Kalimantan (see Fig. 7). On the western side of the Malaysian peninsula, recent records show that the distribution extends as far north as Satun Province in southern Thailand (S. Patamakanthin pers. comm.). Jousseaume (1875) went further, giving the distribution as extending into the Bay of Bengal, but recent records do not corroborate this. It is the confusion between *C. ventricosa* and two members of the *Cryptospira elegans* group, *C. glauca* and *C. marchii*, which has caused these identification problems and introduced errors in recorded range distributions. Even Coomans (1969) who drew attention to the differences between *C. ventricosa* and *C. glauca* was unable to completely rectify the situation because he too made errors in the identification of *C. glauca* (see later discussion on that species). *Cryptospira ventricosa* (as *M. quinqueplicata* Lamarck, 1822) was one of 18 marginellids listed as part of the fauna of the mollusca of the Persian Gulf, Gulf of Oman and Arabian Sea by Melvill & Standen (1901), but again, this is in error as *Cryptospira* does not range that far West. After morphological comparison of large numbers of specimens, the differences in shell morphology between *C. ventricosa* and species in other groups are quite clear and are demonstrated herein.

Taxonomic aspects. *C. ventricosa* (G. Fischer, 1807) has a chequered taxonomic history. It is arguably the most commonly encountered large marginellid species in 19th Century European museum collections, where specimens are frequently labelled *Marginella quinqueplicata* Lamarck, 1822. The holotype of *M. quinqueplicata* (Fig. 105) is clearly a specimen of *C. ventricosa* and is already established as a junior synonym of it (Tomlin, 1917), as are the highly callused *Marginella Hainesii* Petit, 1851 and the eroded *Marginella vermiculata* Redfield, 1851. *M. Hainesii* is represented by 2 syntypes in the Collection du Journal de Conchyliologie (MNHN). The figured type is the larger of the two (Figs 103, 104). There are two specimens labelled *M. Hainesii*, with no data, in the Saul Collection (CMZ) and it is also present in the BM(NH) collection. All of these shells appear to be merely heavy, worn, highly callused specimens, which have been shown to fall within the variability range of *C. ventricosa* by Dharma & Dunlap (1994). *M. vermiculata* has no taxonomic value as it was proposed in a privately printed catalogue, and Redfield later withdrew it (1870, Amer. Journ. Conch. vi, 254). This shell is now no. 29063 in Coll. Redfield, ANSP. None of these taxa were published with locality data. All of these extra names are testament to the fact that Fischer's taxon, as rightful name-bearer of the species, was poorly known by the *Marginella* workers of the time. Neither Weinkauff, Tryon or Redfield mentioned the name in their monographs. Perhaps this was not surprising, since the description of *C. ventricosa* was but a brief entry in the 1807 catalogue of the Paul Demidoff collection (Zoological Museum of the University of Moscow) and was limited to two lines of text with no locality data, no measurements and no figure to support it. Copies of this catalogue did not appear to be freely available in the research libraries of the major institutions. Jousseaume (1875) went as far as to list the places where he had searched for, and failed, to find it. He was eventually provided with the description of *M. ventricosa* by Professor Deshayes, which translated from the original French text reads; 'humped marginella, blueish, pot-bellied, very short spire, the columella has five plaits, lip strongly rolled, smooth.' Sufficiently enlightened by this brief but surprisingly accurate description, Jousseaume (1875) was the first to suggest that it was the same species as *M. quinqueplicata*. Tomlin (1917) followed Jousseaume, listing *M. ventricosa* as valid and declaring that 'the name *ventricosa* supersedes *quinqueplicata*'. This confirmation that Fischer's taxon should be the name-bearer of the species is now generally accepted and universally used.

Dubious Taxa. *Voluta porcellana* Perry, 1811 was regarded as a synonym of *M. ventricosa* by Tomlin

(1917), but it had previously been included in the synonymy of both *M. strigata* Dillwyn, 1817 by Redfield (1870) and *M. elegans*, Gmelin, 1791 by Tryon (1882-83). More recently Coomans (1969) also included it in the synonymy of *M. elegans*. Tomlin noted: "The colourization of the figure is probably fantastic and certainly unrecognizable. The description points to *ventricosa* and the five strong plaits in the figure are exactly as in *ventricosa*." With a few exceptions, Perry's work is largely discredited due to the fanciful nature of the figures and this explains why it was completely ignored by all the other major 19th century *Marginella* workers. The pattern on his figure of *Voluta porcellana* (Fig. 89) is indeed unusual and the columella plications are not accurately depicted. There are historical clues as to the whereabouts of the specimen illustrated. Dance (1986) mentions how Perry used some of H.C. Jennings (1731-1819) shells for his book. The Jennings collection in part was purchased at auction in 1816 by W.J. Broderip, and the Broderip collection is now in the BM(NH). However, a search of the *Marginella* and *Voluta* collections at the BM(NH) was unsuccessful in rediscovering this shell. Taking all the factors into account, *V. porcellana* Perry should continue to be considered as a *nomen dubium*.

There is, however, a further twist to the tale. *Marginella odoriyci* Bernardi, 1852, was described from a single worn specimen originally in the Dinan Museum (France) but now lost (Tomlin, 1917 and subsequent enquiry by the author). It was considered to be a valid species by all the 19th century reviewers and also by Tomlin (1917) but it was Jousseaume (1875) who suggested that due to its five plications it was probably a *Cryptospira*. Weinkauff (1879) figured the shell (Figs 93, 94). The pattern of 'jumping figures' bears a remarkable similarity to the pattern on the figure of *Voluta porcellana*, and although it cannot be proven, the fact that they may have been the same species needs to be considered. The shell has an elevated spire (too high for *Cryptospira*) and is rather small (18 x 11 mm) for most specimens of axially patterned *Cryptospira* such as *C. elegans* and *C. strigata*. The original description also mentions that the aperture is an orange colour, and the body whorl is white with broad yellow bands which are axially strigate with orange brown, again not seen in *Cryptospira*. Its morphology, I believe, is far more suggestive of the genus *Prunum*, yet the columella undeniably has five plications. The *Prunum/Volvarina* complex generally have four columellar plications, but there are a few exceptions, including a small complex of species centred around *Prunum fulminata* Kiener, 1841 which have five plications, a strong wavy axial pattern and are the right size. It is possible therefore that *M. odoriyci* and maybe also *V. porcellana* are this species or one closely related to it. No further deductions can be made about either taxa until the holotypes are rediscovered and examined and attempts are currently underway to do just that. For the time being therefore, both taxa should be removed from consideration in the genus *Cryptospira*.

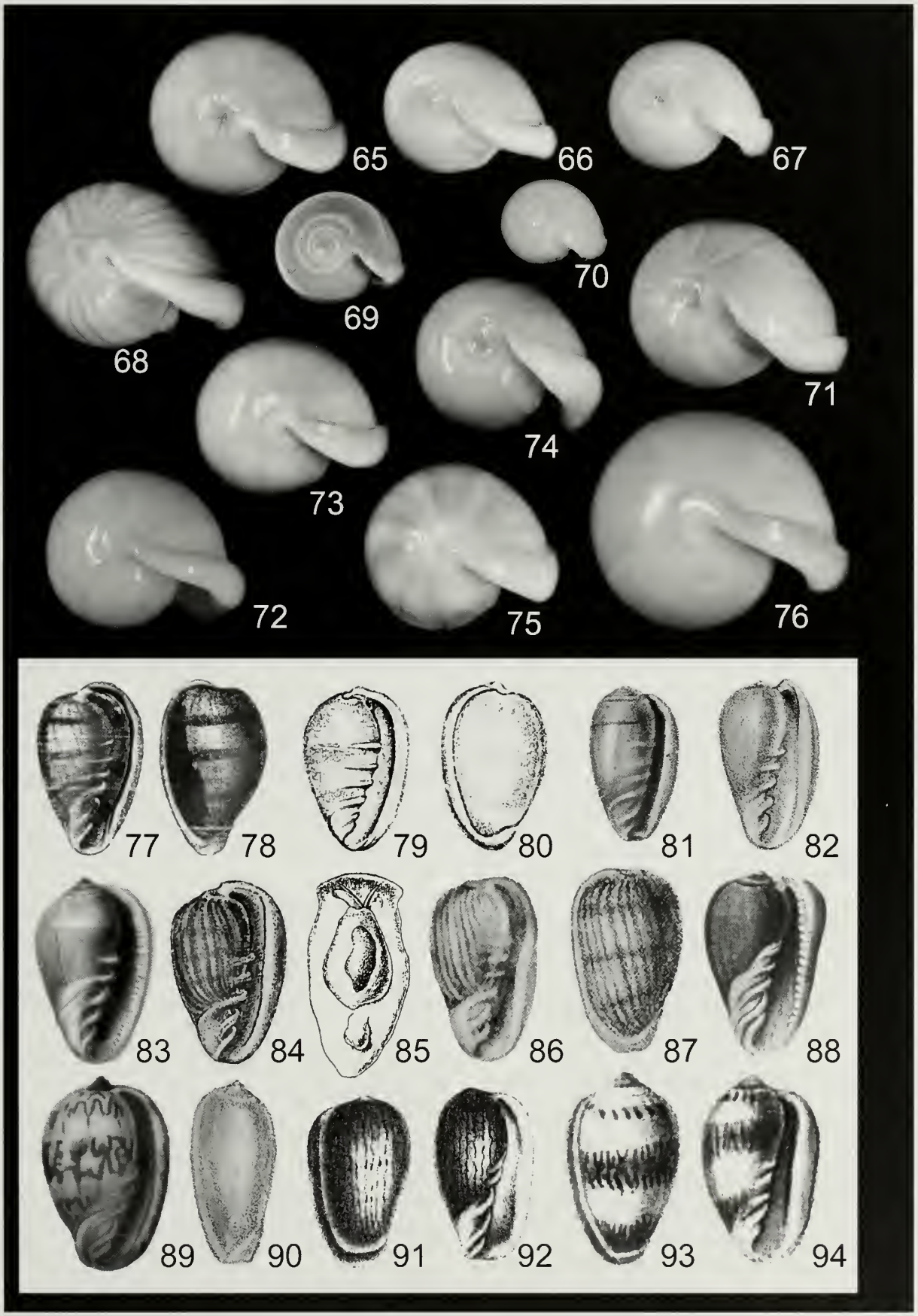
Figures 65-94.

65-76. Spire morphologies.

65. *C. tricincta* Hinds, 1844, Taiwan, AWC; **66.** *C. immersa* Reeve, 1865, Holotype, NHM; **67.** *C. immersa* Reeve, 1865, Palawan, Balabac Is., AWC; **68.** *C. onychina* A. Adams & Reeve, 1848, Holotype, NHM; **69.** *C. fischeri* Bavay, 1902, Palawan, AWC; **70.** *C. sabellii* Cossignani, 2006, Pejantan, N. Borneo, AWC; **71.** *C. onychina* A. Adams & Reeve, 1848, NHM; **72.** *C. quadrilineata* Gaskoin, 1849, Palawan, AWC; **73.** *C. tricincta* Hinds, 1844, Palawan, AWC; **74.** *C. onychina* A. Adams & Reeve, 1848, Palawan, AWC; **75.** *C. wallacei* n. sp., Makassar, Pulau Balabalangan; **76.** *C. dactylus* Lamarck, 1822, Pontianak, West Kalimantan.

77-94. Miscellaneous illustrations

77-78. *Marginella tricincta* Hinds, 1844, first figure from Hinds 1844b; **79-80.** *Marginella (Cryptospira) ovalis* Marrat, original figure; **81.** *Marginella fischeri* Bavay, 1902, original figure; **82.** *Marginella immersa* Reeve, 1865, original figure; **83.** *Cryptospira glauca* Jousseaume, 1875, original figure; **84.** *Marginella onychina* A. Adams & Reeve, 1848, original figure; **85.** *Marginella ventricosa,* live animal (after Souleyet, 1852); **86-87.** Figures of *Marginella onychina*, incorrectly named as *Marginella Bernardii* Largilliert, 1845, in Reeve, 1864/5; **88.** *Marginella loebbeckeana* Weinkauff, 1878, original figure; **89.** *Voluta porcellana* Perry, 1811, original figure; **90.** *Marginella trailii* Reeve, 1864, original figure; **91-92.** *Marginella Bernardii* Largilliert, 1845, original figures; **93-94.** *Marginella odoriyci* Bernardi, 1852, figures from Weinkauff, 1879.


65
66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87
88
89
90
91
92
93
94

Persistent identification problems.
Whilst the synonymy is established and the correct name for the species is now accepted as being beyond reasonable doubt, there remains considerable taxonomic confusion between the typical *C. ventricosa* and another species, *C. glauca* Jousseaume, 1875. Jousseaume showed that he had a good working knowledge of these species because in his Marginella monograph of 1875 he remarked how *C. ventricosa* (as *M. quinqueplicata* and *M. Hainesii*) differed from *M. glauca*. However, later authors were unable to grasp the morphological distinction between the two, including Tomlin (1917) who regarded *C. glauca* as "rather doubtfully distinct from *ventricosa*", and Wagner & Abbott (1967) who noted that *M. glauca* "may be *ventricosa*".
Coomans (1969) was well aware of the confusion between *C. glauca* and *C. ventricosa* and dealt with it comprehensively in a comparative review of the two species utilising the material available to him in the ZMA. He also designated a type locality for the species based upon the provenance of the material he was studying, safe in the knowledge that "the type of *M. ventricosa* is kept in the Zoological Museum of the University of Moscow, being a part of the collection Demidoff from which it was described by G. Fischer". However, according to a paper on the molluscan type specimens of the Museum Demidoff Collection (Ivanov, Kantor, Sysoev & Egorov, 1991) the type of *C. ventricosa* was in fact lost before 1872, and most probably earlier than that during the 1812 war. The current curator has, upon my request, checked the collection again and confirms that the type is indeed lost. Perhaps Coomans would have designated a neotype in addition to a type locality for this species had he been aware that his pronouncement about the existence of the type specimen was erroneous. However, the original description and the clarification by Coomans of what exactly constitutes this species are probably sufficient to avoid the need to now designate a neotype (Article 75, ICZN).
So is the morphology of *C. ventricosa* understood any better by researchers and authors today? Evidence of continued confusion is not hard to find. The shell photograph issued on card No 75 (Kaicher, 1973) of *C. ventricosa* is in fact *C. marchii*. Cossignani (2006, p. 322) correctly identified the depicted specimens as *C. ventricosa*, yet on p. 292 he repeated Kaichers error by incorrectly identifying the specimens of *C. marchii* (top row, centre) and *C. glauca* (the remaining images of *Cryptospira* on that page) as *C. ventricosa*. Finally, any search of shell websites with marginellid content will reveal photographs of specimens of *C. glauca* identified as *C. ventricosa*, and vice versa. It is clear therefore, that there is still considerable misunderstanding over the morphology of all of these species. A comparison of the key features of the *ventricosa* group with the remaining two groups is required to deal with this confusion once and for all.

Usage of species group characteristics in solving species identification problems.
The confusion in the literature between *C. ventricosa* and *C. glauca* is compounded by the fact that several species are commonly referred to as *C. glauca*. Fortunately, the two primary diagnostic characters of the *ventricosa* group enable straightforward separation of *C. ventricosa* from these other species (Figs 119-124). A principal diagnostic difference lies in the morphology of the first plication. All of these species, including *C. ventricosa*, have a thin first plication when compared with the remaining four, but in the *ventricosa* group this plication extends further then sharply angles back forming the truncated anterior end of the shell. In the *elegans* group this angle is absent and instead the first plication sweeps back in an elegant curve forming a more rounded anterior profile. This also has an effect upon the orientation of the siphonal canal, which is best observed laterally, from the opposite side to the lip. In the *ventricosa* group the siphonal canal is in line with or turns slightly upwards (dorsally) away from the columella axis and the truncated anterior end lies at a right angle to it (Figs 122-124). In the *elegans* group the siphonal canal inclines noticeably downwards (ventrally) and the anterior end of the shell forms an acute angle to the columella axis (Figs 119-121). This will always reliably separate *C. ventricosa*, *C. dactylus*, *C. trailii* and *C. sangiranensis* from other species. The orientation of the siphonal canal towards/away from the substrate may have a functional significance in relation to the position occupied by the animal in or on it, but this will only be ascertained by direct observation of the animal.
C. dactylus, though undoubtedly possessing the anterior end primary shell characters of the *Cryptospira ventricosa* group, resembles the morphology of *Cryptospira tricincta* at its posterior end and this is considered to be a convergent character.

Cryptospira ventricosa (G. Fischer von Waldheim, 1807)
Figs 85, 95 - 107, 114, 122, 125, 258, 259

Marginella ventricosa G. Fischer von Waldheim, 1807. Mus. Demidoff, iii, p. 172
Marginella quinqueplicata Lamarck, 1822
Marginella vermiculata Redfield, 1851
Marginella Hainesii Petit, 1851
Marginella ventricosa Hedley, 1903 (non-*Marginella ventricosa* G. Fischer, 1807)
? *Voluta porcellana* Perry, 1811 (*nomen dubium*)
† *Marginella ventricosa* var. *minor*, Martin 1895

Type material. Holotype of *Marginella ventricosa* G. Fischer, 1807 stated as lost from Demidoff collection, ZMUM (Ivanov, Kantor, Sysoev & Egorov, 1991).
Marginella quinqueplicata Lamarck, 1822. holotype MHNG Reg No. 1103.44, 31.8 x 20.8 mm (Fig. 105).

Marginella Hainesii Petit, 1851, syntype, 24.3 mm, MNHN (Figs 103, 104).

Other material. Na Trang, Vietnam: 2 spm, 19.1 mm & 23.25 mm, FBC; 4 spm, 38.0 x 24 mm (Fig. 101), 35.6 x 23.1 mm, 35.5 x 21.5 mm, 30.5 x 20.5 mm, AWC.
'Malacca': 3 spm on tablet, 8 fathoms, coarse gravel, 36.0 x 23.3 mm, 30.6 x 20.0 mm, 37.2 x 23.55 mm, BM(NH), (Fig. 102). [Note: this shell, the largest, was figured in Reeve's Conch Icon. Pl. X f. 40a, b].
Singapore: 1 spm, 33.5 x 21.4 mm, AWC (Figs. 99, 100); 2 spm, ex. C.T. Trenchman coll., 33.0 x 21.9 mm, 32.2 x 22.5 mm, BM(NH); 6 spm, ex. Miss Archer coll., 22-34.5 mm, BM(NH).
West Malaysia, Pulau Pangkor, Pres. R.D. Purchon, 26.2 mm, BM(NH).
Karang Hantu, Banten, West Java, 2 spm, in 5-10 m, 28.0 x 18.3 mm, 23.8 x 15.7 mm, AWC.
Karang Hantu, Banten, West Java, growth series; in 0.5 m, 17.3 mm, 21.9 mm, 23.5 mm, AWC, (Fig. 107).
Brebes, central Java, 5 spm, dredged by fisherman in 5-10 m, 24.1 - 25.2 mm, AWC.
Indramaya, Java, 6 spm, in fishermans net, 31 - 38.5 mm, AWC (Figs 95-97).
Jakarta Bay, West Java, in fishermans net, 25.7 x 17.0 mm, AWC.
Kepulauan, Seribu, Java, 2 spm, 27.1 mm & 27.3 mm, FBC.
Bali, 3 spm, 30 - 32.3 mm, FBC.
Santubong, Sarawak, washed up among rocks on shore of muddy sand at river mouth, coll. D.G. Reid, 1 spm, 24.4 x 14.9 mm, BM(NH).
Singkep Is., eastern Sumatra, dredged in 20 metres, 33.2 x 19.3 mm, AWC (Fig. 98).
La N'gu Bay, Satun Province, Southern Thailand (Andaman Sea), dredged in 5 - 10 m, 3 spm, 38.0 mm, 38.0 mm, 37.8 mm, SPC.

Type locality. Designated as Surabaya, north coast of Java (Coomans, 1969).

Distribution. Vietnam to Singapore and the Strait of Malacca, north and east Sumatra, the north coast of Java, to Lombok and eastern Kalimantan.

Habitat. Mud, sand and gravel substrates in 10-30 m. Has been recorded in an estuarine environment (Dharma & Dunlap, 1994) and in fine muddy sand in 10 metres off mangroves in Satun Province, Thailand (pers. comm. S. Patamakanthin).

Descriptive notes. Shell medium to large (L = 25 - 45 mm, W:L = 56-72 %), thick, heavy, pyriform to ovate, inflated posteriorly, tapering to truncated base. Colour even bluish pale grey, with sparse axial growth markings. Lip opaque white, thick to very thick. Spire exposed, low to elevated with a raised crest at the suture, of 3.5 whorls including protoconch. Shoulder rounded, smooth. Labial shoulder forming a sharp right angle with the lip. Posteriorly, aperture as wide as labial varix, widening to 1.5 times as wide anteriorly. Lip thickened as a single varix with a smooth rolled edge. Internal aspect of lip smooth. External varix groove present. Anterior and posterior notches present. Lip extending to level of suture, but generally below the apex, inserting into callus on the body whorl just beow the surture. Columella with five plications; all oblique, strong. An elongated denticle resembling a remote 6th plication extends horizontally across parietal surface further than the plications. Posterior ventral callus opposite labial insertion present, resulting in a well demarcated posterior notch. Anterior ventral callus widening columella base and forming a fasciole which merges with the first three plications, its edge well defined between the third and fourth plications.

Remarks. The shell, from 25 - 45 mm in length matures according to the growth series presented in fig. 107. The truncated base is present throughout development, the last adult whorl often develops a raised crest at the suture, and the lip matures by increasing its internal thickness except at the posterior end where it forms the extended and angulate posterior shoulder.
The animal of *C. ventricosa* was reported upon by Coovert (1987) who referred to an illustration of it in Souleyet (1852). The animal is uniformly coloured, with a rather large siphon. The mantle extends from all sides, covering spire with the central area uncovered. The foot has a large bulbous protuberance posteriomedially. Souleyet's drawing was subsequently reproduced by Tryon (1882-83, Pl. 9, fig 64). Tryon's figure is shown here (Fig. 85).
Dharma & Dunlap (1994) reported that heavily callused shells are found at Tembilahan, Sumatra, in the region of the estuary of the Indragiri River, and also in many localities in Java where shells of this species are generally thicker and fatter than they are in Sumatra. Slender shells have been found in 20 – 30 metres near Singkep Is., east Sumatra (Fig. 98), but all are clearly identifiable as *C. ventricosa* due to the columella morphology, truncated anterior end, colour, and sub-pyriform to pyriform profile.

Cryptospira dactylus (Lamarck, 1822)
Figs 76, 108, 109, 254 - 257

Marginella dactylus Lamarck, 1822. Anim Sans Vert., vii, 360
† *Marginella dactylus* var. *inflata* Martin, 1895.
† *Marginella dactylus* var. *minor* Pannekoek, 1936.

Type material. 1 spm, holotype, MHNG Reg. No. 1103/53, 23.9 x 14.3 mm (Fig. 108).

Other material examined. Makassar Strait, 00°58'S 119°29'E, dredged in 62 m, CORINDON Exped., st. DR254, 1 spm, 26.3 x 12.2 mm, MNHN.
Makassar Strait, 01°11'S 117°06'E, trawled in 21 m, CORINDON Exped., st. CH201, 1 spm, 21.0 x 9.6 mm, MNHN.
Makassar Strait, 01°08'S 117°18'E, trawled in 49 m, CORINDON Exped., st. CH205, 7 spm, 30 x 13.5 mm, 27.5 x 12.4 mm, 27.0 x 12.3 mm, 29.3 x 13.4 mm, 23.0 x 10.0 mm, 25.0 x 11.0 mm, 25.2 x 11.0 mm, & 2 juv. spm, 32.6 x 14.2 mm, 15.1 x 6.1 mm, MNHN.
East Sumatra, Bangka Is., trawled in 10 m, 1 spm, 19.0 x 8.5 mm, AWC.
Sunda Strait, Fisherman's net in 20 m, 1 spm, 21.0 x 9.4 mm, AWC.
Java, Surabaya, 1 spm, 32 mm, FBC.
Java, Madura Strait, 2 spm, 37 mm & 37 mm, TMC.
West Kalimantan, Pontianak, trawled in 25-30 m, 1 spm, 33.5 x 15.9 mm (Fig. 109), AWC.
West Malaysia, Johor, 1 spm, 34 mm, AWC.
Lombok Island, 2 ad spm, 36.8 x 17.8 mm, 33.7 x 16.3 mm, AWC.

Type locality. Unknown.

Distribution. Reliably recorded from West Malaysia, east into the Java Sea including the Karimata, Makassar, and Sunda Straits, but populations appear to be fragmented in their distribution. A large population exists in Lombok. The range may extend north into the South China Sea; some old museum specimens state Hong Kong as their locality, but this requires confirmation.

Habitat. From 8 to 62 m on muddy substrates.

Descriptive notes. Shell medium to large (L = 21 - 37 mm, W:L = 46 - 48 %), moderately thin, light, elongate and sub-cylindrical, narrow posteriorly, tapering slightly to truncated base. Colour pale bluish-grey. Lip white. Pattern absent. Spire immersed, concealed under apical callus. Shoulder smooth, rounded. Aperture evenly narrow and straight, widening to 1.5 times the width of the labial varix anteriorly. Lip thickened slightly as a single varix with a smooth rolled edge. Internal aspect of lip smooth, lacking denticles. External varix groove present. Anterior notch weak, posterior notch absent. Lip extending beyond end of shell curving round to insert into callus directly over apex. Columella with five oblique plications; first slightly sinuous, second and third strongest, then weakening to fifth. Anterior ventral callus with distinct, slightly raised edge between third and fourth plications. Anterior end somewhat truncated, parietal surface posterior to plications is smooth and parietal callus is absent.

Remarks. The characteristically elongate cylindrical shape, with its five anteriorly positioned, evenly oblique columellar plications, consistent shell morphology (W:L ratio 45% - 47.7%) and solid grey colour lacking any spiral pattern make the identification of this graceful species quite straightforward, and it is hard to see how it could be confused with anything else. Its group is, however, not intuitive. The immersed spire and the arching of the posterior labial insertion onto the spire are characters converging upon those of the *Cryptospira tricincta* group, but the lack of any spiral pattern, the position of the columellar plications, the truncated base, the angulation of the anterior canal, and the range of distribution place this species firmly in the *Cryptospira ventricosa* group. It has an interesting fossil record, but the extinction of one of its fossil forms and its sporadic occurrence in the recent could imply that this elegant species may be on the decline.

Cryptospira trailii (Reeve, 1865)
Figs 110 - 113, 115 - 118, 124

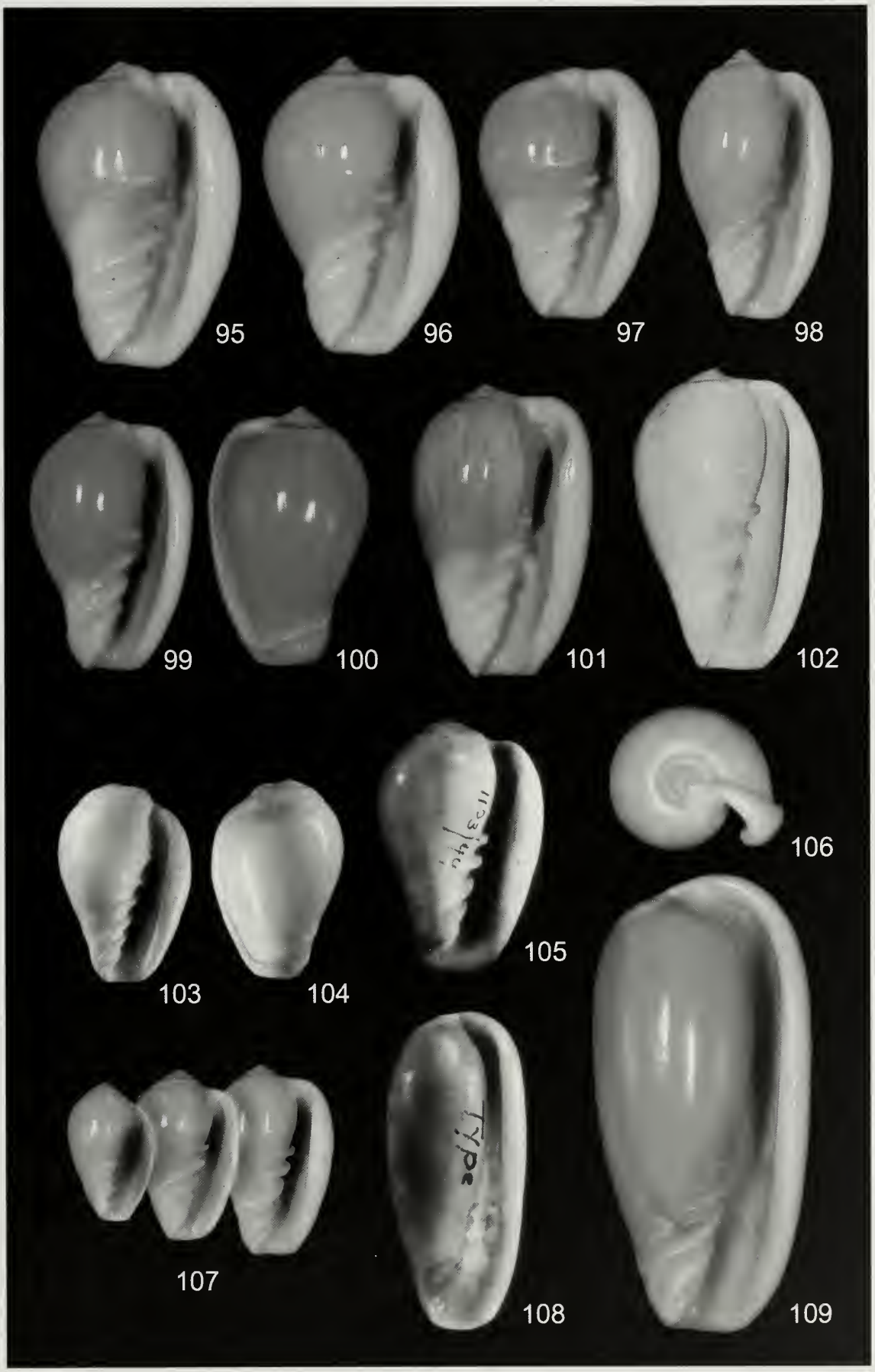
Marginella trailii Reeve, 1865 (5th Jan.) Conch. Icon., xv, pl. xxi, fig. 114.

Type material. Malacca, 2 spm, syntypes, Reg. No. 1975011/012, 13.4 x 6.6 mm (Figs 110, 111), 12.9 x 6.5 mm (Figs 112, 113), BM(NH). [Note: the larger of the two is the figured specimen in Reeve].

Figures 95-109. *Cryptospira ventricosa* group.

95-107. ***C. ventricosa*** Fischer von Waldheim, 1807
95-97. Indramaya, Java Sea, 36.7 x 24.5 mm, 36.8 x 24.5 mm, 31.0 x 22.4 mm, AWC; **98.** Singkep Is., Sumatra, 33.2 x 19.3 mm, AWC; **99-100.** Singapore. 33.5 x 21.4 mm, AWC; **101.** Nha Trang, Vietnam, 38.0 x 24.0 mm, AWC; **102.** Malacca. 37.2 x 23.55 mm, BM(NH) (Shell depicted by Reeve, 1864); **103-104.** Syntype of *M. Hainesii*. Jousseaume, 1875, 24.3 mm, MNHN; **105.** Holotype of *M. quinqueplicata*, Lamarck, 1822, 31.8 x 20.8 mm, MHNG. Reg. No. 1103.44; **106.** Spire view showing posterior notch and internal labial callus; **107.** Growth series, Karang Hantu, Banten, west Java, 17.3 mm, 21.9 mm, 23.5 mm, AWC;

108-109. ***Cryptospira dactylus*** Lamarck, 1822
108. Holotype, MHNG Reg. no. 1103/53, 23.9 x 14.3 mm; **109.** West Kalimantan, Pontianak, 33.5 x 15.9 mm, 25-30 m, AWC.


95
96
97
98
99
100
101
102
103
104
105
106
107
108
109

Other material. 2 spm, 10.77 x 5.28 mm, 11.45 x 5.46 mm, Singkep Is. East Sumatra, 20 m, collected June 1992, AWC (Figs 115 - 118, 124).
Several further specimens with same data in BDC.

Type locality. 'Malacca'

Distribution. Strait of Malacca to Singkep Is, Sumatra.

Habitat. Muddy sand at about 20 m.

Descriptive notes. Shell small (L = 11-13.4mm, W:L = 49-50%), moderately thin, elongate, narrow posteriorly, tapering smoothly to truncated base of columella. Colour pale straw or cream, without axial or spiral pattern. Lip same colour as body whorl. Spire elevated, 3.5 whorls including protoconch. Shoulder smoothly rounded, labial shoulder forming a right-angle with the lip. Aperture straight, as wide as labial varix in posterior half, flaring to twice this size anteriorly. Lip thickened externally as a single varix with a smooth edge. Lip smooth, denticles absent. External varix groove present. Anterior notch present, posterior notch absent. Labial insertion at shoulder. Columella with five oblique, square-crested plications occupying anterior 2/3 of the aperture; first and second plications closest and most oblique. Anterior ventral callus merging with distal ends of first three plications.

Remarks. This is perhaps the most elusive species of the genus, and as such it is poorly known. Until specimens were recently collected at Singkep Island, Sumatra, the only other known examples were the two syntypes in the BM(NH). The species is very distinctive, with its elevated spire, elongate, sub-rectangular shape, straight, thick labial margin and an almost right-angled labial shoulder creating a strong posterior notch.

(C) *CRYPTOSPIRA ELEGANS* GROUP

The *Cryptospira elegans* group comprises an aggregation of 6 species with characteristic combinations of shell morphologies and colour patterns. It is the dominant group in the western arm of the geographical distribution of the genus. Its valid species are; *C. elegans* (Gmelin, 1791), *C. strigata* (Dillwyn, 1817), *C. marchii* Jousseaume, 1875, *C. praecallosa* (Higgins, 1876), *C. glauca* Jousseaume, 1875, *C. grisea* (Jousseaume, 1875), *C. scripta* (Hinds, 1844) and *C. bridgettae* n. sp.
C. elegans and *C. strigata* together have the longest lists of synonyms in the whole family and despite clear differences, have at various times also been included in the synonymy of each other. Most of the group's species are common and familiar to conchologists because of their relatively large sizes and the colourful patterns of their shells, but *C. scripta* and *C. grisea* remain rather rare in collections, and *C. bridgettae* n. sp. is only known from limited type material.

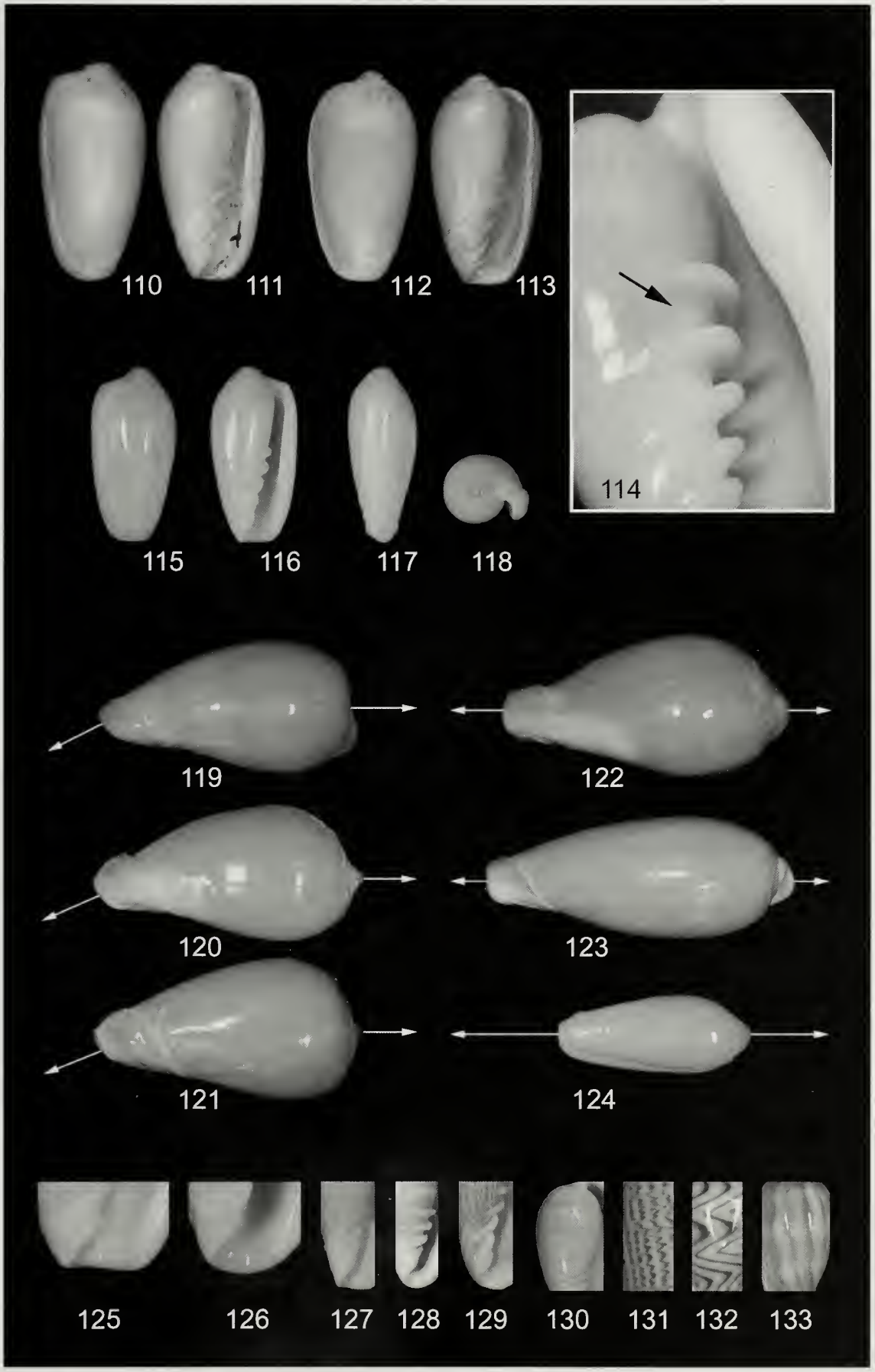
Figures 110-133. *Cryptospira ventricosa* group and shell characters.

110-113, 115-118. *Cryptospira trailii* Reeve, 1865

110-111. Syntype figured by Reeve, Malacca, 13.4 x 6.6 mm, BM(NH) Reg. No. 1975011; **112-113.** Syntype, Malacca, 12.9 x 6.5 mm, BM(NH) Reg. No. 1975012; **115-118.** Singkep Is., Sumatra, 11.4 x 5.4 mm, AWC.

119-124. Orientation of the siphonal canal.
119. *C. tricincta* Hinds, 1844, Palawan (*Cryptospira tricincta group*); **120.** *C. glauca* Jousseaume, 1875, Madras (*Cryptospira elegans* group); **121.** *C. marchii* Jousseaume, 1875, Andaman Sea (*Cryptospira elegans* group); **122.** *C. ventricosa*, Fischer, 1807, (*Cryptospira ventricosa* group); **123.** *C. dactylus*, Lamarck, 1822, (*Cryptospira ventricosa* group); **124.** *C. trailli*, Reeve, 1865, (*Cryptospira ventricosa* group).

114, 125-133. Shell characters
114. Detail of columella of *C. ventricosa* showing denticle between 4th and 5th plication; **125.** truncated anterior end of *C. ventricosa*; **126.** rounded anterior end of *C. tricincta*; **127.** anterior end and ventral callus of *C. dactylus*; **128.** columella of *C. tricincta* with relatively horizontal plications; **129.** columella of *C. strigata* with relatively oblique plications; **130.** Fine spiral lined pattern seen in *Cryptospira tricincta* group species (*C. quadrilineata* shown); **131.** Finely zig-zagged axial lined pattern of some *Cryptospira elegans* group species (*C. strigata* shown); **132.** Strongly zig-zagged pattern of some *Cryptospira elegans* group species (*C. scripta* shown); **133.** Smooth axial pattern along growth lines, seen in *Cryptospira tricincta* group species (*C. wallacei* shown).


110
111
112
113
114
115
116
117
118
119
122
120
123
121
124
125
126
127
128
129
130
131
132
133

Principal characteristics of the *Cryptospira elegans* group

The *C. elegans* group is the only *Cryptospira* group having member species which bear well-formed denticles on the inner aspect of the labial margin and this can be said to be one of its two primary shell characters. Having said that, some species, for example *C. glauca*, are always heavily denticulate whereas they are very weak to absent in specimens of other species such as *C. elegans*, so care has to be exercised when applying this shell character during identifications. Although heavier denticulation often goes hand in hand with increasing shell maturity, this is not always the case. Within populations of normally denticulate species, for example *C. strigata*, there will also be mature specimens with denticles so reduced that they are hardly detectable. The '*elegans*' group can always be differentiated from the '*ventricosa*' group by the angle the anterior end of the shell makes with the horizontal plane in lateral view (see figs 119-124). With the exception of fluctuations in base colour as a result of growth lines, no other group exhibits an axial pattern. It consists of well developed fine zig-zags in *C. elegans* and in most specimens of *C.strigata*, and it is so well developed in *C. scripta* that it forms an elaborate and striking pattern. However, axial pattern is absent in *C. glauca*, *C. grisea* and in some varieties of *C. strigata*. Such inconsistencies in individual shell characters make diagnosis of *Cryptopira elegans* group species reliant upon primary and secondary character combinations.
The principal shell characters of the elegans group are therefore as follows:

- Lip smooth to denticulate (up to 30 elongated denticles). Deeply denticulate callus bevel often present at posterior end of internal aspect of lip (Fig. 159).
- Axial pattern of irregular wavy lines to zig-zags, often heavily disrupted (Fig. 154). Production of darker pigment at specific zones along the growing edge of the shell creates repeating axial micro-patterns which result in a macroscopic spiral pattern effect (Figs 139-146).
- Shell sizes from very small (5 mm) to very large (50 mm) for the family.
- Shells ovate, ob-ovate, elongate-ovate, and subtriangular in profile.
- Colour of labial margin often concentrated at the marginal groove. Ground colour varies from pale grey and pale cream to bluish-grey and greenish-brown.
- Five strong columellar plications. First two plications as in other groups of *Cryptospira*, are very close together.
- Weak to moderate anterior ventral callus which extends to between the third and fourth plication, often well demarcated by a ridge extending from between these two plications, round to join up with the edge of the varix adjacent to the varix groove.
- Weak to moderate parietal callus extending from the level of the posterior end of the lip is often present.
- Spire exposed and flat to slightly elevated. Protoconch always visible.

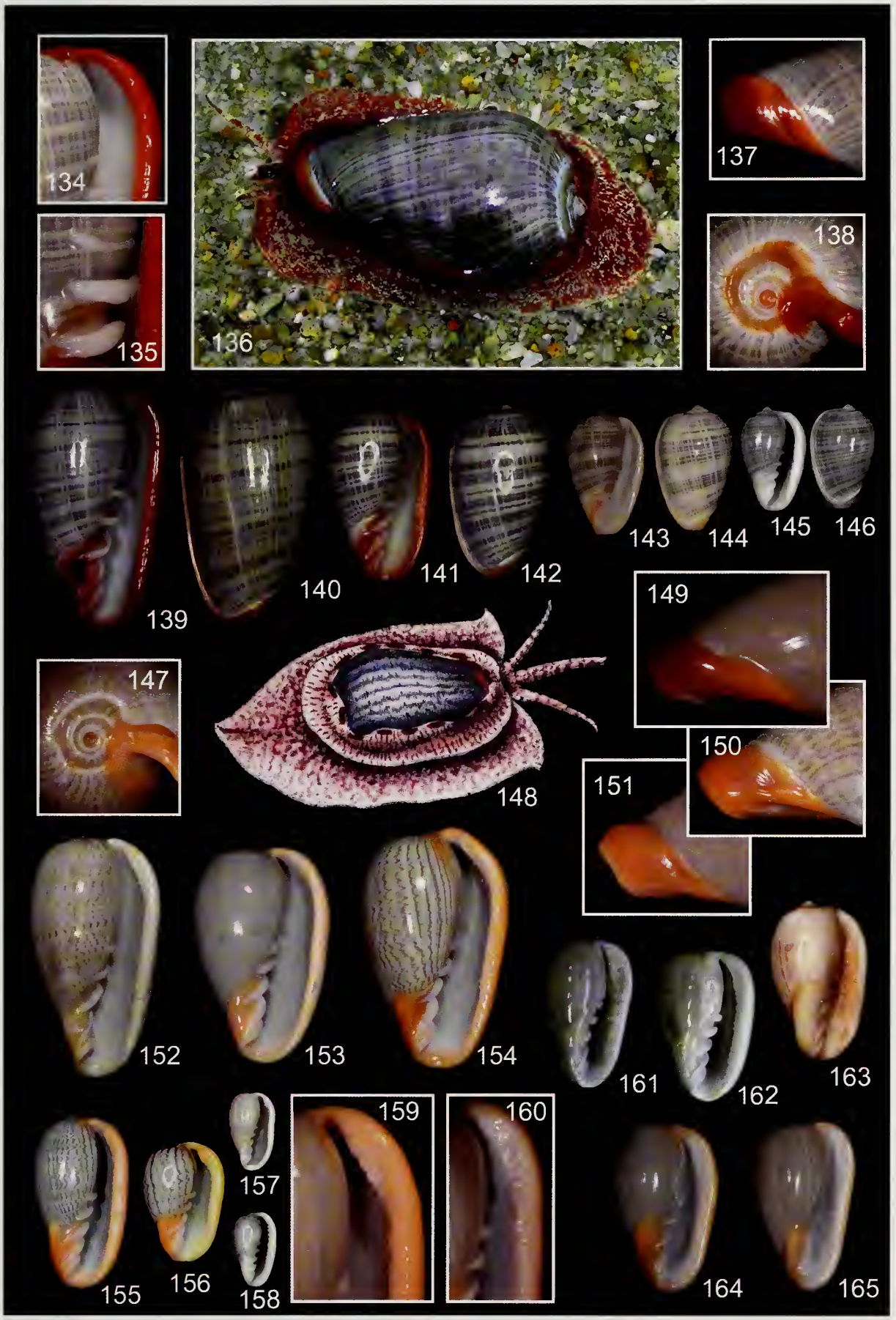
Figures 134-165. *Cryptospira elegans* group.

134-144. ***Cryptospira elegans*** Gmelin, 1791;
134. Posterior end of lip; **135.** 4th & 5th plications and parietal lira; **136.** Live animal, low tide, Laemson National Park, Ranong Province, Thailand; **137.** Anterior callus; **138.** Spire; **139-140.** Andaman Sea, dredged 60 m. 49.0 x 28.0 mm, AWC; **141-142.** Andaman Sea, 33.0 x 20.0 mm, AWC; **143-144.** Racha Island, Phuket, Thailand, 25.0 x 16.0 mm, AWC.

145-146. ***Cryptospira bridgettae*** n. sp., Bang-Rin to Nang Yon, Ranong Province, S. Thailand, holotype, 20.05 x 12.58 mm, BM(NH) Reg. no. 20100327

147-148, 150-159. ***Cryptospira strigata*** Dillwyn, 1817;
147. Spire; **148.** *M. undulata* Deshayes, illustration from Adams & Reeve, 1848; **150-151.** Anterior callus morphologies; **152.** Strait of Malacca, narrow form, 46.0 x 25.0 mm, AWC;
153. Andaman Sea, dredged 60 m, the var. 'unicolor', 44.0 x 26.0 mm, AWC; **154.** Andaman Sea, 49.0 x 28.5 mm,(= *Marginella undulata* of Deshayes),AWC; **155.** Strait of Malacca, 33.0 x 18.5 mm, AWC; **156.** Rawa Bay, low tide on sand, 23.0 x 15.5 mm, AWC; **157.** Singkep, E. Sumatra, 16.0 x 9.0 mm, AWC; **158.** Bay of Bengal, 14.3 mm, FBC; **159.** Denticulated bevel at posterior end of lip.

161-165, 149. ***M. praecallosa*** Higgins, 1876;
161-162. *M. loebbeckeana* Weinkauff, 1878, holotype, 29.8 x 19.0 mm, LMD;
163. Holotype, 25.0 x 12.0 mm, MCM; **164.** Andaman, Sea, 34.0 x 21.0 mm, AWC; **165.** Andaman Sea, 33.5 x 20.0 mm, AWC; **149.** Anterior callus formation in *M. praecallosa*.


134
135
136
137
138
139
140
141
142
143
144
145
146
147
148
149
150
151
152
153
154
155
156
157
158
159
160
161
162
163
164
165

Distribution Pattern. The distribution of the *elegans* group is the most distinctive of all the three groups in the genus. It is the sole occupant of the western arm of the range of distribution of the genus (see Fig. 8). It extends from western Borneo, eastern Sumatra (Karimata Strait) and the southern end of the Straits of Malacca, Malaysia (2 *elegans* group species), passes up into the Andaman Sea between the Nicobar and Andaman Islands and Thailand then north to Burmese waters (4 *elegans* group species), and then into the Bay of Bengal and down the east coast of India to Sri Lanka (1 *elegans* group species). The only overlap of the *C. elegans* group distribution with *Cryptospira* species from other groups is from the Northern end of the Malacca strait to the Karimata Strait and southern Kalimantan. The type locality of *C. scripta* is 'Macassar', so theoretically the overlap could extend further East to the Wallace line. It should be noted however that all other records of *C. scripta* are from Malacca or the Andaman Islands.

Taxonomic aspects. There are three unresolved taxonomic issues to address in this group:

1. To clarify the morphologic species definition of *C. glauca* Jousseaume, 1875: Several grey-coloured species from across the range of distribution of the group, and involving a wide range of morphologies, are currently being referred to as *C. glauca*.

2. To reveal the correct taxonomic placement of *C. loebbeckeana* (Weinkauff, 1878) by examination of the type specimen: *C. loebbeckeana* is frequently and confusingly used as a varietal name for specimens of *C. glauca* from the Bay of Bengal (eastern coast of India).

3. To reconsider the taxonomic position of phena currently considered synonymous with *C. strigata* in the literature: *M. undulata* Chemnitz, 1788, *M. Burchardi* Reeve, 1864, *M. marchii* Jousseaume, 1875, and *M. Bernardii* Largilliert, 1845

The true identity of *C. glauca* Jousseaume, 1875

To properly define *C. glauca* we need to consider the original description, study the type specimen and make comparisons with the morphologies of superficially similar grey '*Cryptospira elegans*' group species. In addition, an understanding of the distribution of the various phenotypes occurring in the Bay of Bengal and the Andaman Sea is absolutely essential.

In his monograph of the Marginellidae, Jousseaume (1875) provided a very detailed description of *C. glauca*, including an accurate, exquisitely drawn colour figure, with remarks about how the species differed from *M. quinqueplicata* Lamarck, 1822 and *M. luiuesii* Petit, 1851 (both presented earlier as synonyms of *C. ventricosa* G. Fischer von Waldheim, 1807). Jousseaume therefore left us in no doubt about its morphology. All specimens have a heavily denticulate lip and a moderate to strong basal callus (Fig. 172) giving shells a stout, subtriangular to ovoid appearance (Figs 166-177). It is important to note that it was described without a type locality, but that Coomans (1969) designated it as being Singapore. The description and original figure of *C. glauca* clearly indicate a basally callused shell of the type exclusively found in the western Bay of Bengal, from Sri Lanka northwards up the east coast of India. The syntype (Figs 170, 171) was rediscovered in the Jousseaume collection (MNHN) by Dr. E. Fischer-Piette at the request of Coomans in 1969, and its morphology is in accordance with the observations made above. The length of the syntype is 24 mm and the size range of the many specimens I have studied is from 21-28 mm, with most specimens being around 24 mm in length. Similarly coloured shells (Figs 180-198) sourced from the Mergui Archipelago (Burma) and further south along the coast of Thailand and peninsular Malaysia through the Straits of Malacca down to Singapore and northeast Sumatra could not be more different, in that in even very mature adult specimens the basal callus is always absent (Fig. 185), and the shells often attain a larger size (though there is an overlap with the size range of *C. glauca*). Because the basal callus is a constant shell character in *C. glauca*, we should regard it as important in defining the species, and by default the shells with no basal callus found further east need to be regarded as a separate species (see below). When considered in this way, *C. glauca* is easy to identify in terms of size, shape and distribution. It is also necessary to re-designate the type locality of Singapore, designated by Coomans (1969). The majority of specimens I have seen are sourced from Chennai (Madras), and so the type locality of *C. glauca* is hereby redesignated as Chennai, Tamilnadu, India.

The true identity of *C. loebbeckeana* (Weinkauff, 1878)

Three years after Jousseaume's description of *C. glauca*, *M. loebbeckeana* Weinkauff, 1878 was described. Tomlin (1917) stated that it was 'rather doubtfully distinct from *ventricosa*, G. Fischer' but nevertheless he listed it as a valid species. It was considered to be a synonym of *C. glauca* by Coomans (1969), and has been commonly used as a varietal name for that species ever since ('*C. glauca var. loebbeckeana* '). Weinkauff's figures of the dorsal and ventral views lack detail, and in his descriptive text he gives the size as 31 x 19 mm (W:L ratio of 61%). He was of the opinion that the *M. elegans* specimen figured in Sowerby (1846, fig. 149), was the same as his species, and that *M. Burchardi* Reeve was also a synonym. Clearly, a very confused state of affairs.

In 1969, Coomans was denied access to the type lot of *M. loebbeckeana* due to lack of curatorial presence at

the Loebbecke Museum, Dusseldorf. Today, we are more fortunate because the museum now has a curator, and excellent photographs of the type specimen taken from several angles have been secured (Figs 161, 162). These were compared and contrasted with the syntype of *C. glauca* (Figs 170, 171), in order to check Coomans' assignation. The clear differences in the size and shape of the shells indicate that they are not, in fact, the same species. This comes as no real surprise because Weinkauff gave the measurements of the type of *M. loebbeckeana* as 31 x 19 mm and as noted earlier I have not seen any example of the true *C. glauca* over 28mm. Coomans (1969) did not spot this of course, because he included the larger, uncallused, more eastern ranging species (here called *C. marchii*) in his definition of *C. glauca*.

Apart from the size difference, when making a comparison between *C. loebbeckeana* and *C. glauca,* the morphology of the lip should be regarded as a particularly important character because in these species comparison of the basal callus is not diagnostic – it is strongly present in both. When viewed from the ventral aspect, the internal labial surface of *C. glauca* is straighter than that of *M. loebbeckeana.* In cross section, *C. glauca* has a more rounded denticulate labial border with denticles relatively close to the edge, whereas in *M. loebbeckeana* the denticles are present on a raised ridge more deeply situated in the aperture. This is demonstrated in cut-away sections (Figs 178, 179).

M. loebbeckeana also has consistently different labial morphology to *C. strigata.* Along the entire length of the inner lip, it has a very strong, curved, sloping surface, bearing moderately strong lirae which terminate as raised denticles along a crest which runs the entire length of this sloped surface (Fig. 160). In contrast *C. strigata* has a deeply denticulate sloping bevel at the posterior insertion of the lip only (Fig. 159). *M. loebbeckeana* is a good match morphologically with the slightly more callused *M. praecallosa* Higgins, 1876 (Fig. 163) and it is considered herein to be a synonym of it. We have the benefit of a recently collected lot of shells from a population in the straits of Malacca to compare with the types of *M. loebbeckeana* and *M. praecallosa* and these consistently demonstrate the diagnostic labial morphology. In conclusion, *M. loebbeckeana* is not a synonym or a variety of *C. glauca* as stated by Coomans (1969), and because it was described later it becomes a a junior synonym of the valid *M. praecallosa* Higgins.

The taxonomic position of phena closely allied to *C. strigata*

From Burma down to southern Thailand (and probably further into the Straits of Malacca), populations of medium-sized, very weakly denticulate, uniformly pale grey shells are found (Figs 180 - 198). As noted above these are often erroneously referred to as *C. glauca*, possibly because they were lumped together with that species by Coomans (1969). [Note; The largest of the ten specimens Coomans used for his study was a 31.5 mm long shell from Sumatra - clearly not *C. glauca* on account of both its size and its provenance]. They are also much more variable in size and shape than the relatively morphologically constant *C. glauca.* The lack of taxonomic clarity with this species has come about because within its range of completely intergrading morphologies are subtriangular shells superficially resembling *C. glauca*, and ob-ovate shells resembling *C. strigata.* Unlike *C. strigata* or *C. glauca* however, the basal callus is limited to a fine wash and the labial denticulation is much reduced or absent, The edge of the ventral callus wash is clearly marked by a prominent ridge emerging from between the 3rd and 4th plications and continuing around the base of the shell to link up with the edge of the labial margin at the marginal groove. I have had the good fortune of obtaining a substantial lot of thirty unsorted specimens, sourced from La N'gu, Satun Province, southern Thailand, in which the full range of their morphological variability is expressed. Firstly, it was possible to separate out two quite typical *C. strigata* of similar size by the presence of a denticulate bevel at the inner aspect of the posterior end of the lip. The remaining morphologies are presented in figs 180-185, 187-191, and 193-198. When the whole range of morphologies are familiarized and compared with the type material of relevant taxa, namely *M. Burchardi* Reeve, 1864 and *M. marchii* Jousseaume, 1875, we find that both fit in the range of morphologies at different points. The three syntypes of *M. Burchardi* (one shown in Fig. 186) are in the BM(NH) and their morphology is a close match for ob-ovate specimens from the population sample from La N'gu, Thailand (Fig. 187). The morphology is very close to *C. strigata* and that they are small, faded examples of this species was declared by Redfield (1870) and Tomlin (1917). Jousseaume pointed out that the name *M. Burchardi* was preoccupied and he renamed it *M. marchii* Jousseaume, 1875. The syntype (Fig. 192) is in MNHN. *C. marchii* is a much smaller and lighter shell than *M. Burchardi* but still falls within the range of normal variation of the species as noted above. As I cautiously consider this species to be distinct from *C. strigata*, and completely distinct from *C. glauca*, *C. marchii* Jousseaume, 1875 is designated here as being the correct name for this species, with *M. Burchardi* Reeve 1864 being synonymous.

There are two other taxa which need to be considered in relation to *C. strigata* ; *M. Bernardii* Largilliert, 1845 and *M. undulata* Deshayes, 1844. *M. Bernardii* has been the name given to Taiwanese *C. cloveriana* by some recent authors. Earlier in this paper this assignment was shown to be erroneous, the rightful place of *M. Bernardii* being in the synonymy of *C. strigata. M. undulata* is simply a *C. strigata* with a particularly clear wavy axial pattern (Fig. 154).

Adams and Reeve (1848) collected and recorded the living animal of *C. strigata*, referring to it as *M. undulata* Deshayes (Fig. 148). The animal was particularly well illustrated and described thus: 'This fine species was also taken alive, the tentacles, siphon foot and mantle are of a delicate, semitransparent yellowish ground colour, streaked and mottled with carmine, the border of the mantle being mildly spotted with the same. The left lobe of the mantle is more produced over the shell than the right.' The animal of *C. strigata* is clearly paler and more of the yellowish colour is evident than in the animal of *C. elegans* (Fig. 136).

Cryptospira elegans (Gmelin, 1791)
Figs 134 -144

Lister, Conch., 1688. Pl. 803, Fig. 11.
Martini, Conch., 1773. i, p. 106, pl. 42, Fig. 424, 425.
Voluta No. 98, Schroeter, 1786. Einleitung, i, 269.
Murex monilis, 1787. Meusch., Mus. Gevers., p. 328, No. 713.
Voluta elegans Gmelin, 1791. Ed. Syst. Nat., p. 3448.
Voluta cancellata var., 1793. Schreibers, Conchylien-Kentnniss, i, p. 118. (nomen dubium)
Voluta elegans, in Wood, 1828, Index Testac., pl. 20, Fig. 69 (copied from Martini).
Marginella elegans, in Kiener, 1834. Coq. Viv., p. 15, pl. 8, Fig. 35.
Marginella bullata, in Reichenbach, 1842, Conch., p. 62, pl. 37, Figs 530, 531.
Marginella elegans, in Reeve, 1843. Conch. Systemat. Ii, 249, pl. 277, Figs 5, 6 ; Catlow, 1843, Pop. Conchology, p. 251 ; Deshayes, 1844, ed. Lam. Anim. Sans Vert. X, p. 450 ; Sowerby, 1846, Thes. Conch., i, p. 385, pl. 77, Fig. 147 (not 148, 149); Chenu, 1859, Manuel de Conchyl., i, p. 199, Fig. 1056 ; Reeve, 1864, Conch Icon., *Marginella*, pl. 2, Figs 4a, b ; Redfield, 1870, Catalogue Fam. Marginellidae, p. 231, no. 52 ; Tryon, 1882-83, Man. Conch., Fam. Marginellidae, p. 30, pl. 9, Figs 67-70, 82; pl. 2, Fig. 8.

Type material. Not found.

Other material. W. Malaya, trawled off Pulau Pangkor, 2 spm., 31.0 mm & 26.0 mm; trawled off Pulau Langkawi, 2 spm., 32.0 mm & 32.5 mm, Coll. R.D. Purchon, BM(NH).
West Thailand, 3 miles Southeast of Phuket in 80 feet on 20/2/1963, 1 spm., 28.5 mm, Coll. by R.T. Abbott, BM(NH).
Phuket, 30 m, 1 spm., 34 mm, BM(NH); 2 spm., 39.3 & 39.4 mm, FBC; 20 spm., 26.0 mm to 49.0 mm, AWC (Figs. 134, 135, 137 - 140); 7 spm., 28.7 – 50.0 mm, SPC.
Phuket, east Racha Is. and Mactan Is., pale shelled dwarf form, 2 spm., 24.3 mm & 24.4 mm, SPC.
Phuket, east Racha and Mactan Is., typical patterned dwarf form, 4 spm., 19.8 mm, 22.7 mm, 24.2 mm, 28.4 mm, SPC.
Phuket, east Racha and Mactan Is., dwarf with very clear spiral pattern, less rounded shoulders and pale yellow labial margin, 4 spm., 19.9 mm, 19.7 mm, 21.8 mm, 24.8 mm, SPC (Figs 143, 144).

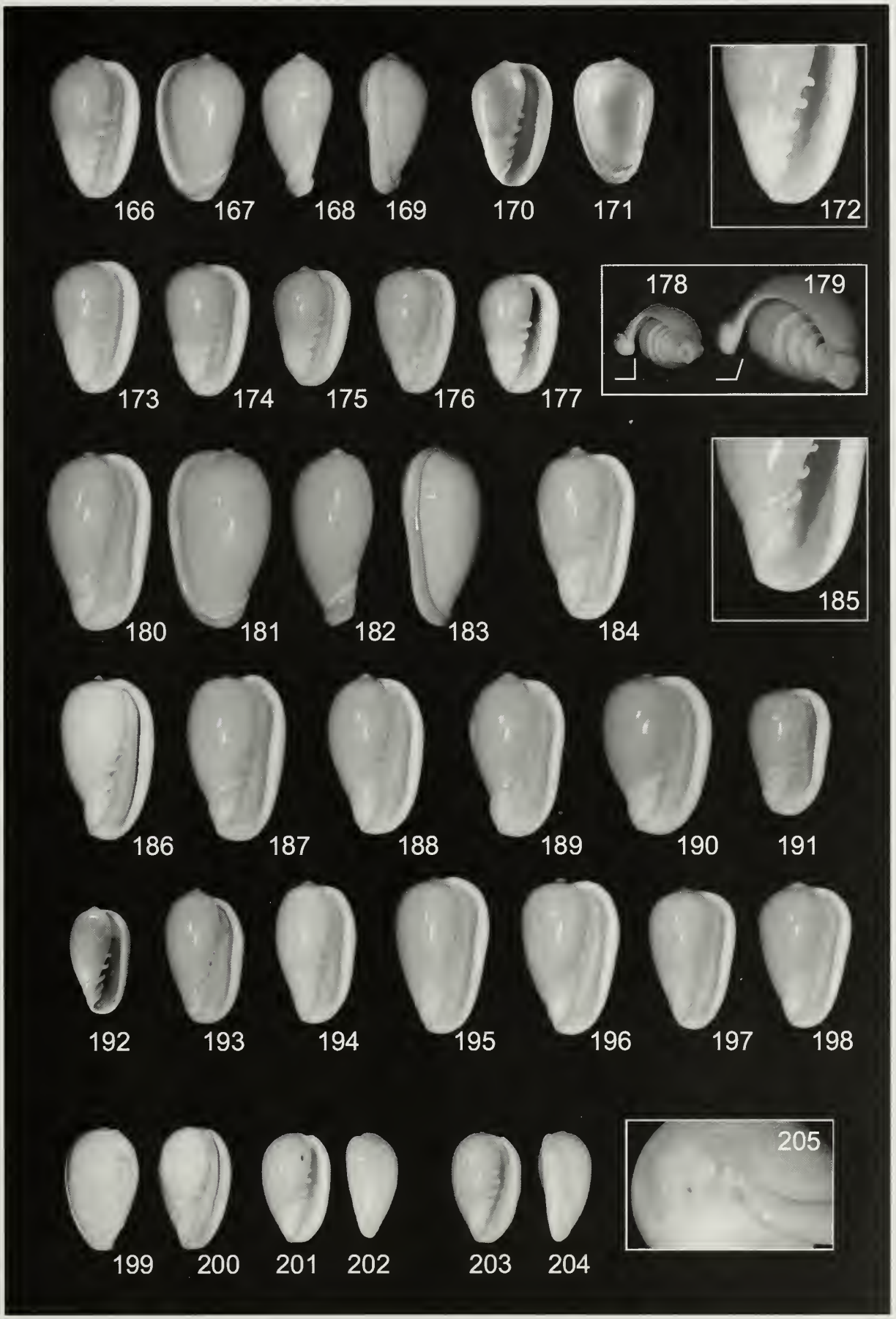
Figures. 166-205. *Cryptospira elegans* group ctd.

166-178. ***Cryptospira glauca*** Jousseaume, 1875; **166-169.** Rameswarem, S. India, 28.0 x 17.9 mm, AWC; **170, 171.** *C. glauca*, syntype, 24.0 x 15.5 mm, MNHN; 172. Closeup of basal callus; **173.** Rameswarem, 25.7 x 17.1 mm, AWC; **174.** Rameswarem, 25.5 x 16.8 mm, AWC; **175.** Rameswarem, 23.1 x 15.3 mm, AWC; 176. Rameswarem, 25.0 x 16.1 mm, AWC; **177.** Madras, 23.8 x 15.3 mm, AWC; **178.** Cut-away labial section of *C. glauca*.

179. ***C. strigata*** Dillwyn, 1817, cut-away labial section.

180-198. ***Cryptospira marchii*** Jousseaume, 1875; **180-183.** La N'gu, Satun Province, Thailand, 34.0 x 20.0 mm, AWC; **184.** La N'gu, Thailand, 33.2 x 18.8 mm, AWC; **185.** Close-up of columella base; **186.** *Marginella Burchardi* Reeve, 1864, syntype, 31.9 x 19.1 mm, BM(NH) Reg. no. 1989146; **187-191.** La N'gu, Satun Province, Thailand, 32.0 x 19.0 mm, 31.0 x 18.4 mm, 31.2 x 18.3 mm, 30.7 x 21.2 mm, 24.2 x 15.7 mm, AWC; **192.** *C. marchii* Jousseaume, 1875, holotype, 20.4 x 11.7 mm, MNHN; **193-198.** La N'gu, Satun Province, Thailand, 25.8 x 15.0 mm, 27.2 x 15.6 mm, 30.0 x 18.1 mm, 29.5 x 19.0 mm, 27.2 x 17.0 mm, 27.8 x 17.7 mm, AWC.

199-205. ***Cryptospira grisea*** Jousseaume, 1875;
199-200. *Marginella obtusa*, Sowerby, 1870, holotype, Gulf of Martaban, Burma, 24.0 x 14.9 mm, BM(NH) reg. No. 1874.12.11.93; **201-204.** 21.2 x 13.4 mm, 19.7 x 12.4 mm, AWC; **205.** Close-up of spire and posterior end of lip.


166
167
168
169
170
171
172
173
174
175
176
177
178
179
180
181
182
183
184
185
186
187
188
189
190
191
192
193
194
195
196
197
198
199
200
201
202
203
204
205

Type locality. Not given in original description.

Distribution. West coast and islands of the Malaysian peninsula, including Thailand and the Nicobar Islands.

Descriptive notes. Shell solid, thick, glossy, length 17.5 - 50.0 mm (W:L = 56 - 65 %), obovate to subtriangular. Colour pale grey with darker bluish-grey fine axial markings which line up successionally to form a spiral pattern of randomly thick and thin lines. Labial margin classically deep orange-brown, occasionally cream, rarely opaque white. Lip straight to slightly inflexed, finely nodulose, rarely developing into weak labial denticles, even then only 10-15 in number and present in the middle third of the lip (Fig. 141). Spire of 3.5 whorls not including protoconch, low to moderately elevated. Protoconch pinkish-brown. Suture obscured by dark callus on last adult whorl (Fig. 138). Aperture straight, twice as wide as lip, flaring slightly anteriorly. Posterior end of lip lacking bevel, thinning and inserting on spire at level of suture (Fig. 134).
Columella with five plications, always with a thiner parietal lira posterior to, but not remote from fifth plication (Fig. 135). Plications bifurcate as they terminate, square topped. Gaining strength from 1st to 3rd, then progressively weaker to 5th. Basal callus (Fig. 137) absent to moderately strong, in region of first three plications. First three plications oblique, 4th and 5th and parietal lira lying more horizontally.

Remarks. This species was first published in the literature as a rudimentary illustration in Lister (1688). Redfield (1870) noted that this species had subsequently been referred to by at least six different names. It was confused with *C. strigata* by Sowerby (1846, Pl. LXXVII, figs. 148, 149) yet there are clear differences between the two species.
It can be distinguished from *C. strigata* on shell morphology alone. The single diminutive parietal lira (Fig. 134) masquerading as a 6th columella plication, is a constant shell character in *C. elegans* - it is always absent in *C. strigata*. In addition, the lip of *C. elegans*, though not entirely smooth edged, generally lacks denticles, and the posterior denticulated labial bevel seen so often in *C. strigata* (Fig. 159) is always absent in *C. elegans* (Fig. 134).
The differences in pattern and colour are less stable but the general trend is for a blue-grey spiral pattern to predominate in *C. elegans*, and an undulating axial one to feature more in *C. strigata*. The reddish-brown labial margin in *C. elegans* has been regarded as diagnostic but the form from Racha Island, Phuket (Figs 143, 144) has a pale yellow lip.
Troschel (1867) provided a rudimentary drawing of the radula of this species. The radula is 0.06 mm wide, the basal edge of each rachidian plate is convex and the cutting edge bears 9 cusps which gradually increase in size towards the middle.
The animal of this species is recorded here for the first time (Fig. 136). It was photographed by Mr. Komson Hongpattharakeeree (Thailand), at Laemson National Park, Ranong Province, Thailand (Andaman Sea, near to the Southern Mergui Archipelago) in 2010. This dwarf form was found crawling on the sand at low tide. The animal of *C. elegans* appears to be more intensely crimson-coloured than the animal of *C. strigata* decribed by Adams & Reeve, but photography of living *C. strigata* will be necessary for an accurate comparison to be made.

Cryptospira strigata (Dillwyn, 1817)
Figs 129, 131, 147, 148, 150 - 159

Voluta glabella undulata Chemnitz, 1788, Conch. X, p. 166, pl.150, figs 1423-4.
Voluta glabella var *0*, Gmelin, 1788, ed. Syst. Nat., p. 3445.
Voluta glabella var c, Schreibers, i, p. 115, 1793, and Encyl. Meth. Vers. Pl. 377, fig. 7, 1798.
?Voluta porcellana Perry, 1811, Conch., pl. 17, fig. 2.
Voluta strigata Dillwyn, 1817, descr. Cat., p. 530. and in Wood, 1828, Index Testac., pl. 20, fig. 67.
Marginella strigata Kiener, 1834, Coq. Viv. p. 14, pl. 8, fig. 37.
Marginella undulata Deshayes, 1844, ed. Lam. Anim. Sans Vert. X, p. 451.
Marginella elegans var. Sowerby 1846, Thes. Conch. i., p. 385, pl. 77, fig. 148.
Marginella Bernardii Largilliert, 1845
Marginella undulata in Roberts, 1851, Pop. Hist. Moll. Pl. 4, fig.4 (animal); Chenu, 1859, Manuel de Conch., i, p. 199, fig. 1055; Reeve, 1864, Conch. Icon. *Marginella*, pl. 2, figs 5, 6a, b.

Type material. Not found.

Other material. Thailand, Andaman Sea, 15 spm., 25.2 - 49.1 mm, trawled offshore at 60 - 120 m, SPC; 25 spm, 27.0 - 45.0 mm (Figs 153, 154), AWC.
Malaysia, Strait of Malacca, elongated form, 3 spm., 38.5 - 45.9 mm, SPC; 37.0 - 47.0 mm, (Fig. 152), AWC.
Phuket, Rawai Beach, dwarf population, 20.8 - 27.5 mm, SPC; 2 spm., 22.5 mm, 26.9 mm (Fig. 156), AWC.
South Thailand, Kontong, 6 spm., 33.8 - 44.4 mm, AWC.
West Thailand, Satun, trawled in 85 m, 2 spm., 36.0 & 35.7 mm, AWC; Phuket, 2 spm., 42.0 mm & 40.3 mm, FBC; 2 spm., 42.0 mm & 43.0 mm, AWC; Knala Kedah, 1 spm., 36.0 mm, labelled '*M. elegans*', R.D. Purchon coll., BM(NH).
Malacca Strait, in prawn boat net at 60 m, 1 spm., 40.0 mm, AWC.
East Sumatra, Singkep Is, net in 60 m, 3 spm., 16.2 mm to 26.4 mm, AWC.
South Borneo, South Banjarmasin, net in 60 m, 1 spm., 27.0 mm, AWC.

West Kalimantan, Alan Tiga Is., net in 60 m, 2 spm., 21.0 mm & 23.0 mm, AWC.
'Malaysia', 1 spm., 21.4 mm, FBC.
Burma, 6 spm., 20.5mm to 22.5 mm, ATC.
Mergui Archipelago, 1 spm., 21.8 mm, BM(NH).
Singapore, 1 spm., labelled *M. undulata*, ex. Mrs DeBurgh coll, 30.5 x 19.6 mm, BM(NH).
China, 3 spm., labelled *M. undulata*, 19.5 - 23.0 mm, BM(NH).
Penang, 4 spm., 26.0 - 41.0 mm, BM(NH).
East Indies, Moulmein, 3 spm., unmeasured, BM(NH).
East Africa (err.), 2 spm., unmeasured, Ex. Mrs J. Lombe-Taylor coll., BM(NH).
West Thailand, Phuket, 2 spm., 44.3 mm & 37.5 mm, FBC; 16 spm., 38.0 mm - 45.0 mm, AWC; 1 spm., 35.5 mm, ATC.
South Thailand, Kantong, 1 spm., 33.5 mm, FBC.

Type locality. Given in error in the original description as 'Coasts of Guinea', a West African locality.

Distribution. Andaman Sea (west Thailand, Nicobar and Andaman Is, northeast Sumatra), Straits of Malacca (west Malaysian and east Sumatran coasts), across the Karimata Strait to western Borneo and its offshore islands.

Descriptive notes. Shell small to large (L=12 - 50mm, W:L= 53-68%), glossy, moderately thin and light to thick and heavy, elongate-ovate to obovate, narrowish to inflated posteriorly, tapering smoothly to base of columella. Colour khaki, pale grey, pale cream, fading to white. Spiral pattern of lines of fine dashes and chevrons densely grouped together at irregular intervals on body whorl resulting in denser spiral lines and zones. Dashes and chevrons line up and joined up axially to create axial pattern of irregular lines (Fig. 154) or larger zig-zags. Spiral pattern unrelated to position of plications. Spire exposed and moderately elevated or flat, protoconch raised (Fig. 147). Shoulder smooth, rounded. Aperture posteriorly immediately starts to widen to twice as wide as the labial varix, the widening continuing anteriorly to reach three times as wide. Lip thickened externally as a single varix with a smooth rolled edge (cutaway of lip shown in fig. 179 alongside that of *C. glauca*). Internal aspect of the lip irregular to denticulate. Denticles strongest posteriorly, 10-15 grouped on a bevelled straight edge at the posterior end of the lip, then gradually diminishing in strength from posterior to anterior. Anterior notch absent, moderate posterior notch. Lip extends to level of or slightly beyond apex, curving round to insert into callus at suture level. Columella with five placations; first moderately strong, oblique. Second very close to the first, also oblique. Columella somewhat excavated between 2nd and 3rd plications. Thick anterior ventral callus, cream to orange, merging with the distal ends of the first three plications, and strongly present around anterior end to merge with lip (Figs 150, 151). Parietal surface posterior to plications is smooth.

Remarks. As well as colour pattern variability, this species is also tremendously variable in size, and to a lesser extent shape;

i. Pattern variation
The axial pattern varies from heavily marked shells with a distinct undulating effect [the *M. undulata* of Deshayes, (Figs 148, 154)] through ones where the pattern becomes progressively more faint and disorganised (Fig. 153), to creamy coloured unpatterned shells which are often called *C. strigata* var. 'unicolor', and in old collections, *M. Burchardi* Reeve. Intergrading series of fully patterned to unpatterned shells are seen.

ii. Size variation
The specimens dredged from down to 60 metres in the Andaman Sea by prawn fishermen are the largest, frequently reaching 50 mm in length.
Smaller specimens are found at the lower end of the Straits of Malacca (Sumatra and Peninsular Malaysia). The smallest specimens (Fig. 157), as little as 12 mm in length, are found at the extreme southern end of the range in the Karimata Strait and the islands of western Kalimantan and eastern Sumatra.

iii. Shape variation
The shape varies from inflated (W:L 68 %) to narrow and elongate (W:L 53 %). Specimens deep dredged in the Andaman Sea are generally very inflated and have wide apertures and lack extensive callus formation (Fig. 153). Narrow specimens with a khaki colouration matching the description and figure of *M. Bernardii* Largilliert very closely, can be found in West Kalimantan (see Dharma, 2005, p. 151, pl. 50, 15a, c.) Localised internal callus formation at the posterior end of the labrum is frequently seen and it forms a sharply angulated internal bevel, which is often deeply denticulate when compared with the rest of the lip (Fig. 159). This character can also be present on otherwise non-callused specimens of *C. strigata*. It is always absent in *C. elegans* (Fig 134), is very weak in *C. marchii* (Fig. 180), and takes on a different shape altogether in *C. praecallosa* (Fig. 160). The ab-apertural callus is variable and different extents are shown of it in figs 150 and 151. Compare this callus with that of *C. praecallosa* (Fig. 149) – in the latter the callus extends much further, onto the bodywhorl.
In the Strait of Malacca, a very elongate and pale form can be found (Fig. 152). It used to be possible to find a very short and squat form (Fig. 156) at low tide at Rawa Island, Phuket, but due to habitat destruction this form is now locally extinct (communication from Somwang and Somnuek Patamakanthin).

Cryptospira praecallosa (Higgins, 1876)
Figs 149, 160 - 165

Marginella praecallosa Higgins, 1876. Journ Conch., 1, p. 136.
Marginella loebbeckeana Weinkauff, 1878 Syst. Conch. Cab., p.33, pl. v, f.9,12.
Marginella lobbekeana "kob", Paetel, 1888 (in error)

Type material. *Marginella praecallosa* Higgins, 1876, 1 ad spm, holotype, 25 x 12 mm (Fig. 163), MCM.
Marginella loebbeckeana Weinkauff, 1878, 1 ad sh, holotype, no locality, 29.8 x 19 mm (Figs. 161, 162), LMD. [Note: there is a 1.2 mm discrepancy between the actual length measurement of this shell (29.8 mm) and that recorded by Weinkauff (31 mm). The widths are the same. That this is still the type specimen is, in my opinion, beyond reasonable doubt; It is the only specimen of *C. loebbeckeana* present in LMD and has a label handwritten by Weinkauff. It matches the original but inaccurately drawn figure very well, and the colour is the same. As for the length measurement discrepancy, Weinkauff only provided shell measurements in whole millimetres throughout his monograph, which introduces a margin of inaccuracy of all of his measurements].

Other material. Ranong, Andaman Sea, Thailand, 4 ad. spm., 33.9 x 20.9 mm, 34.5 x 21.7 mm, 33.8 x 19.8 mm, 36.2 x 21.6 mm, and 1 subadult spm., 32.0 x 20.1 mm, (Figs 160, 164, 165), AWC.

Type locality. Unknown

Distribution. Andaman Sea coast of Thailand to Sumatra.

Descriptive notes. Shell medium sized (L = 25-36 mm, W:L = 48-62%), smooth, glossy, very thick, heavy, ob-ovate, inflated posteriorly, anterior end very rounded. Colour pale cream, pale grey to brownish grey, with very weak pattern of irregular and broken axial and spiral lines. Spire exposed, flat to moderately elevated, protoconch elevated. Shoulder smooth, rounded. Posteriorly, aperture narrower than the varix, widening anteriorly to as wide as the varix. Lip thickened externally as a single very thick varix with a smooth rolled edge. Internal aspect of entire lip thickened, forming a sloping ridge along its entire length. Ridge grooved with 30 or more irregular lirae which terminate at a crest deeper into the aperture as denticles, strongest from posterior end of lip to a position level with the second plication, then rapidly weakening. External varix groove present. Anterior notch absent, posterior notch deep. Lip extends to shoulder level or slightly beyond, curving round to insert into callus at shoulder level. Columella slightly concave in region of first three plications. Five strong flat crested plications occupying 2/3 of the apertural length; first two close, oblique, curving anteriorly. Plications 3 to 5 stronger, grooved along their crest so they appear double, becoming more perpendicular to the axis. Parietal surface posterior to fifth plication is smooth but heavily callused, the callus often linking up with the anterior ventral callus which forms a distinct pad at the terminal ends of the plications, resulting in a very wide columella base.

Remarks. It is the heavy callus and the morphology of the inner aspect of the lip which distinguishes this species from its closest relative, *C. strigata*. The recently collected examples in AWC from the Strait of Malacca are a deep greenish brown with very heavy callus and distinctive labial denticles and lirae (Figs 160, 164, 165) which certainly concur with the degree of circum-apertural thickening seen in the holotypes of both *M. praecallosa* Higgins, 1876 (Fig. 163) and *M. loebbeckeana* Weinkauff, 1878 (Figs 161, 162). Tomlin (1917) regarded these taxa to be junior synonyms of *C. strigata*, but the differences between *C. praecallosa* and *C. strigata* are clear;

1. the angulated and heavily denticulate inner labial bevel seen in *C. strigata* (Fig. 159) is replaced in *C. praecallosa* and *C. loebbeckeana* by a more gently sweeping, lirae-covered callus 'slope' which runs the entire length of the lip and ends as a denticulated ridge within the aperture (Figs 160, 161).
2. The plications in *C. strigata* are also a little more oblique than in *C. praecallosa*, and
3. the very thick anterior ventral callus in *C. praecallosa* which is only matched by that of *C. glauca*.

C. praecallosa and *C. loebbeckeana* should be regarded as conspecific, and *C. praecallosa* is the valid name of this species since its description predates that of *C. loebbeckeana*.

Cryptospira glauca Jousseaume, 1875
Figs 120, 166-178

Cryptospira glauca, Jousseaume, 1875, Rev. Mag. Zool., p. 234-235, pl. 8, f.1,
(non-*Marginella glauca* G. Fischer, 1807 = *Bullata bullata*, Born, 1778).

Type material. 1 lot of 1 sh., conserved dry, Syntype, 24 x 15.5 mm, locality unknown, (Figs 170, 171), MNHN.

Other material. Rameswarem, India, 6 spm., 25.0 x 16.1 mm, 25.9 x 16.8 mm, 25.8 x 17.1 mm, 28.0 x 17.8 mm, 23.1 x 15.3 mm, 22.5 x 14.9 mm, (Figs 166-169, 173-176), AWC; 2 spm., 21.35 mm & 22.0 mm, FBC.
Pondicherry, 22.0 mm, BM(NH).

Madras, Tamilnadu, India, 2 spm., 23.8 mm & 24.0 mm, trawled in 10 fathoms on muddy sand, FBC; 1 spm., 25.9 mm, trawled in 20 fathoms on muddy sand, FBC; 4 spm., 23.5 x 15.9 mm, 23.8 x 15.3 mm (Fig. 177), 23.1 x 15.5 mm, 24.1 x 15.4 mm, trawled, AWC.

Type locality. Originally unknown. Designated as Singapore (Coomans, 1969). Herein redesignated as Chennai (Madras), India.

Distribution. Bay of Bengal – northeast Sri Lanka and along the eastern coast of India.

Descriptive notes. Shell medium sized (L = 21 - 28 mm, W:L = 63.5 to 66 %). smooth, glossy, solid. Shape variable; ovate, obovate, subtriangular. Colour an even pale bluish to greenish - grey. Labial margin same as base colour at the deep marginal groove, fading to pale cream at the labial border. Inner labial surface finely denticulated with 30 or so irregular denticles, strongest in middle third. Aperture slightly wider than labial margin, more or less straight, not widening to any extent anteriorly.
Spire of 3.5 whorls not including protoconch, moderately elevated, brownish. Suture only distinct on last adult whorl, and white coloured. Posterior end of inner lip narrowing only slightly, and slightly bevelled on inner surface extending to apical level.
Columella with five plications, occupying 2/3 of aperture. First three oblique; first weak and close to stronger second. Opaque white basal callus in region of terminus of first three plications, extending strongly up the anterior ab-apertural shell surface. Posterior labial insertion callused to level of edge of the protoconch. Third plication strongest and longest. Fourth and fifth reducing in strength and becoming more horizontal.

Remarks. Tomlin (1917) noted incorrectly that *C. loebbeckeana* and *C. glauca* were one and the same, which may account for current specimens often being labelled *C. glauca loebbeckeana*. *C. loebbeckeana* has been shown herein to be a synonym of *C. praecallosa,* a close relative of *C. strigata.*
The main character with which *C. glauca* can be reliably separated from *C. marchii* is the anterior ab-apertural callus which is always present in *C. glauca* (Figs 120, 172) and always absent in *C. marchii* (Figs 121, 185). Secondary charcters are size differences (*C. glauca* does not exceed 28 mm whereas *C. marchii* regularly does), and labial morphology (the inner lip of *C. glauca* is always denticulate whilst that of *C. marchii* is usually smooth). The locality data, if to be relied upon, is also a giveaway as the ranges do not overlap; any Bay of Bengal / Indian locality will be *C. glauca*, whereas any Andaman Sea / Burmese / Thailand / Malaysian locality will always be *C. marchii*.

Cryptospira marchii Jousseaume, 1875
Figs 121, 180 - 198

?*Marginella Burchardi* Reeve, 1864, pl. 2, f. 3a,b. (non *M. burchardi* Dunker, 1852).
Marginella elegans var. Sowerby 1846, pl. 77, fig. 149.
Cryptospira marchii Jousseaume, 1875, 3(3), p. 235-236.

Type Material. *Marginella Burchardi* Reeve, 1864 (Label; Nicobar Is., annotated "*strigata* Dillwyn"), 3 spm., preserved dry, syntypes, 31.9 x 19.1 mm (Fig. 186), 31.9 x 18.7 mm, 31.7 x 19.0 mm, BM(NH) Reg. No. 1989146.
Cryptospira marchii Jousseaume, 1875. 1 lot of 1 spm., preserved dry, Malacca, Syntype, 20.4mm, (Fig. 192), MNHN.

Other material. Southern Thailand, Andaman Sea, Ranong Province, Bang-Kin to Nang-Yon, 4 spm., pale grey form, 25.3 mm – 31.3 mm, taken by prawn and sea cucumber trawlers in 5-15 metres on muddy sand, SPC; Satun Province, N'gu, 25 spm., 28.0 mm - 34.0 mm (Figs 180-185, 187-191, 193-198), AWC.

Type locality. Malacca

Distribution. Andaman Sea from the Mergui Archipelago (Burma), west Thailand, Straits of Malacca (Sumatra and peninsular Malaysia) to the islands of the Karimata Strait.

Habitat. 5-15 metres on muddy sand.

Descriptive notes. Shell medium sized (L= 20-40 mm, W:L ratio 56-65%), light, thin, glossy, plain bluish grey or cream, Shape variable; ovate, obovate, elongate ovate and subtriangular. Labial margin darker externally, fading to opaque white at its edges and internal surface. Inner labial surface smooth, rarely finely denticulated with approximately 30 denticles or undulations, and either straight, to slightly inflexed at its mid-point. Spire low to moderately elevated, of 3.5 whorls including the protoconch, suture visible as an opaque white line. Aperture wide (2-3 times as wide as lip thickness). Columella occupying 2/3 of apertural length, with five oblique plications; 1st very thin, 2nd and 3rd increasing in strength, 4th and 5th weakening again, and remaining relatively oblique. Parietal lira and callus always absent. Weak to moderate anterior ventral callus extending to between the third and fourth plications, its edge being well demarcated by a ridge extending from between these two plications, which passes round to join up with the edge of the varix adjacent to the varix groove.

Remarks. The syntypes of *M. Burchardi* are labelled as coming from Nicobar Is., a good locality for the species, but Reeve (1864) cites Ceylon and E. Africa

as the type locality. Specimens so labelled are not present in the collection at the BM(NH), (K. Way label, 1989, and subsequent searching by the first author). As *M. Burchardi* Reeve, was a preoccupied name, Jousseaumes name is the valid one for this species.
The raised ridge between the third and fourth plication, bordering the weak anterior ventral callus is strongly evident in this very variable species, and it is easily distinguishable from *C. glauca*, a species with which it is frequently confused, by its lack of both anterior ab-apertural callus and labial denticles.

Cryptospira grisea Jousseaume, 1875
Figs 199 - 205

Marginella obtusa Sowerby, 1870
Persicula grisea Jousseaume, 1875, 3(3):268 (*nomen novum* for *M. obtusa*, Sowerby, 1870, non-Sowerby, 1846).
Marginella sexplicata Weinkauff, 1879, p. 85, 86, Taf. 16, figs 6, 7.

Type material. Gulf of Martaban, 1 ad sh, 24.0 x 14.9 mm, holotype of *M. obtusa* Sowerby, 1870, BM(NH) Reg. No. 1874.12.11.93, ex. Mrs J. Lombe-Taylor coll., Indian Museum, (Figs 199, 205).

Other material. 2 spm., Locality unknown, 21.2 x 13.4mm, 19.7 x 12.4mm, AWC (Figs 201-205).

Type locality. Gulf of Martaban (Burma). The name 'Pegu' is written on the original label, although this is 80km inland.

Distribution. Unknown. Possibly restricted to Burmese waters.

Descriptive notes. Shell medium sized (L=19.7-24.0 mm, W:L ratio 60 – 62 %). Shell ovate, solid, thick, uniformly pale cream. Shoulder very rounded, shell tending towards pyriform, tapering to a more pointed anterior end. Spire very low, of 3.5 whorls, with raised crest at suture of last adult whorl only, forming a callus ring on the top of the spire. Labial margin thick, same colour as rest of shell. Thinning lip sharply angled in lateral view at posterior end creating a deep posterior notch (Fig. 205). Aperture evenly narrow, widening very little anteriorly. Inner labial margin with up to 30 small denticles which reach to edge of labial margin and along a ridge internally. Columella with five plications and always an obvious parietal lira mimicking a 6th plication. First plication thin and weak, second to third stronger, flat topped, fourth and fifth getting weaker. Parietal lira posterior to fifth plication but not remote from it. Only callus deposition parietally at posterior labial insertion, and no callus at the rather pointed base of the columella.

Remarks. Since Sowerby's name was preoccupied, Jousseaume was perfectly entitled to rename this species. Under either name it has always been poorly known because until now, as far as I am aware, the only known specimen has been the holotype of *M. obtusa*. The two examples of this species in the authors collection match the morphology of the holotype of *M. obtusa* perfectly, and confirm that *C. grisea* is indeed a valid species and that the holotype is not simply a malformed shell of another species. The distinctive shell characters include a uniformly narrow aperture, five very strong, flat topped plications and a smaller parietal lira mimicking a 6th plication. The raised, circular beading of callus present at the suture (Fig. 205) is very obvious and diagnostic. The morphology of the posterior end of the lip is unlike any other '*elegans*' group species in that its edge thins noticeably, and from a lateral view, the posterior end of the lip is sharply angled apically (Fig. 205) unlike the more sweeping profiles seen in other members of the genus, and this helps to create the characteristic deep posterior notch.

Cryptospira scripta (Hinds, 1844)
Figs 132, 206 - 217

Marginella scripta Hinds, 1844, Proc. Lond. Zool. Soc., p. 73; Hinds, 1844, Moll. Voyage Sulphur, p. 45, pl. 13, figs 16, 17.
Sowerby, 1846, Thes Conch., i, pl. 75, figs 83-85.
Chenu, 1859, Manuel de Conch., i, p. 197, fig. 1037.
Reeve, 1865, Conch. Icon., pl. 14, fig. 58.

Type material. Makassar Strait, 1 lot of 5 spm preserved dry, 6.6 mm, 6.6 mm, 6.5 mm (Figs 212, 213), 6.0 mm, & 5.6 mm, & 1 juv., 4.2mm, syntypes (cab. Belcher), BM(NH) Reg. No. 1844.6.7.44-48.

Other material examined. Malaysia, 1 spm, 5.75 mm, FBC.
Andaman Is, Port Blair, 12 spm, 8.6 - 10.6 mm, FBC.
Andaman Is, 70 spm (Figs 202-211), BM(NH) Reg. No. 1901.7.11.39
Malacca Strait, 6 spm, 5.0 - 8.7 mm (Figs 214-217), BM(NH).
Malacca Strait, numerous spm, 5.0 mm - 6.0 mm, MCM.

Type locality. 'Straits of Macassar' (Makassar Strait), Indonesia.

Distribution. An apparently fragmented distribution from the Makassar Strait, through the Strait of Malacca and on to the Andaman and Nicobar Islands.

Habitat. Originally recorded in the Makassar Strait as being found on coarse sand in 11-15 fathoms.

Descriptive notes. Shell small (L= 5-11 mm, W:L ratio 60 – 81 %), solid, smooth, glossy, stocky, ovate to obovate. Colour opaque white to cream, strong axial pattern of dark brown wavy lines. Rounded arrowheads pointing away from the aperture bearing thicker, darker markings in three zones, shoulder, midbody and anteriorly. The pattern can be regular or disorganised. Spire flat to elevated, 3 whorls, protoconch rounded, glazed over, suture indistinct. Labial margin thickened externally and internally, cream to white. Inner labial surface slightly rippled to strongly denticulate. Lip with 20-25 irregular denticles, strongest in middle third of lip, becoming progressively weaker posteriorly and anteriorly. Five columellar plications, occupying 2/3 of aperture; 1st weak and thin, 2nd strong, oblique and very close to 1st. 3rd strongest and much less obliquely positioned. 4th and 5th progressively weakening and lying more horizontal. Occasionally a small denticle posterior to the 5th plication is present. Aperture narrow, widening slightly anteriorly.

Remarks. Hinds' original description was published concurrently with that of *M. tricincta*, both being unfigured. Figures were published a month later in an account of the Zoology of the Voyage of HMS Sulphur 1836-1842. The type locality has to be regarded with caution as it is outside the normal range of distribution of '*Cryptospira elegans*' group species, and it is well known that locality records of Marginellids from both the Sulphur and the Samarang expeditions were often mixed up (Coovert, 1989a).
This is an unmistakeable little species, but when sufficient lots from different localities are examined, its variability becomes apparrent and it has to be conceded that several species may be concealed within the taxon. In Indonesian localities (Makassar and Malacca Straits) the shells are small (5.5 - 6.6 mm in length) and stocky. The shells from the Andaman Islands in the Indian Ocean are up to twice as large, more elongate, have a more rounded shoulder and generally a more depressed spire. The wavy axial lines can be thick and widely spaced or they can be fine and tightly grouped together. They may also be very regular or, somewhat haphazard in their orientation. In one particular specimen (Figs 210, 211) they are particularly fine and close together, and the shell morphology approaches that of small specimens of *C. strigata*, suggesting a close relationship to that species. Large numbers of specimens are present in most 19th Century European museum collections, but recently acquired specimens are decidedly rare. Occasional specimens are claimed as being sourced from Mauritius, but unless they have been transported there, this is unlikely as the marginellids of Mauritius are known to be more typical of an oceanic island fauna. Mauritius also lies on the Mascarene Ridge, outside the restricted distribution of the genus, which is confined to the Eurasian continental shelf.

Figures 206-217. ***Cryptospira elegans*** **group ctd.**

206-217. ***Cryptospira scripta*** (Hinds, 1844);
206, 207. Port Blair, Andaman Is, 9.75 x 6.55, AWC; **208, 209.** Port Blair, Andaman Is., 9.3 x 6.1 mm, AWC; **210, 211.** Andaman Is., 10.7 x 6.5 mm, BMNH; **212, 213.** Syntype, Makassar, 6.5 x 4.3 mm, BM(NH) Reg. no. 1844.6.7.44-48; **214, 215.** Strait of Malacca, 6.5 x 4.5 mm (MCM); **216, 217.** Strait of Malacca, 8.75 x 5.7 mm, BM(NH).

Cryptospira bridgettae n. sp.
Figs 145, 146, 218-222

Type material. Thailand, Ranong Province, Bang-Rin to Nang Yon, 5-15 m muddy sand, by prawn and sea cucumber trawlers.
1 ad spm., holotype, 20.05 x 12.58 mm, BM(NH) Reg. No. 20100327, (Figs 145, 146, 218-220).
1 ad spm., paratype, 17.57 x 11.08 mm, Reg. No. NMW.Z.2010.011.00001, (Figs 221, 222).

Type locality. Ranong Province, Thailand (Andaman Sea).

Distribution. Bang-Rin to Nang Yon, Ranong Province, Thailand

Description. Holotype small (L=20.0 mm, W:L = 63%), moderately thick, rounded subtriangular, tapering to rounded columella base. Colour of body whorl pale grey with occasional very fine opaque white axial growth marks, Clear spiral pattern of 21 darkr blue-grey regularly spaced narrow lines, some 2-3 times as wide as the narrowest but not organised at any particular position on the body whorl. On ventral surface pattern stops just posterior to third plication. Lip and base of columella and placations and protoconch opaque white. Spire moderately elevated, callus-free, of 3.5 whorls including protoconch. Shoulder smooth, rounded. Posteriorly, aperture as wide as lip, flaring only slightly anteriorly. Lip thickened externally as a single varix with a smooth rolled edge. Internal aspect of lip with 25-30 irregular denticles, strongest in posterior 2/3, weakening rapidly in anterior 1/3. External varix groove present. Anterior notch absent, posterior notch weak. Lip extending to and inserting at shoulder, just below apex. Columella with 5 plications occupying anterior 2/3 of aperture; first and second oblique, close together, moderately strong. Third strongest and less oblique, longer than the first two, slightly square edged. Fourth and fifth becoming more perpendicular to axis, and slightly square-edged. Fifth thinner, weaker and shorter than the fourth. Modcrate basal callus. Parietal surface posterior to placations is smooth and parietal callus is very weak.

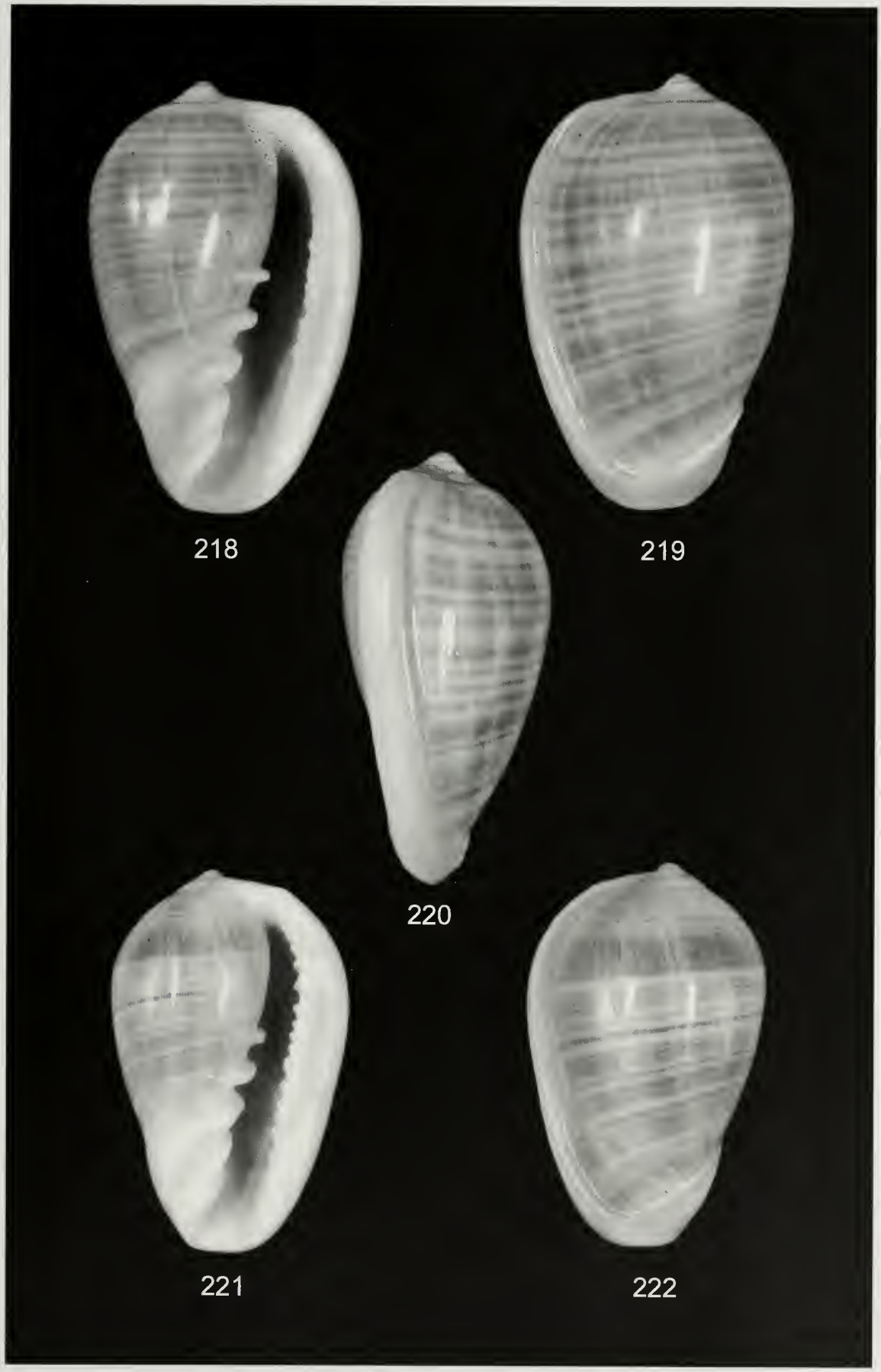
Remarks. This very distinctive, beautiful small species is closely related to *C. elegans* and can be easily distinguished from that species by virtue of its relatively small size, the pure opaque white and heavily denticulated lip, and the absence of a posterior parietal denticle. It is rare, known only from the two type specimens and is named in honour of Bridget Wakefield, wife of the author.

(D) THE INDONESIAN CRYPTOSPIRA FOSSIL RECORD

Beginning with the Pleistocene period (from approx. 2 million years to about 10,000 years ago) the global climate tended towards glacial. This was characterised by a generally drier climate than we experience now, with much of the worlds water being locked up in vast ice sheets extending from the poles and reaching as far as the tropics, including the Malaysian and Indonesian region. During these glaciations, Kalimantan, Sumatra, Java, Bali and Peninsular Malaysia were all connected into one large continental landmass, either icebound or as dry savannah punctuated by huge river systems, and Kalimantan was connected to the Philippines by a narrow strip of land, now Palawan. The fact that we are able to discover fossils of *Cryptospira* at inland sites in Java and Sumatra indicates that at other times during the Pleistocene (and even earlier in the Pliocene 2-5 MYA) these areas were submerged. Vertical tectonic plate movements partially explain this, but a more important contribution was made by climatic events. In fact, during the Pleistocene, sea levels rose and fell a total of 25 times between glacial and interglacial periods. Alluvial sediments from the giant river systems rapidly buried dead shells and created ideal conditions for their preservation in the fossilized state, with some specimens even retaining their colour patterns. As a result, the late tertiary / early quaternary fossil record of the genus in Indonesia is rich and remarkably complete. It is even possible to discover *Cryptospira* species that have long since gone extinct, telling us that the genus was probably even more diverse during this period than it is today.

Figures 218-222. *Cryptospira elegans* group ctd.

218-222. ***Cryptospira bridgettae*** n. sp.;
218-220. Holotype, 20.05 x 12.58 mm, BM(NH) Reg. no. 20100327; **221-222.** Paratype, 17.57 x 11.08 mm, Reg. no. NMW.Z.2010.011.00001.


218
219
220
221
222

The principal sites for fossil *Cryptospira* are at Sangiran in central Java, and Pasir Ipis and Cimanceurih in west Java, although fossil shells are also found on beaches facing the Indian Ocean at Suka Hujan, as a result of coastal erosion. It is relatively straightforward to associate species of living *Cryptospira* with their ancestral forms as revealed by their late Pliocene and Pleistocene fossils. A total of 12 fossil *Cryptospira* taxa have now been listed, including the two new species described herein. They can all be allocated to each of the three species groups defined earlier. As far as the recent taxon *C. tricincta* (of authors) is concerned, in it's fossil state we can assemble a complex of four non-intergrading morphologies, reinforcing the multiple species concept of that taxon promoted earlier, and demonstrating that the separation into the various morphospecies took place well before the Pliocene period, 3-5 MYA. The '*Cryptospira tricincta*' and '*Cryptospira ventricosa*' groups, having their centres of distribution in Indonesia, are unsurprisingly the ones most frequently encountered in the Tertiary strata of Java.

Fossils of the '*Cryptospira tricincta*' group

'*Cryptospira tricincta*' group fossils are commonly found in late Pliocene strata at Sangiran in central Java. When studied in quantity, series of four distinctly different and non-intergrading morphologies are observed. The first three of these are;

(i) The typical three-banded form.

(ii) A narrow, thick-shelled, more callused form with a narrow aperture and a broad columella base, with faint spiral banding evident in well preserved specimens. This form was given the name *C. quinqueplicata* var. *minor* Martin, 1931 but Oostinghe (1938-1939) later relegated it to the synonymy of *C. tricincta*, Hinds.

(iii) A large, ovate, thin shelled, inflated form with a wide aperture.

Material examined

C. tricincta, Form (i), 1 lot:
5 ad. sh. examined from Sambung Macan, Sangiran, central Java, late Pliocene. Largest 17.51 x 11.43 mm, smallest 15.75 x 10.64 mm, average W:L = 65 %, (Figs 233-236).

C. cf. C tricincta Form (ii), 2 lots:
16 ad. sh. studied from Sangiran, central Java, late Pliocene, Largest 20.06 x 11.25 mm, smallest 17.09 x 9.67 mm, average W:L = 54% (Figs 241-243).
8 ad. sh, Sambung Macan, central Java, late Pliocene, Largest 19.47 x 11.35 mm, smallest 16.55 x 10.31 mm, average W:L = 60% (Figs 244-248).

C. cf. C tricincta Form (iii) 2 lots:
10 ad. sh from Sangiran , central Java, late Pliocene, largest 30.61 x 17.93 mm, smallest 24.52 x 13.43 mm, average W:L = 57%, (Figs 251-253).
4 ad. sh. Sambung Macan, Sangiran, late Pliocene, largest 30.44 x 17.78 mm, smallest 26.72 x 16.45 mm, average W:L = 60% (Figs 249-250).

Comments. No intergrades between these morphologies have been found - they are always easily separable, and perhaps all three could be considered as different (morpho) species. While it is, of course, not possible to state with total confidence the ancestral relationship of living species to fossil forms, it seems reasonable from morphologic comparison to conclude that form (i) is analogous to typical *C. tricincta*. Form (ii) could be analogous to the dwarf, narrow *Cryptospira cf. C. tricincta*, like those dredged in the Makassar Strait (Figs 21, 22), or to *C. wallacei* (Figs 34-37) although the parietal denticle between the fifth and sixth plications in that species are not present in the fossil. The distinctive giant ovate Form (iii) is not uncommon as a fossil, but seems to be scarce in the present. I am only aware of a single recent example in BM(NH), (Fig. 17) and a juvenile specimen recorded from deep water in the Makassar Strait by the CORINDON expedition (MNHN). The ability of these non-intergrading fossil forms to reflect almost identical present day forms suggests that the evolutionary splitting from an ancestral 'tricincta' form(s) occurred at least as long as 3-5MYA, and very possibly longer, and lends weight to the multiple species complex argument for *C. tricincta.*
A fourth, very distinctive form has recently been discovered (Figs 223-232). It is small, ovate, has a thick shell with very strong plications and a strong, open, regular axial pattern. Due to its morphologic originality and its pattern, it is herein named *C. bundharmai* n. sp. It is considered to now be extinct.
C. cloveriana has not been seen as a fossil. This is not unexpected as it has a more north-easterly distribution.

Fossils of the *Cryptospira ventricosa* group

The fossils of the *Cryptospira ventricosa* group are represented by the following taxa;

†*C. ventricosa* G. Fischer von Waldheim, 1807 (typical form)
†*C. ventricosa* var. *minor* Martin, 1895 (dwarf form)
†*C. sangiranenesis* Martin, 1906 (a distinct and valid species, extinct since the Pleistocene)
†*C. trailii* Reeve, 1865 (listed as a form of *C sangiranensis* Martin, 1938) in Oostinghe, 1938
†*C. dactylus* var. *minor* Pannekoek, 1936
†*C. dactylus* var. *inflata* Martin, 1895

Material examined

C. ventricosa G. Fischer von Waldheim, 1807 (typical form), 1 lot;
7 ad. sh. from Pasir Ipis, west Java, Middle Pliocene, 7 ad. sh., largest 38.25 x 25.89 mm, smallest 26.17 x 18.44 mm, average W:L = 66 %, AWC (Figs 258, 259).

C. ventricosa var. *minor* Martin, 1895 (dwarf form), 1 lot;
3 ad. sh. from Pasir Ipis, west Java, middle Pliocene, 23.96 x 16.28 mm, 22.71 x 14.84 mm, 20.37 x 13.44 mm, AWC.

C. sangiranenesis Martin, 1906. 3 lots:
11 ad. sh. from Pasir Ipis, west Java, middle Pliocene, largest 19.05 x 10.33 mm, smallest 12.38 x 7.29 mm, average W:L = 56%, AWC (Figs 260, 261).
4 ad. sh. from Cimanceurih, west Java, Pliocene, largest 15.82 x 10.22 mm, smallest 11.1 x 7.07 mm, W:L = 64%, AWC.
7 beach worn ad. sh. from Suka Hujan, west Java, largest 16.91 x 10.80 mm, smallest 10.34 x 7.05 mm, AWC.

C. dactylus var. *minor* Pannekoek, 1936. 2 lots:
8 ad. sh. from Pasir Ipis, west Java, middle Pliocene, largest 30.14 x 14.74 mm, smallest 20.04 x 9.53 mm, average W:L = 48%, AWC.
3 ad. sh. from Sambung Macan, Sangiran, central Java, late Pliocene, 23.96 x 11.54 mm, 32.78 x 16.55 mm, 33.00 x 15.44 mm, average W:L = 49%, (Figs 254, 255), AWC.

C. dactylus var. *inflata* Martin, 1895. 3 lots:
1 ad. sh. from Pasir Ipis, west Java, middle Pliocene, 39.71 x 18.90 mm, AWC.
2 sh. from Sambung Macan, Sangiran, central Java, late Pliocene, 52.79 x 24.91 mm (Fig. 257), 44.54 x 20.61 mm (juv.), AWC.
5 ad. sh. from Sangiran, central Java, late Pliocene, largest 41.18 x 22.33 mm, (Fig. 256), smallest 33.65 x 17.65 mm, average W:L = 53%, AWC.

Comments. All the various shell morphologies of recent specimens of *C. ventricosa* are found at Pasir Ipis in the middle Pliocene fossil record of West Java (Figs 258, 259). An evolutionary tendency for an overall reduction in the thickness of parietal callus deposits and in the thickness of the shell itself has been reported (Dharma, 2005). Martin (1895), described a dwarf form, *C. v. minor*, from the younger Tertiary of Java, and it is also known from Sumatra and Kalimantan (Oostingh, 1935:96-98).
C. sangiranenesis Martin, 1906 is a commonly occurring fossil from this group, although this species appears to have gone extinct (Figs 260, 261). The highly angular shoulder and extended posterior labrum are its distinctive features, and in this respect it resembles *C. trailii* and narrow *C. ventricosa*. It is possible that it is a precursor to the recent *C. trailii* although the latter has made its own appearance as a fossil in the literature. It was figured by Oostinghe (1938-39, pl. 8, figs 154 a, b), but was recorded by him as a form of *M. (C.) ventricosa sangiranensis* Martin, 1906. Clearly the two species are very close, but *C. sangiranensis* attains a much larger size and is broader.
Although only represented in the recent as a single species, there are two fossil morphologies making up a *C. dactylus* complex, and these are found at two different sites in Java. The middle Pliocene deposits of Pasir Ipis and the late Pliocene of Sangiran contain a large form (35 to 52mm in length) which has a wide aperture, often a very strong parietal callus pad, and a much more tapering shell (Figs 256, 257). This form was given the varietal name '*inflata*' by Martin (1895), but is so different to recent *C. dactylus* that it was probably a distinct species in its own right. It has not been collected in the recent and is probably extinct. Both sites also contain a smaller form which has a relatively narrow aperture, proportionally thicker lip, more cylindrical shell, and no parietal callus (Figs 254, 255). It was figured by Pannekoek (1936) as *C. dactylus* var. *minor* and is morphologically indistinguishable from the extant *C. dactylus*.

Fossils of the *Cryptospira elegans* group

The *Cryptospira elegans* group has only the eastern fringe of its recent distribution in Indonesia and therefore is not as well represented in the fossil record. In fact, to date there are only three published examples from Java;

'*Marginella* (*Cryptospira*) *ex aff. elegans*' (Oostinghe, 1938).
'*Marginella* (*Cryptospira*) *aff. loebbeckeana*' (Oostinghe, 1938)
Marginella birmanica Vredenburg, 1923 (apparently extinct)

A new fossil species of the '*Cryptospira elegans*' group has been found in late Pliocene deposits at Kemukus, Sangiran, Central Java. It appears to be closely related to *C. strigata*, and is described and named herein as *C. kemukusi* n. sp.
Sub-fossil *C. elegans* and *C. marchii* are brought up by tin dredging vessels working off Chalong Bay, Phuket, Thailand (Somwang Patamakanthin, pers. comm.).

† ***Cryptospira bundharmai*** n. sp.
Figs 223 – 232, 268-277

Type material. Holotype, central Java, Sangiran, Sumber Lawang, late Pliocene, 1 ad. sh., 13.44 x 8.68 mm, (Figs 225, 226, 268, 269), MGB 0000548.

Paratype 1, central Java, Sangiran, Kemukus, late Pliocene, 1 ad. sh, 13.01 x 8.83 mm, (Figs 229, 230), MZB Fos. 0056.
Paratype 2, central Java, Sangiran, Sumber Lawang, late Pliocene, 1 ad. sh., 17.36 x 11.38 mm, (Figs 223, 224, 270, 271), BDC.
Paratype 3, central Java, Sangiran, Kemukus, late Pliocene,1 ad. sh., 13.75 x 8.80 mm, (Figs 227, 228, 272, 273), AWC.
Paratype 4, central Java, Sangiran, Kemukus, late Pliocene,1 ad. sh., 14.63 x 9.77 mm, AWC.
Paratype 5, central Java, Sangiran, Kemukus, late Pliocene,1 ad. sh., 13.98 x 9.33 mm, (Figs 231, 232, 276, 277), AWC.

Other material. Central Java, Sangiran, Kemukus, 5 ad. sh., 18.3 x 12.1 mm, 17.5 x 11.4 mm, 13.9 x 9.4 mm, 15.0 x 10.0 mm, 14.1 x 9.5 mm, collected May 2000.
Central Java, Sangiran, 4 ad. sh., 15.02 x 10.03 mm, 14.39 x 10.46 mm, 18.17 x 11.36 mm, 15.33 x 10.92 mm, and 3 fragments, collected October 2000, AWC.

Type locality. Sumber Lawang, Sangiran, central Java.

Distribution. Only known from Sumber Lawang and Kemukus, Sangiran, central Java.

Description. Holotype small (L = 13.44 mm, W:L = 65%), moderately thick, heavy, ovoid, inflated, tapering to base of columella. Colour pale tan, with axial pattern of brown, equally and widely spaced, straight to slightly undulating lines, numbering 13 on the body whorl, and which follow previous growing edge of shell. Lip and columella cream coloured. Spire involute, immersed in callus. Shoulder smooth, rounded. Aperture very curved, posteriorly as wide as labial varix, only widening slightly anteriorly, extending to level of posterior end of the shell. Lip thickened externally as a single varix with a smooth rolled edge, internal aspect smooth, lacking denticles. External varix groove present. Anterior notch absent, posterior notch weak. Lip inserts to top of spire. Columella with six strong square-cresteded and very emergent plications, occupying 2/3 of aperture. First two oblique, second to sixth increasingly perpendicular to long axis. Anterior ventral callus in region of first four plications merges with thick parietal callus which extends over all of the parietal surface to the labial insertion.

Remarks. The very oval shape, strong plications and above all the strong axial pattern will distinguish this species from most specimens of fossil *C. tricincta*. It is named after Bunjamin Dharma, renowned author and expert on Indonesian mollusca, and discoverer of this species.

Figures 223-261. Indonesian Pliocene and Pleistocene fossil *Cryptospira*.

223-232. †***C. bundharmai*** n. sp., Sumber Lawang, Sangiran, central Java, late Pliocene; **223-224.** Paratype 2, 17.3 x 11.3 mm, BDC; **225-226.** Holotype, 13.4 x 8.6 mm, reg. no. MGB 0000548; **227-228.** Paratype 3, 13.7 x 8.8 mm, AWC; **229-230.** Paratype 1, 13.0 x 8.8 mm, reg. no. MZB Fos. 0056; **231-232.** Paratype 5, 13.9 x 9.3 mm, AWC.

233-236. †***C. tricincta*** form (i), Sambung Macan, Sangiran, central Java, Late Pliocene;
233-234. 16.1 x 10.8 mm, AWC; **235-236.** 16.4 x 10.9 mm, AWC.

237-240. †***C. kemukusi*** n. sp., Kemukus, Sangiran, Central Java, Late Pliocene;
237-238. Paratype 2, 17.3 x 11.3 mm, BDC; **239-240.** Holotype, 13.6 x 8.0 mm, reg. no. MGB 0000549.

241-248. †***C. tricincta*** form (ii);
241-243. Sangiran, central Java, late Pliocene, 17.5 – 19.5 mm, AWC; **244-248.** Sambung Macan, Sangiran, central Java, late Pliocene, 19.6 – 17.0 mm, AWC.

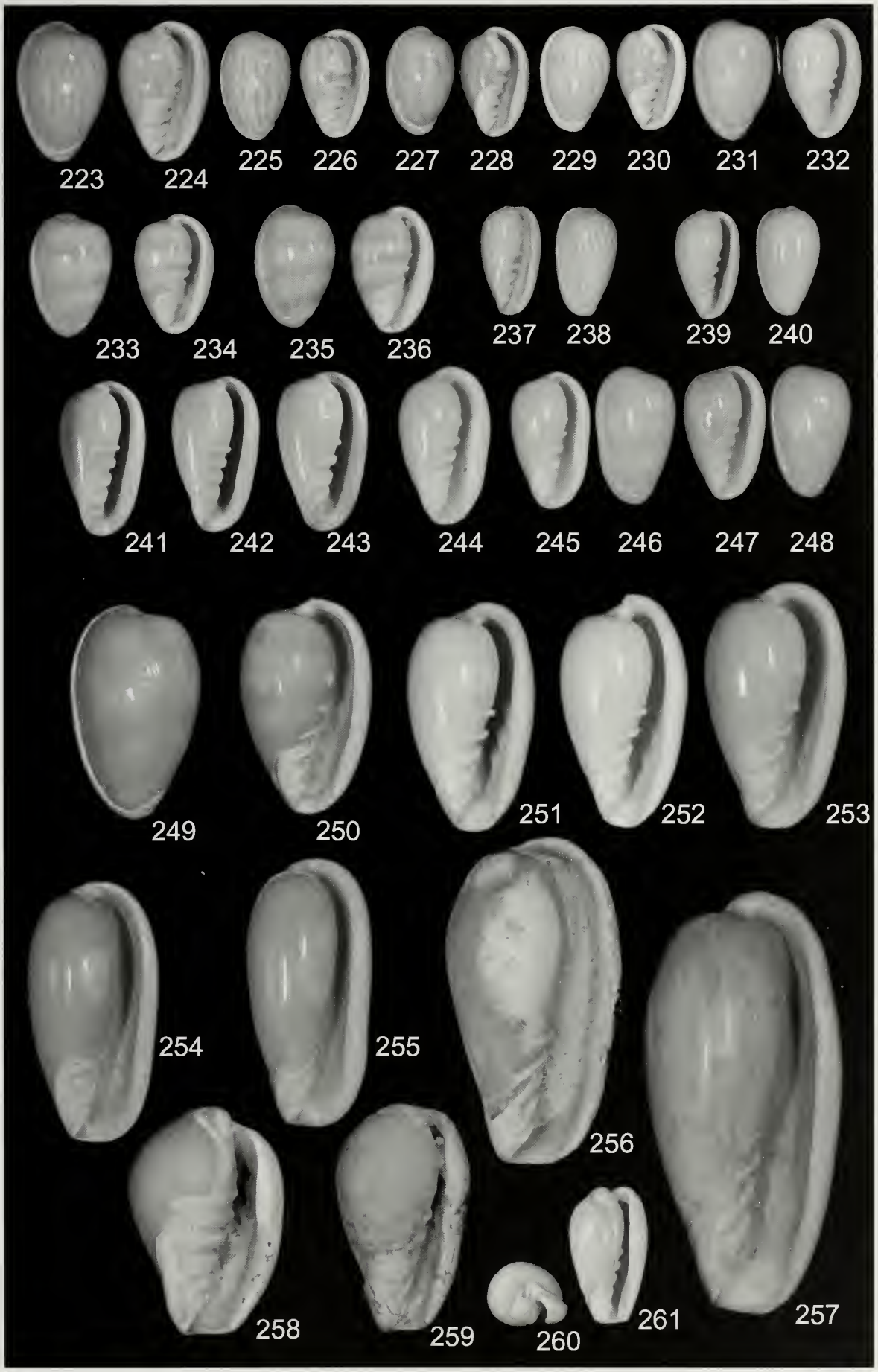
249-253. †***C. tricincta*** form (iii);
249-250. Sambung Macan, Sangiran, late Pliocene, 26.6 x 16.5 mm, AWC; **251-253.** Sangiran, central Java, late Pliocene, 30.0 x 18.2 mm, 30.5 x 17.9 mm, 30.61 x 18.0 mm, AWC.

254-255. †***C. dactylus* var. *minor*** Pannekoek, 1936 (=*C. dactylus* Lamarck, 1822);
Sambung Macan, Sangiran, central Java, late Pliocene, 32.7 x 16.5 mm, 33.0 x 15.4 mm, AWC.

256-257. †***C. dactylus* var. *inflata*** Martin, 1895;
256. Sangiran, central Java, late Pliocene, 41.1 x 22.3 mm, AWC; **257.** Sambung Macan, Sangiran, central Java, late Pliocene, 52.7 x 24.9 mm, AWC.

258-259. †***C. ventricosa*** Fischer von Waldheim, 1807. Pasir Ipis, west Java, mid-Pleistocene;
258. 36.8 x 23.5 mm, AWC; **259.** 28.6 x 16.6 mm, AWC.

260-261. †***C. sangiranensis*** Martin, 1906. Pasir Ipis, west Java, mid-Pliocene, 17.0 x 9.8 mm, AWC.


223
224
225
226
227
228
229
230
231
232
233
234
235
236
237
238
239
240
241
242
243
244
245
246
247
248
249
250
251
252
253
254
255
256
257
258
259
260
261

† ***Cryptospira kemukusi*** n. sp.
Figs 237 – 240, 262-267

Type material. Central Java, Sangiran, Kemukus, 6 ad. sh., late Pliocene, Collected April 2009;
Holotype, 13.62 x 8.01 mm, (Figs 239, 240, 264, 265), MGB 0000549.
Paratype 1, 11.65 x 6.85 mm,(Figs 266, 267), MZB Fos. 0057.
Paratype 2, 13.37 x 7.52 mm, (Figs 237, 238, 262, 263), BDC
Paratype 3, 12.55 x 6.99 mm, BDC
Paratype 4, 12.12 x 7.12 mm, AWC
Paratype 5, 13.5 x 7.67 mm, BDC

Type locality. Kemukus, Sangiran, Central Java.

Distribution. Only known from the type locality.

Description. Holotype small (L = 13.6 mm, W:L = 59%), rather thin, light, narrow-ovate, tapering smoothly to base of columella. Colour pale cream, overlaid with 22 regular fine axial lines of darker colour on the body whorl. Spire exposed, slightly elevated, of 3.5 whorls including slightly raised protoconch. Aperture rather straight, of even width along its length, as wide as the labial varix. Lip thickened externally as a single varix with a smooth rolled edge, denticles absent. External varix groove present. Anterior notch absent, posterior notch weak. Lip extends to shoulder level, inserting at suture. Columella with six oblique plications; first two very close, all plications very thin, sixth diminutive. Parietal surface posterior to plications is smooth. Anterior ventral callus absent, anterior end rounded.

Remarks. The exposed spire, narrow elongated shape, oblique plications and fine axial pattern clearly places this species in the *Cryptospira elegans* group, and is most likely closely related to *C. strigata*, but differs from it in that it has an extra plication and a narrower aperture. It is named after the type locality, and is probably an extinct species.

DISCUSSION

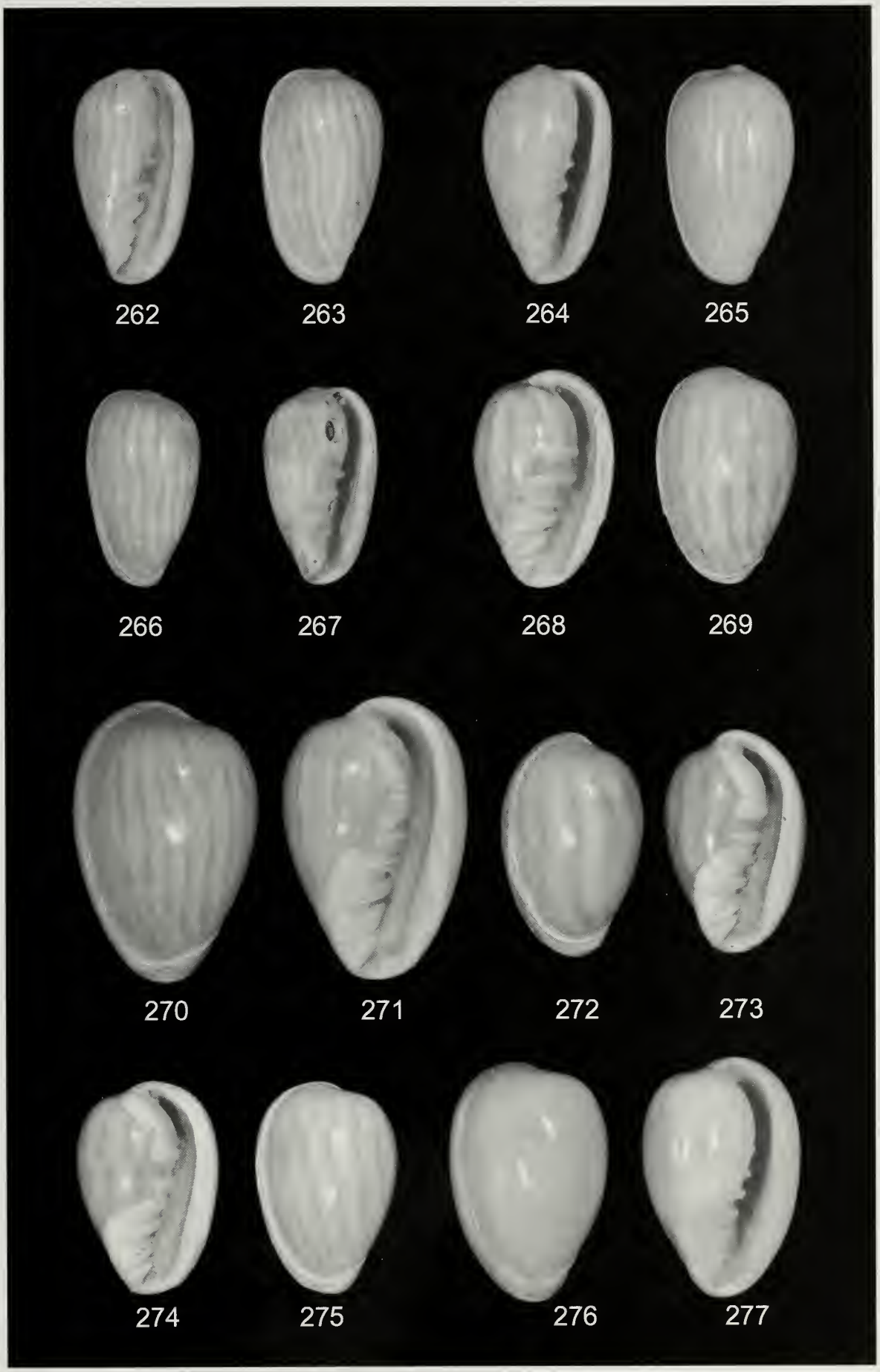
Phyletic Analysis

The radula morphologies of two *Cryptospira* species have been published. Coovert & Coovert (1990) extracted and examined the radulae of four specimens of *C. fischeri*, and Troeschel (1867) published a drawing of the radula of *C. elegans*. The rachidian plates of the radula of *Cryptospira* are wide, flat and 'comb-like' (Fig. 4) and resemble closely those of *Volvarina* and *Primum*. It is necessary to compare the relatively low numbers of cusps present (21-28 cusps per plate in *C. fischeri* and 9 cusps per plate in *C. elegans*) with the cusp counts of the radulae of the Marginellid subfamily Marginelloninae, which is suggested by Harasewych and Kantor (1991) to be the most primitive group in the Marginellidae: *Marginellona gigas* (Martens, 1904) has from 58-59 to 83-85 cusps, and *Afrivoluta pringlei* (Tomlin, 1947) has 70-80 (Coovert & Coovert (1995). From this, Boyer (2001) deduced a high number of radular cusps to be a plesiomorphic character in this type of uniserial modified rachiglossan radula. Though statistically a very small sample size, the *Cryptospira* radulae examined have a considerably smaller number of cusps than those of the Marginelloninae, and a tendency to a smaller number than that seen in the *Primum / Volvarina* complex. Further radular analyses across the range of *Cryptospira* species will be necessary before any concrete phylogenetic conclusions can be drawn, but if shown to be a consistent character, the relatively small cusp count could provide evidence to support the view that the genus split off relatively recently from the main *Primum / Volvarina* lineage, and much later than other genera such as *Serrata* and *Dentimargo* which evolved during the Eocene.
More observations about the evolutionary development of *Cryptospira* in southeast Asia can be made by looking for clues in the fossil record and by making appropriate comparisons with recent forms. The fossil record of the genus is restricted to the Indonesian archipelago (Sunda Shelf Zone) and is completely absent from other major marginellid fossil assemblages worldwide. No fossils have been discovered which could be regarded as intermediate in form between *Primum / Volvarina* and *Cryptospira* morphologies, and fossil species are very close morphologically to recent ones. From this we can infer that the genus evolved exclusively, rapidly and recently in the Sunda Shelf zone, approximately 3-5 million years ago.

Figures 262-277. New *Cryptospira tricincta* group late Pliocene fossil species;

262-267. †*C. kemukusi* n. sp., Kemukus, Sangiran, central Java, Late Pliocene; **262-263.** Paratype 2, 17.3 x 11.3 mm, BDC; **264-265.** Holotype, 13.6 x 8.0 mm, reg. no. MGB 0000549; **266-267.** Paratype 1, 11.6 x 6.8 mm, reg. no. MZB Fos. 0057.

268-277. †*C. bundharmai* n. sp., Sumber Lawang, Sangiran, central Java, late Pliocene;
268-269. Holotype, 13.4 x 8.6 mm, reg. no. MGB 0000548; **270-271.** Paratype 2, 17.3 x 11.3 mm, BDC;
272-273. Paratype 3, 13.7 x 8.8 mm, AWC; **274-275.** Paratype 1, 13.0 x 8.8 mm, reg. no. MZB Fos. 0056;
276-277. Paratype 5, 13.9 x 9.3 mm, AWC.


262
263
264
265
266
267
268
269
270
271
272
273
274
275
276
277

The shell characters of the genus are heterogenous with the range of morphologies and shell characters encountered in the *Primum / Volvarina* complex, and the basic radula pattern and external animal anatomy also indicate a close ancestral relationship. *Cryptospira* therefore can be regarded as an offshoot of the main *Primum / Volvarina* lineage. Although distribution of the genus now extends further than this, the Sunda Shelf remains the zone of maximum species diversity (both recent and fossil) and the place where there is overlap of all three of its species groups. The initial radiation away from the main *Primum* lineage is therefore likely to have begun here. The three distinct species groups subsequently launched adaptive radiations from this central zone, becoming the dominant marginellid genus of medium to large shelled species in the vast Indo-west Pacific geographical area, and probably forcing other marginellid genera into retreat. Representing other genera there are currently only two species of large sized marginellid in this geographic region; *Volvarina obscura* (Reeve, 1865) and the deep water relict species *Marginellona gigas* (Martens, 1904). Such disharmonious representation of the family would imply that the ancestral *Cryptospira* explosively radiated into the Sunda Shelf zone, rapidly evolving into new species to take advantage of available niches to the exclusion of others. The great speciation potential of the genus may have also been driven by the hydroclimatic disturbances occurring throughout the Pleistocene period. The pressure thus exerted upon older *Primum / Volvarina / Dentimargo* stocks may account for the disappearance in the recent of other medium - sized Indonesian fossil species such as *Marginella berberkiriana* (Martin, 1906) from the middle – Miocene, and may be a manifestation of the displacement of species from other genera by *Cryptospira* later coming to dominate their habitat. That dominance, so evident during the Pleistocene from the diversity of the fossil record may be on the wane in the recent. The fact that at least five fossil species have gone extinct since the Pleistocene, and the discovery of new fossil species and forms in the *Cryptospira tricincta* group that do not appear in the recent fauna could be telling us that the diversity of the genus was probably greater then than it is now. At least four fossil species have gone extinct (*C. sangiranenis, C. dactylus* var. *inflata, C. bmdharmai* and *C. kemnknsi*) and this could indicate that several *Cryptospira* lineages present in the Pleistocene are currently on the decline. For example, only one of the two *C. dactylus* forms present in the Pleistocene is extant, and the one remaining, *C. dactylus* of Lamarck, is uncommonly encountered. Another example is the extinction of one of the most common Pleistocene *Cryptospira* species, *C. sangiranensis*, leaving only the related and exceedingly rare species *C. trailii* as its closest relative. Falling diversity since the Pleistocene evident from these extinctions, coupled with the scarcity of some recent species which are common as fossils, may indicate that the genus has passed its adaptive potential and is currently in a state of gradual decline.

Biogeographic observations

Moving on from interpretations of the fossil record, it is necessary to examine the current biogeographic distribution of the genus, and to analyze the diversity of the species groups and sub-groups within it. Once the three *Cryptospira* groups were established and defined, individual species were allocated to their various groups and the resulting distributions were examined to check for continuity. In accordance with the 'Sarawak Law' of the English Biogeographer, Alfred Russel Wallace (1855), the species within each of the three groups were indeed found in patterns of continuous distribution, with the '*Cryptospira elegans*' group forming the most distinctive radiation and providing the supporting biogeographic evidence required for the exclusion of *M. mabellae* and *M. angustata* from the genus. Very closely related species, for example those forming sub-groups, were also found to occupy adjacent areas, as expected. The distribution maps of each group (Figs 5 - 8), show that there is a degree of central overlap in the region of the Java Sea. It appears that the three groups radiated outwards from here; the *Cryptospira elegans* group to the northwest along the Asian continental shelf towards India, the *Cryptospira tricincta* group to the northeast into Kalimantan, Palawan and the central Philippines, and the *Cryptospira ventricosa* group remaining, in the main, in the Java Sea but also extending north where it occurs sporadically in the South China Sea.

It is likely that the sea floor substrate of muddy sand provided a homogenous environment that allowed *Cryptospira* to easily disperse. The continuity of these shallow water substrates which lie on the continental shelf in the northeast Indian Ocean, from northern Thailand around the Bay of Bengal westwards to the eastern side of India and Sri Lanka, albeit punctuated by large river delta's, have allowed species of the *Cryptospira elegans* group to spread westward to these areas. In the same way, the continuity of habitat along the Asian mainland around the northern rim of the South China Sea has allowed several species from the *Cryptospira tricincta* group and the *Cryptospira ventricosa* group to disperse, with one species (*C. cloveriana*) reaching as far north as Taiwan. Elsewhere it is a different story. To the south and west of the Sunda Shelf the Indian Ocean coasts of Sumatra and Java are predominated by coral reefs and deep water, neither of which is favoured by *Cryptospira*. To the east of the central range lies the deep water of the Makassar Strait. Examples of *Cryptospira* from the ever insular Sulawesi, forming the eastern side of the Makassar Strait, do not appear to be available, although this would be important to check in any field study there. The Makassar Strait, coincides with the

mid-section of the Wallace line, the imaginary biogeographic boundary separating the Eurasian and Australinean faunas, and here the deep water does appear to present a formidable barrier to the eastern dispersal of *Cryptospira*, just as it does for mammals, birds, insects and freshwater fish. The Philippine island of Palawan is different in that in geological terms it is an offshore island of the Asian mainland, separated from Kalimantan by the Balabac Strait, a shallow channel 145m deep. Palawan is indeed a hotspot of *Cryptospira* diversity with at least 5 *Cryptospira tricincta* group species represented.

The southern section of the Wallace line passes between the islands of Lombok (Lesser Sunda's or Nusa Tenggara) and Bali (Indonesia), but this has had limited influence upon eastern dispersal of two species of *Cryptospira*; *C. ventricosa* occurs in Lombok (Dharma & Dunlap, 1994), and a population of *C. dactylus* has also recently been discovered there (B. Dharma, pers. comm.). *Cryptospira* has not been recorded further into Nusa Tenggara than Lombok and is not found in the Banda, Arafura or Timor Seas. Apart from this small incursion, the south- eastern edge of the range of distribution of *Cryptospira* in the shallow seas of Indonesia is demarcated by the Wallace line, and coincides with the edge of the Asian continental shelf, beyond which the marginellid fauna reverts to relatively small oceanic species from numerous other genera.

ACKNOWLEDGEMENTS

This project would not have been possible without the considerable support of Bunjamin Dharma (Indonesia), who provided me with much needed information and study material. Many other friends and colleagues also made a significant contribution; Franck Boyer (France), Phil Clover (USA), Gary Coovert (USA), Marcus Coltro (Brazil), Komson Hongpattharakeeree (Thailand), Roland Houart (Belgium), Felix Lorenz (Germany), Tony McCleery (UK), Alistair Moncur (UK), Somwang and Somnuek Patamakanthin (Thailand), and Andrew Tournier (France). To them all I extend my grateful thanks.

Thanks are also due for assistance given by professional Malacologists. Kathie Way and Amelia MacLellan (BMNH), Harriet Wood and Jennifer Gallichan (NMW), Virginie Héros & Philippe Bouchet (MNHN), Elina Sufiati (MGB), Ristiyanti Marwoto (MZB), Tiziano Cossignani (MMM), Dr. R. Preece (CMZ), Nora MacMillan (MCM) and Alexander Sysoev (ZMUM) allowed access to museum type material and literature. In particular, I am deeply indebted to Dr. Silke Stohl and Mr. Boscheinen of the Loebbecke Museum, Dusseldorf, Germany, for providing vital photographs of the holotype of *M. loebbeckeana*, to my two referee's who encouraged me to stick to the facts, and to Roland Houart for his editorial support and infinite patience.

REFERENCES

Adams, A. & Reeve, L. 1850. In 1848-1850. Mollusca, in A. Adams, *The Zoology of the Voyage of HMS Samarang; under the command of Captain Sir Edward Belcher during the years* 1843-1846. London.

Bavay, A. 1902. Description d'une espèce nouvelle du genre Marginella. *Journal de Conchyliologie* 50(4): 407-408.

Bernardi, A.C. 1852. Description d'une Marginelle nouvelle. *Journal de Conchyliologie* 3(1): 59-60, Pl. 2, figs 6, 7.

Boyer, F. 2001. Espèces nouvelles de Marginellidae du niveau bathyal de la Nouvelle-Caledonie. *Novapex* 2 (4): 157-169.

Clover, P. W. 1968. *Marginella ventricosa* G. Fischer, 1807. *Hawaiian Shell News* 16(5): 6

Clover, P. W. 1979. Philippine *Marginella*. *Of Sea and Shore.* 10(1): 59-60.

Clover, P. W. 1981. The Marginellas of Southeast Asia. *Conchologists of America Bulletin*, 24: 6-7.

Coan, E. V. 1965. A proposed reclassification of the family Marginellidae. *The Veliger* 7(3): 184-194.

Coovert, G. 1987. A literature review and summary of marginellid external anatomy. *Marginella Marginalia* 3: 2/3, 10.

Coovert, G.1989(a). The *Marginella musica – diadochus* Group. *Marginella Marginalia* 6 (3-5): 17.

Coovert, G., 1989(b). A literature review and summary of published Marginellid radulae. *Marginella Marginalia* 7 (1-6), 1-37.

Coovert, G. 1990. A study of Marginellid Radulae Part 1: Type 6 Radula, '*Prunum / Volvarina* type. *Marginella Marginalia* 8 (1-6) Jan-June 1990, & 9 (1-6) July-Dec 1990, pp. 1-68.

Coovert, G. A. & Coovert, H. K. 1995. Revision of the Supraspecific Classification of Marginelliform Gastropods. *The Nautilus* 109(2-3): 43-110.

Coomans, H.E. 1969. On the identity of *Cryptospira glauca* and the related *Cryptospira ventricosa* (Gastropoda: Marginellidae). *Basteria,* 33(5-6): 85-92.

Cossignani, T. 2006a. Marginellidae and Cystiscidae of the world. Atlas with over 2,600 photos. L'Informatore Piceno, Ancona, Italy: pp. 1 - 408.

Cossignani, T. 2006b. Due nuove Cryptospira dall'Indo-Pacifico (Gastropoda: Prosobranchia, Marginellidae). *Malacologia Mostra Mondiale* 51: 5,6.

Dance, S.P. 1986. *A History of Shell Collecting*. Pp. I-xv, 1-265, 32 pls. 17 text figs. E.J. Brill, Leiden.

Dharma, B. 2005. *Recent & Fossil Indonesian Shells*. Pp. 1-424, Publ. Conchbooks, Hackenheim, Germany and by the author, Jackarta, Indonesia. ISBN 3.92 5919-70-8

Dharma, B. & Dunlap, F. 1994. The variability of *Marginella ventricosa* in the Java Sea. *Hawaiian Shell News*. XLII(9): 7.

Dillwyn, L.W. 1817. *A descriptive catalogue of Recent shells arranged according to the Linnean method: with particular attention to the synonymy*. 1: 1-580. London, John & Arthur Arch.

Fischer (Von-Waldheim), G. 1807. *Museum Demidoff 3. Végétaux et Animaux*: I-IX, 1-330, Moscow.

Gaskoin, J. S. 1849. Descriptions of seven new species of *Marginella* and two of *Cypraea*. *Proceedings of the Zoological Society of London* 19: 17-23.

Gray, J. E. 1847. A list of the genera of Recent Mollusca, their synonyms and types. *Proceedings of the Zoological Society of London, 1847*. Pt 15, (17): 129-219 [Marginellidae: pp.142].

Harasewych M. G. & Kantor Y. 1991. Rediscovery of *Marginellona gigas* (Martens, 1904), with notes on the anatomy and systematic position of the subfamily Marginelloninae (Gastropoda: Marginellidae). *Nemouria* 37: 1 - 19.

Higgins, H. H., 1876, in Marrat F.P. 1876. Descriptions of five new marginellae. *Quarterly Journal of Conchology*, 1: 136.

Hinds, R.B. 1844a. Descriptions of Marginella collected during the voyage of HMS Sulphur, and from the collection of Mr. Cuming. *Proceedings of the Zoological Society of London*, Part 12 = Vol. 14: 72-77.

Hinds, R. B. 1844b, Oct. The zoology of the voyage of H.M.S. Sulphur, under the command of Captain Sir Edward Belcher...during1836-1842, 2 (2): 25-48, pls.8-14. London [Marginellidae: pp. 44-46, pl. 13].

Ivanov, D.L., Kantor, Y.I., Sysoev, A.V., & Egorov, R.V. 1991. Type Specimens of molluscs described by G. Fischer von Waldheim in 1807, *Apex* 8(3): 71-94.

Jousseaume, F. 1875. Coquilles de la famille des Marginelles. Monographie. *Revue et magasin de Zoologie Pure et Appliquée* 3(3): 164-271, 429-435, pls. 7-8.

Kaicher, S.D. 1973. *Card catalogue of world-wide shells*. Publ. by the author. Pack. No. 1, Marginellidae.

Lamarck, J.B.P.A. De M. De. 1822. *Histoire naturelle des animaux sans vertèbres*, 1st ed. Vol.7 "Mollusques" pp. 1-711, Paris, Giraudet. (Marginellidae pp. 355-365).

Largilliert, 1845. *Marginella*. Lamarck. M. Bernardii. Largilliert. *Magasin de Zoologie, D'Anatomie Comparée et de Palaentologie*, Recueil, 1845, ser. II, 7th yr., pl. 116.

Marrat, F. P. 1881. *Marginella (Cryptospira) ovalis*. Marrat, Swatow, China. 1 p. 1 col. Pl. (J. Chard delt.). Dated Jan. 18th, 1881.

Martin, K. 1891-1906. *Die Fossilien Von Java*. E.J. Brill, Leiden.

Martin, K. 1895. Die Fossilien von Java. *Sammlungen des Geologischen Reichsmuseums* 1(2-5): 1-132, E. J. Brill, Leiden.

Martin, K.1906. Die Fossilien von Java. *Sammlungen des Geologischen Reichsmuseums* 42; 301, Pl. XLIII, figs. 716, 716a. E. J. Brill, Leiden.

Melvill, J.C., & Standen, R. 1901. The Mollusca of the Persian Gulf, Gulf of Oman, and Arabian Sea, as evidenced mainly through the collections of Mr F.W. Townsend, 1893-1900; with descriptions of new species. Part 1: Cephalopoda, Gastropoda, Scaphopoda. *Proceedings of the Zoological Society of London, 1901*, 2(1): 327-460, pls. 21-24.

Oostinghe, C. H. 1938-1939. 'Die Mollusken des Pliocans von Sud-Bantam in Java,' 2. Abschnitt (Gastropoda II) mit Tafeln VIII-XVI. Druk van G. Kolff & Co. Batavia, Centrum.

Perry, G. 1811. Conchology, or the Natural history of shells, Containing a New Arrangement of the genera and species, illustr. By coloured engravings executed from the Natural Specimens, and including the latest Discoveries. Pp. 1-4, pls. 1-61.

Petit de la Saussaye, S. 1851. Notice sur le genre Marginelle, *Marginella* Lamarck, suivie d'un catalogue synonymique des espèces de ce genre. *Journal de Conchyliologie* 2: 38-59.

Redfield, J. H. 1851. *Catalogue of Marginellidae*, In the Collection of John H. Redfield. 2 pp. Privately printed. N.Y.

Redfield, J. H. 1870. Catalogue of the known species, recent and fossil, of the family Marginellidae. *American Journal of Conchology*, 6(2): 215-269.

Reeve, L. A. 1864-1865. Monograph of the genus Marginella in *Conchologia Iconica: or illustrations of the shells of molluscous animals* (15), pls. 2-13 [Aug. 1864], pls. 1, 14-27, index, errata [Jan, 1865].

Souleyet, L.F.A. 1852. 'Mollusques', in F. Eydoux & L.F.A. Souleyet, 1852 'Zoologie', in 'Voyages autour du Monde exécuté pendant les années 1836 et 1837 sur la corvette 'La Bonite' commandée par M. Vaillant Capitaine de Vaisseau publié par ordre du gouvernement sous les auspices du Département de la marine'. 2:1-664. Atlas pp. 2-8, pls. 1-45, Arthus Bertrand, Paris.

Sowerby, G. B. 2nd, 1846. Monograph of the genus Marginella *in* Thesaurus Conchyliorum, or Figures and Descriptions of Recent Shells 1(7): 239-406, pls. 68-78, Sowerby, London..

Tomlin, J. R. Le B. 1917. A Systematic list of the Marginellidae, *Proceedings of the Malacological Society of London*, 12 (5): 242-306.

Troschel, F. H. 1867, in 1865-1893. *Das Gebiss der Schnecken zur Begrundungeiner Naturlichen Classification*, 2: 1-409, pls. 1-32. G. Parthey, Berlin.

Tryon, G.W. 1882-1883, *Manual of Conchology* 5:5-58, 197-198. Philadelphia.

Wagner, R.J.L. & Abbott, R.T. 1967. Van Nostrands Standard Catalogue of Shells, 2nd ed. Van Nostrand Co. Princeton, N.J.

Wallace, A. R. 1855. 'On the Law Which Has Regulated the Introduction of New Species'. *Annals and Magazine of Natural History*. 16 (2nd series): 184 – 196.

Weinkauff, H.C. 1879. Die Gattungen *Marginella* und *Erato*. *Systematisches Conchylien-Cabinet* 5(4): 1-166. Nuremberg.