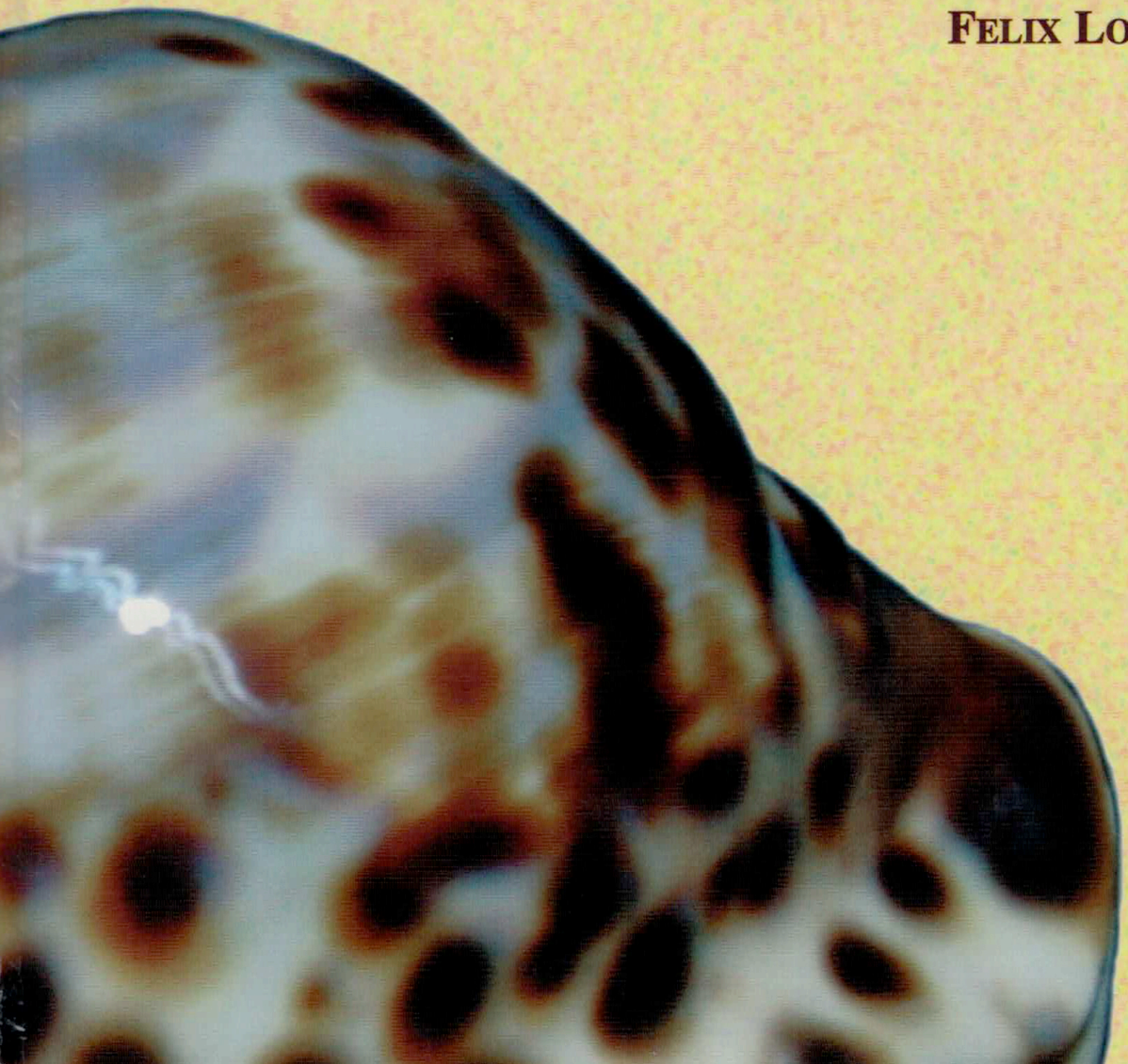
MONOGRAPH OF THE LIVING ZOILA

FELIX LORENZ



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MONOGRAPH OF THE LIVING

ZOILA

A FASCINATING GROUP OF AUSTRALIAN ENDEMIC COWRIES (MOLLUSCA: PROSOBRANCHIA: CYPRAEIDAE).

A systematic-taxonomic and iconographic revision of the genus

by Dr. FELIX LORENZ[1]

with the description of *Zoila ketyana bataviensis* nov. ssp.

by Dr. FELIX LORENZ[1] & HUGH MORRISON[2]

and a foreword by LINDSEY GROVES.

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[1] Institut für Allgemeine und Spezielle Zoologie der Justus-Liebig-Universität, Stephanstr.24, 35390 Giessen, Germany

[2] Ealing Mews 5, Kingsley 6026, Western Australia, Australia

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Foreword

Endemic faunas have always held a certain degree of mystery for the biologist and the endemic populations of Australia are no exception. Both endemic and Indo-Pacific molluscan faunas inhabit Australia and in particular it is the cypraeid genus *Zoila* that continues to capture the imagination of the professional malacologist and shell collector alike. Prior to the 1960's, six species of this magnificent genus were recognized as valid along with a handful of subspecies. Of these six species, all but one (*Zoila rosselli* COTTON 1948) were described in the middle and late 19th century and until fairly recently *Zoila marginata* (GASKOIN 1849) was still considered among the great ultrararities of the shell world.

Early works by GRAY, SOWERBY, GASKOIN, and SMITH were purely descriptive in nature and contributed little to the life habits of the group. Improved scuba diving technology and increased deep–water–trawling activities throughout northwestern and southern Australia during the 1970's and 1980's has increased the number of species, subspecies, and forms. As a result a tremendous wealth of information concerning the biology, ecology, conchology, and biogeography of *Zoila* has been published in the recent works of cypraeid specialists BIRAGHI, BURGESS, CATE, LORENZ & HUBERT, RAYBAUDI, SCHILDER and WILSON. Hence the number of *Zoila* taxa has increased dramatically as well as the understanding and appreciation of this remarkable cowry genus. Herein, FELIX LORENZ has concisely synthesized an enormous amount of data into a single comprehensive volume on the genus *Zoila*. His approach and interpretations may be considered controversial by some but it is indeed a fine effort. The result is a beautiful book on a fascinating group of cowries.

LINDSEY T. GROVES
Natural History Museum of Los Angeles County
February, 2001

Abstract

This book deals with the systematic taxonomy of the living and some fossil members of the cypraeid genus *Zoila*. A revised approach to evaluating the systematic units "species" and "subspecies" in a consistent way is proposed for the living members of the genus, which itself is subdivided into five species–groups. The occurrence and taxonomic importance of intermediate phenotypes is discussed. Ecological and geographical factors are additional features for a systematic treatment of taxa. All species, subspecies, and the various forms and variations are described, discussed, and illustrated in color, including many holotypes of systematically important taxa as well as a wide range of conchological variation. Distributions of the species, subspecies, and geographically defined forms are shown on detailed maps. *Zoila marginata* (Gaskoin 1849) is split into three separate species. The status of *contraria* (Iredale 1935) and conchologically similar shells is discussed, *contraria* itself being a deep water subspecies of *thersites* (Gaskoin 1849). *Zoila orientalis* Raybaudi 1985 and *intermedians* Lobetti 1986 are recognized as earlier names of *Zoila raybaudii* Lorenz 1992, syn. nov.

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Many people have contributed to this book in one way or another. I am greatly indebted to those listed here, without whose cooperation and support this book could not have been completed. Furthermore my sincerest thanks also all whose enthusiasm for the subject has encouraged me to write it.

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My friends and publishers, Christina and Klaus Groh of Hackenheim, Germany, for a pleasant collaboration.

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Lindsey Groves of Los Angeles, USA.

Guido Poppe of Berchem, Belgium, for interesting suggestions, and information.

[1] In this book, Dr. Luigi Raybaudi Massilia will be referred to as "Raybaudi", so as not to confuse with his daughter, Dr. Gabriella Raybaudi, also a well–known malacologist and famous authority on the family Conidae.

Hugh Morrison of Kingsley, Western Australia, helped a lot with detailed field knowledge.
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For material, information, suggestions and criticism (good and bad), I wish to thank Marty Beals, Randy Bridges, Rob Clifton, Jan Deprez, Paul Fischer, Jo van Heesvelde, Anna Holmes, Chris Meyer, Rainer Norpoth, Simone Pfützner, Emilio Jorge Power, Doug Thorn, and Barry Wilson.

Finally my sincerest thanks for the support given by my family, my parents Ingrid and Felix Lorenz, and above all, my loving life companion Jana Kratzsch.



Material and methods

The shells depicted in this book are from my private collection unless otherwise stated. Approximately five thousand specimens of living *Zoila* were studied, including shells from the collections Gabrielli (Neuss) and Hubert (Erlangen). Photographs were taken with a SONY DSC F505V digital camera. Word and image processing was done using NisusWriter™, MacDrawPro™, AdobePhotoshop™, and Grafikkonverter™. The computer setup consisted exclusively of Apple Macintosh™ computers, another factor that helped immensely. Those machines were a pleasure to work with and did not crash but once during the entire making of this book!

Introduction

The family of the cowries (Cypraeidae) consists of approximately 200 living species distributed in all temperate and warm seas. The family is split into four subfamilies with numerous genera, of which *Zoila* is one of the most popular. Its large, colorful shells are among the most coveted collectors' items in the world of malacology, and the most admired items at shell shows worldwide are usually *Zoila*.

The popular–scientific malacological publications are full of articles on *Zoila* and there is no other group in cowries in which the description of a new taxon causes a greater stir and start of debates and discussions. The aim of this book is to revise the systematic taxonomy of the genus, to give an iconographic overview to its vast conchological diversity, and to add some aspects to ongoing debates.

1. The history of the genus *Zoila*

The family of true cowries (Cypraeidae) is subdivided into four subfamilies, of which the most ancient, the Bernayinae is made up of four living genera, among which the genus *Zoila* is the largest, with the widest distribution. The genus was described by F. Jousseaume (1884).

Translated from French it reads: "Shell oval, flat basally, rounded and a little bit callused below. Mantle line indistinct, towards the right side. Spire slightly projecting. Aperture sinuous, slightly widening anteriorly. Columellar border with slight dentition anteriorly and posteriorly. The fosssular region is large and deep, forming a smooth projecting margin. Type species: *Zoila scottii* Broderip (syn. of *Zoila friendii* Gray), others are *Z. marginata* Gaskoin, *Z. thersites* Gaskoin." (see also Wenz 1940). The most recently modified definition was given by Lorenz & Hubert, 1993, and that is adopted in this book (slightly abbreviated and modified, see chapter 4: Systematic Part).

The oldest true cowries are known from the late Jurassic (Tithonian, 150 mill. years old). There were small–shelled species whose minute densely coiled protoconch indicates that these animals had a free–swimming veliger stage (e.g. *Palaeocypraea* Schilder 1928 [see Ranson 1967]). But there were also larger, heavy shelled groups showing a prominent, hardly coiled protoconch, indicating lack of a planktonic dispersal phase (e.g. *Bernaya* Jousseaume 1884).

The basic "primitive" characteristic of these earliest known cypraeids was a reduced or absent dentition, especially on the columellar side, a smooth fossula, and a conspicuous spire.



Fig. 1: *Afrocypraea chubbi* RENNIE, holotype, approx. 8 cm, Durban Natal Science Museum, photo courtesy T. CROUCH

At the end of the Mesozoic era (Late Cretaceous), about ten million years before the modern groups of the cypraeids began do disperse worldwide, a spectacular cowry lived in the Pondoland region of what is now southern Africa: *Afrocypraea chubbi* (RENNIE 1930), text fig. 1. This fascinating cowry was covered with prominent warts. The humped shell was surrounded by a flaring margin and had coarse teeth on the labral side only, whereas the columellar side was smooth. SCHILDER (1939) placed *Afrocypraea* in close generic proximity to *Zoila*, because in addition to the shape of the margins, the characteristics of the dentition are also shared. *A. chubbi* is probably not an ancestor of *Zoila* at all, but probably shared a common ancestor that also produced the genus *Zoila.*

In the Tertiary, a variety of conchologically comparable genera formed the dominating fauna of large–shelled cowries worldwide. Noteworthy examples include *Gisortia* JOUSSEAUME 1884(Cretaceous through Eocene) and *Vicetia* FABIANI 1905 (Eocene) in Europe (text fig. 2), India, northern Africa, and western

America, the archaic, then widespread *Bernaya* (Paleocene through Oligocene[2]) and *Barycypraea* SCHILDER 1927 (Oligocene through recent[3], see text fig. 3). The early forms of large–sized cypraeids resembled each other by having dorsal tubercles and ridges partly surrounding the shells, elegantly rostrate, often fragile siphonal canals (especially anteriorly) and reduced to absent dentition, especially on columellar side. All of them were lacking a planktonic dispersal stage (evident by the characteristic large protoconch showing only 1–2 coils) and were most probably spongivorous like their living descendants.

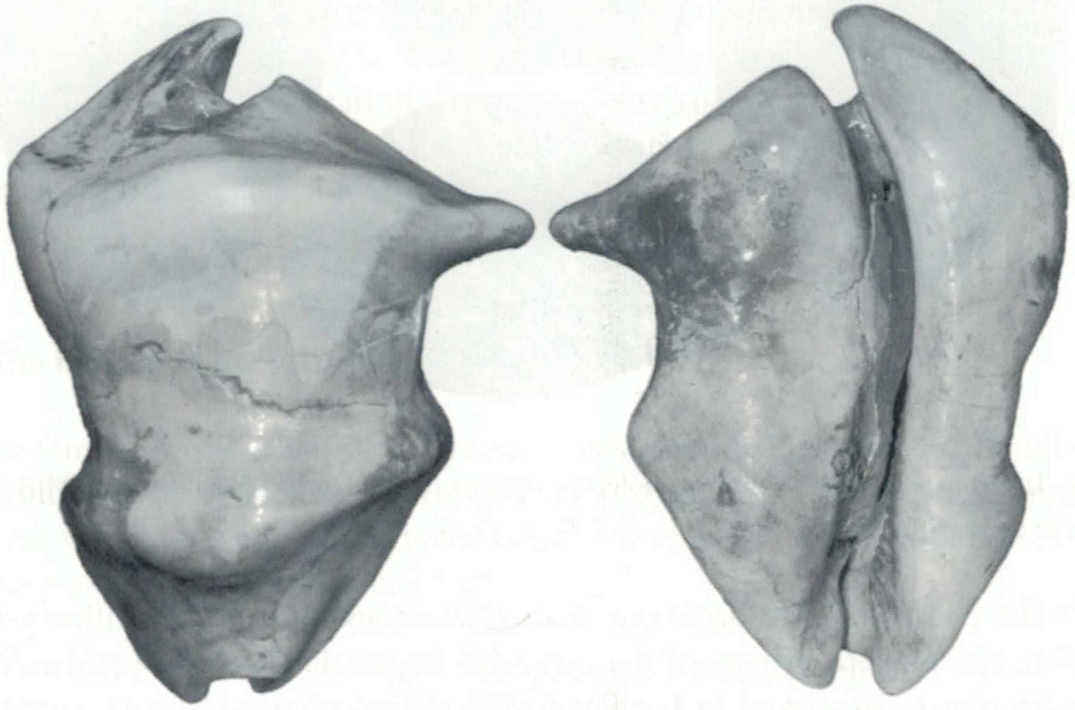


Fig. 2: *Vicetia sp.* Cuisian (Eocene), Gan, France 16 cm.

The earliest fossil species closely related to *Zoila* are found on the Australian continent, the oldest of those are of Miocene age, approximately 20 million years old (see also SCHILDER 1935). Some of them were of enormous size (*Gigantocypraea gigas* MCCOY 1867), others (e.g. *Zoila platypyga* MCCOY 1876)

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[2] The living *teulerei* (CAZENAVETTE 1846) was traditionally placed in the ancient genus *Bernaya* (see SCHILDER & SCHILDER 1971, LORENZ & HUBERT 1993). BRADNER & KAY (1996) have placed this archaic–looking species into *Barycypraea* due to similar radulae. The gap in the fossil record between the early Oligocene *Bernaya* and the living *teulerei* is another argument for this step (L. GROVES, pers. comm. 2001).

[3] Living representatives are found in deep water along the southeast African coast (*fultoni* [see LORENZ 1991]) and the intertidal of Masirah Island, Oman (*teulerei*).

resembled fossil members of *Umbilia* JOUSSEAUME 1884 (e.g. *U. sphaerodoma* TATE 1890), another genus of large–shelled cypraeids known from three living species restricted to Australia[4].

Others again were very similar to the species living today (e.g. *Zoila gabrieli* [CHAPMAN 1912]). Typical *Zoila* are otherwise known only from the Miocene of India (*Zoila schilderi* DEY in SCHILDER 1932a), the Pliocene of Indonesia (*Z. kendengensis* SCHILDER 1941a, b and *Z. gendinganensis* MARTIN 1899) and western Irian Jaya (*Zoila caputavisensis* BEETS 1986, see text fig. 4).



Fig. 3: a) left: *Barycypraea zietsmani* (LILTVED & LEROUX 1988), 61 mm, Pliocene of Port Elizabeth, b) right: *Barycypraea caputviperae*, 41 mm, Miocene of Java, from coll. SCHILDER, photo from FEHSE 2000.



Fig. 4: *Zoila caputavisensis* BEETS, 39 mm, holotype, Pliocene of western Irian Jaya.

[4] The relationship between *Zoila* and *Umbilia* remains debatable. A certain conchological resemblance and the intracapsular development they have in common may be a convergent adaptation to the temperate habitat they share, and not an indication of close phylogenetic relationship.

Florida and European Miocene deposits also bear ancestral forms resembling living species of *Zoila*; some of them were incorrectly described as *Zoila* because of this resemblance (see DOLIN 1991). Most of them belong to the genus *Cypraeorbis* CONRAD 1865, an extinct group from which *Siphocypraea* HEILPRIN 1887 (Florida Pliocene–Pleistocene, see PETUCH 1986, 1987) and the Miocene to recent *Muracypraea* WOODRING 1957 (northern coast of South America) probably evolved. The living *Zoila decipiens* and *Z. venusta* show great resemblance to some fossil *Cypraeorbis* of Florida, both genera may have a common ancestor (see text fig. 5).

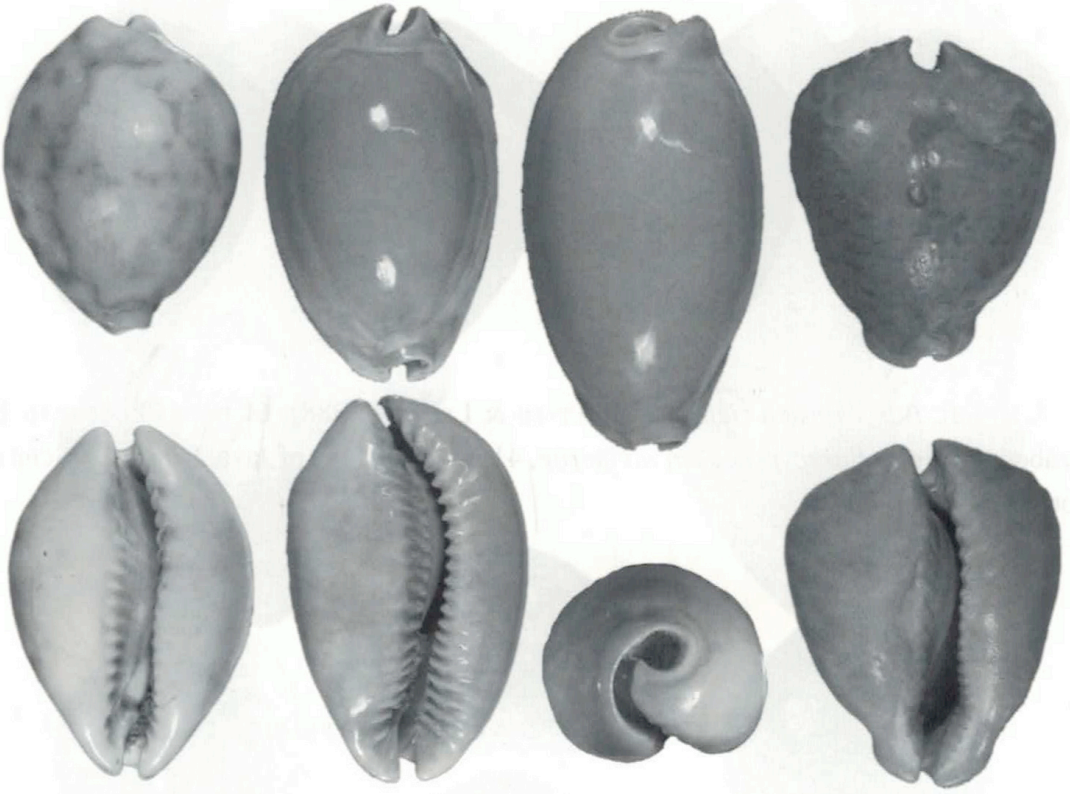


Fig. 5: American fossil species, from left to right: a) *Cypraeorbis* sp. 49 mm, Miocene of Florida coll. PETUCH. b) *Siphocypraea lindae* PETUCH, Paratype, 47 m and c) *S. problematica* (HEILPRIN), 64 mm, both Pliocene of Florida; d) *Muracypraea* sp., 41 mm, Miocene of Colon City, Panama.

How close is the relationship between the fossil and the living *Zoila* ? It is not known whether the resemblance we observe between living members and fossil forms is due to direct relationship or to adaptation to a similar habitat (convergent development). What we do know is that typical *Zoila* already existed in Australia at the time when *Cypraeorbis* flourished in North America and Europe. Judging from the wide distribution of these fossil species, one

may speculate that the paleoecological conditions on the sea floor from the Miocene to the early Pliocene were rather similar to those encountered today in parts of western and southern Australia.

Today, only three groups of the above–mentioned genera still have living representatives. The first is *Muracypraea* (often combined with *Siphocypraea*, see LORENZ & HUBERT 2000) with few taxa in northern South America (usually assigned to a single, variable species, *M. mus* [LINNÉ 1758]), the second *Barycypraea* with at least one species in southeast Africa (*fultoni* [SOWERBY III 1903]) and one in Arabia (*B. teulerei* [CAZENAVETTE 1846]). And finally, the largest group, the genus *Zoila* with its beautiful, variable, and widespread species found along the western and southern coasts of Australia. On text fig. 6, two characteristic fossil species of *Zoila* from Australia are shown.

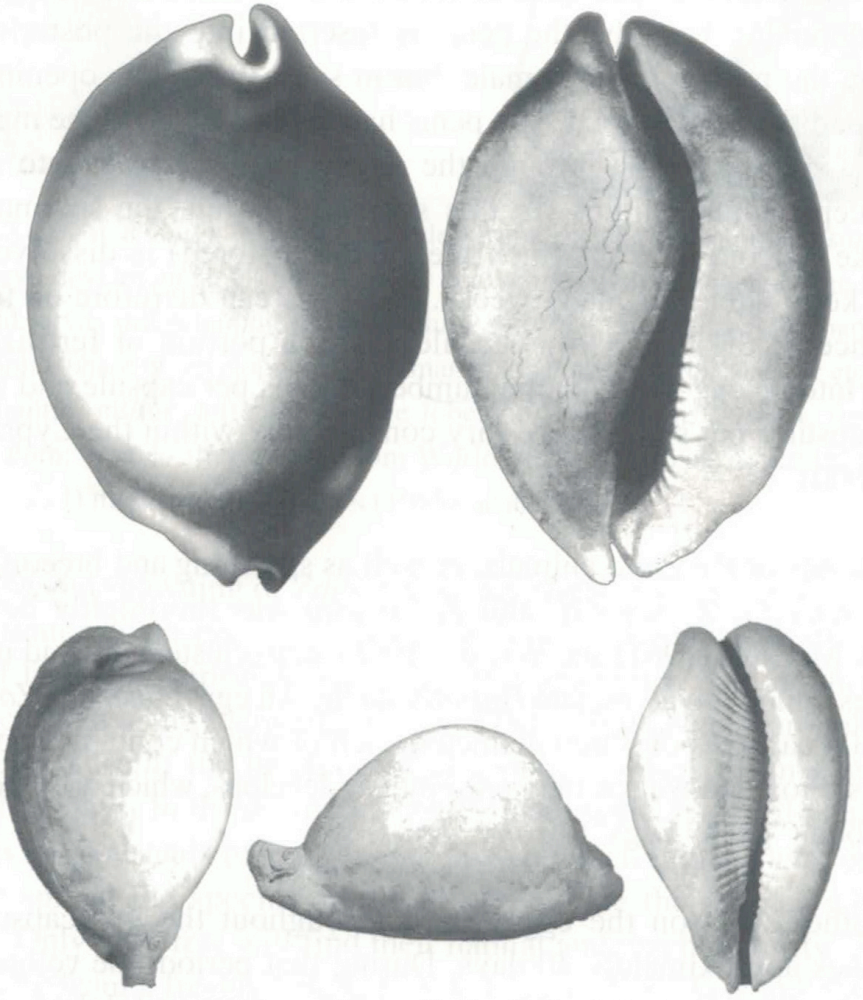


Fig. 6: Australian fossils: Top: *Gigantocypraea gigas* (MCCOY), 24 cm, Miocene of S. Australia, after WENZ 1940. Bottom: *Zoila platypyga* (MCCOY), 61 mm, Miocene of Victoria, coll. SCHILDER, photo FEHSE.

2. The biology and morphology of *Zoila*

This short chapter will give only a brief overview of some biological aspects of cowries and *Zoila* in particular. An exhaustive, richly illustrated scientific treatise on the *Zoila* species, their habitats, animals, genetics, and their biology is in preparation (Wilson, pers. comm.). It will serve as a perfect addition to this book as it will enlighten many aspects less thoroughly discussed herein and also approach the taxonomy of the group from a different angle. I highly recommend both works to be taken into account when objectively evaluating taxa and their proper systematic arrangement.

2.1. The reproductive biology of *Zoila*

Like all cowries, the species of *Zoila* have separate sexes; male and female meet to copulate. Usually, the penis is inserted into the posterior opening formed by the mantle of the female, but in some cases, the opening between the shell and the head is used. The penis has to reach far into the mantle cavity to inject a spermatophore through the vagina of the female into a structure called receptaculum seminis. In this sack–like organ, the spermatophore (a worm–like mucoid tube in which the sperm is stored) is dissolved, and the sperm is kept viable for many weeks. The eggs can therefore be fertilized in the absence of the male. In a capsule gland, a portion of fertilized eggs is enclosed into an egg–capsule, the number of eggs per capsule and the number of egg–capsules per spawn may vary considerably within the Cypraeidae (see Lorenz 2000).

The anatomy of the *Zoila* animals, as well as spawning and breeding behavior of *Zoila friendii, Z. rosselli,* and *Z. venusta* was thoroughly described by Wilson & McComb (1967) and Wilson (1985): egg–clusters are laid into cavities of sponges, empty bivalves, and *Haliotis* shells. An egg–cluster of *Zoila* consists of 200–300 capsules of 3 mm diameter, each of which contains approximately 1000 eggs. From these eggs, only one embryo develops, which uses the remaining eggs as food ("nurse–eggs").

The mother stays on the egg–cluster throughout the intracapsular period, which takes approximately 40 days. During that period, the veliger develops into a pediveliger stage retaining traces of the velum (a bilobed ciliate "sail" enabling the larva to swim). Finally a small cowry hatches, with a shell showing 2.5 whorls and still retaining an operculum, which is absent in older juvenile bulla–stages and adult cowries (see text fig. 7). Opening of the egg–capsules

occurs by pressing the posterior part of the shell against the capsular wall. Young bulla–stage as well as juvenile specimens of most *Zoila* tend to have an orange colored mantle whereas the animals of adult specimens vary from grayish to black in color.

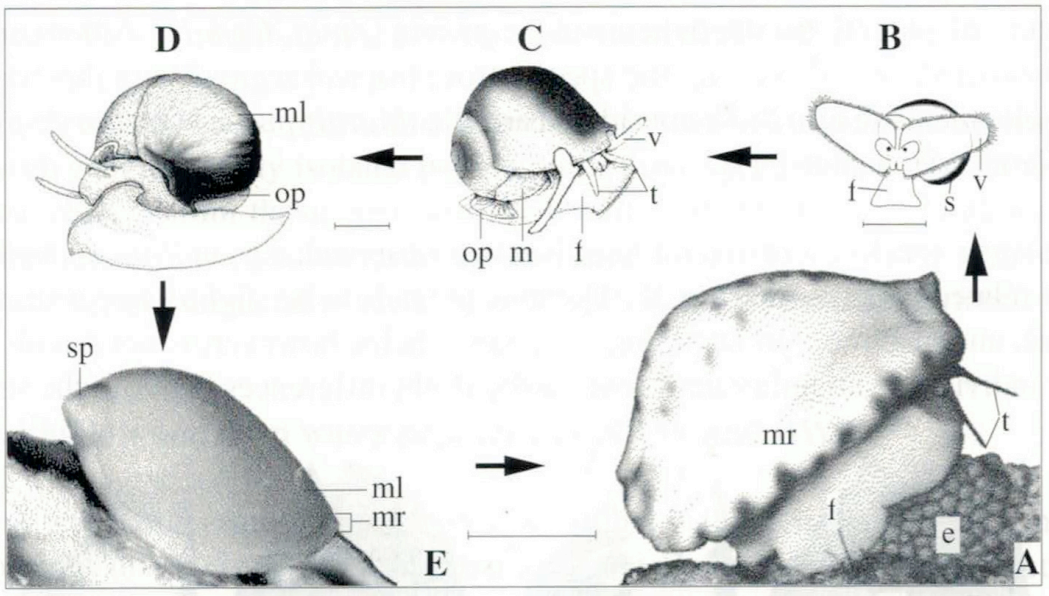


Fig. 7: Life–cycle[5] of a *Zoila*. A: Adult female sitting on eggs. B: Intracapsular veliger phase of embryo development, C: Intracapsular pediveliger with remnants of the velum. D: newly hatched larva, still retaining the operculum, only the left mantle lobe partly covers the shell. E: Bulla–phase of development, both mantle lobes covering the shell. e: egg–cluster; f: foot; m: mantle, ml/mr: left/right mantle lobe; op: operculum; s: shell; sp: spire; t: tentacle; v: velum. A & E after photos from World Shells Magazine, courtesy RAYBAUDI, scale: 1 cm. B, C, D modified after WILSON (1985), scale: 1 mm.

The breeding and spawning of *Zoila* is comparatively ancient. In some cowries with a planktonic veliger phase (e.g. *Erosaria annulus* [LINNÉ 1758]) the veligers are released from the capsules five days after spawning. The mother cowry opens each capsule using its radula (LORENZ 2000). The veligers are released at once, whereas in *Zoila* the hatching of all young cowries of an egg–cluster takes up to five days. In those cowries with a planktonic dispersal phase, there are hundreds of thousands of veligers per spawn which might travel over long distances to spread the species and eventually share their genes with other populations. Only very few will find their habitat and reach maturity. The time needed to grow from a freshly hatched larva to an adult *Zoila* is unknown.

[5] Since the *Zoila* live "down under", the cycle proceeds counterclockwise.

In *Zoila* and other cowries, intracapsular development results in only a few hundred hatching larvae per spawn, but those are at an advanced state of development and are in the right habitat; mortality is lowered, but spreading quickly over long distances is inhibited. Intracapsular development is interpreted as an adaptation to temperate zones (see WILSON 1985); it is a characteristic feature of endemic southern hemisphere genera (*Zoila, Umbilia, Notocypraea, Cypraeovula, Barycypraea*), the species from tropical regions with this type of development are also those considered archaic (*Muracypraea mus*, *Barycypraea teulerei*, see chapter 1.1).

In some species, a sexual dimorphism was observed, e.g. in *Zoila marginata* and related taxa (see text fig. 8). The female tends to be slightly larger than the male, and also more inflated. Sexing empty shells, however, is not possible as the individual variability may obscure the slight differences between the sexes.

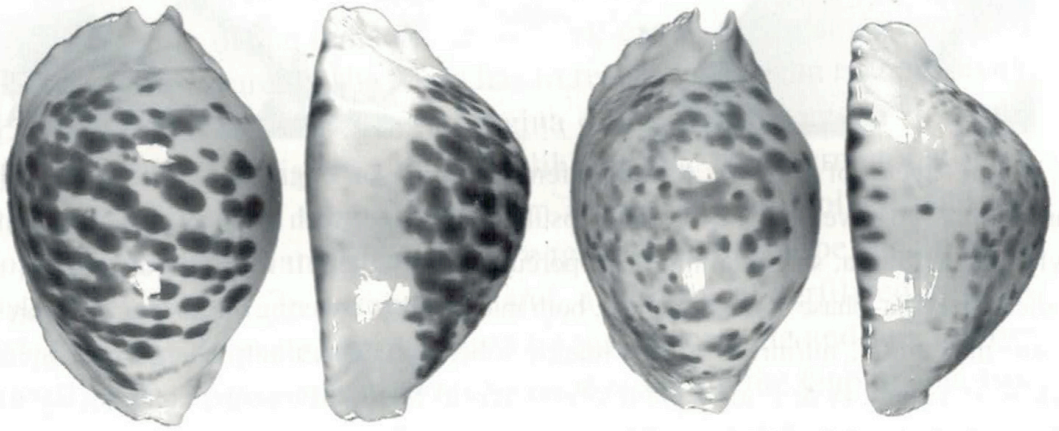


Fig. 8: *Zoila orientalis* RAYBAUDI collected during mating. Left: female (62 mm), right: male (59 mm). Note the difference in shape, and pattern. Kangaroo Is., S. Australia, 19 m depth.

2.2. Genetic isolation versus dispersal in *Zoila*

As mentioned above, *Zoila* species lack a planktonic dispersal phase. How could its species disperse along hundreds of kilometers of coastline? How do isolated micropopulations develop? My hypothesis is that juvenile intracapsular developers can travel long distances on pieces of host sponges torn off the sea floor (phoretic dispersal). At Fullers Bay, South Africa, pieces of sponge containing very juvenile specimens of *Cypraeovula* were repeatedly collected on beaches after heavy storms (COCHRANE, pers. comm. 1984). Especially during cyclones, sponges are torn from their substrate, carried by the current, and subsequently become attached, together with whatever lives on or in them.

The hypothesis appears to be a good explanation for the vast range of some *Zoila* species along thousands of kilometers of coastline. It also explains the phenomenon of occasional isolated individuals being found in areas where no populations of the respective species exist; it also helps to understand how conchologically foreign individuals may occasionally show up in populations where shells with a different set of characteristics are the rule.

A further consequence from this hypothesis is that indeed genetic exchange between geographically isolated populations of one species may exist, at least occasionally, within those areas fed by the same ocean currents. Findings of conchologically intermediate or conchologically deviant shells within otherwise consistent populations may therefore be of very low systematic importance.

2.3. Shallow and deep water populations: SWPs and DWPs

The living *Zoila* are sublittoral cypraeids with a bathymetric dispersal from 2 m to more than 300 m and a distribution from Dampier in the northwest to Gambier in the southeast of the Australian continent. All species feed almost exclusively on sponges (Porifera) with a variable degree of specialization to a particular host. As obligatory ectoparasites lacking a free–swimming veliger stage ("direct developers"[6]), the populations are dependent on the permanent presence of their hosts. A certain degree of distinction can be made between shallow water populations (SWP) and deep water populations (DWP) known from nearly all species of *Zoila*.

SWPs range from a few meters depth to approximately 50 m. Within this depth range (which may of course vary depending on numerous regional factors), climate changes, cyclones and variable oceanic currents have a greater impact on ocean floor communities than at greater depth. The growth rate and species composition of sponges in the shallow water force the species feeding on them to adapt quickly to those changes.

High genetic variability provides a greater tolerance of a population to survive fluctuations in their habitat. As a result, a high degree of conchological variability

[6] The term "direct developers" for species without a planktonic veliger stage should no longer be used, the term "intracapsular developers" is more appropriate for those species in which the veliger is not planktonic (Lorenz 2000).

occurs in widespread coherent SWPs. In cases of genetic drift[7], scattered micropopulations have formed in shallower water, showing a reduced variability in size, shape, and shell pigmentation and ornamentation.

DWPs usually have wide ranges bordering on the ranges of SWPs. Their conchological features, however, are usually more constant, sometimes along hundreds of kilometers of coastline (e.g. *contraria* IREDALE 1935). Temporary climate changes on the surface lose their impact on the sea floor with increasing depth. Accordingly, the evolutionary pressure (the necessity to adapt to changing environments) is lower in deep water. The distinction between SWPs and DWPs must be understood as a hypothetic model; in many taxa there are numerous transitional habitats and populations.

The various populations of the genus *Zoila* (and of most other genera in the Cypraeidae) appear to be in different phases of speciation: on one hand, there are several well–defined species not forming conchological intermediates with others (*venusta* SOWERBY 1846, *rosselli* COTTON 1948); on the other hand, there are species complexes retaining conchologically intergrading populations (*friendii*–group, see chapter 3.5). It is these complexes, often widespread and highly variable, that challenge taxonomists: the status of the geographically defined SWPs as either subspecies or full species is subject of continuing discussion, especially in cases where conchological intermediates exist.

2.4. Distinct and intermediate populations

In *Zoila*, some populations are well defined by conchological characteristics not overlapping with those of others. To call those valid species represents no problem. *Zoila venusta* is an example: there are no conchological intermediates between *venusta* and other species of the genus. The same is true for *Z. decipiens*, but the superficial resemblance to *Z. perlae* and *Z. mariellae* has led some authors to question the status of these as mere "forms" or subspecies of *Z. decipiens* (see BURGESS 1985). This is of course a pragmatic procedure but simply not correct: The shells of *decipiens*, *perlae* and *mariellae* are conchologically similar, but have little in common unless lined up next to each other on a table. In an artificially assembled sequence, one may show a gradual change of a single characteristic from a completely white *mariellae* via a

[7] One or few individuals separated from their population and founded a new one, isolated, and with reduced genetic variability.

sparsely spotted *perlae* to a densely spotted *decipiens* in this example. Other conchological features such as dentition, as well as the ecological, geographic, bathymetric, and evolutionary distance between the three taxa are not taken into account in such an exercise. Such manipulations are commonly found in the malacological literature of recent years, and they were almost exclusively used by authors trying to keep the account of species to a minimum ("lumpers", see also SCHILDER 1963c).

In the genus *Zoila* (like in many other genera of the Cypraeidae and other families) taxonomists are confronted with a vast variety of "intermediate" specimens linking two otherwise distinct populations conchologically by at least one or two features. In some cases, there are whole populations showing intermediate features of some kind, and in one case (*vercoi* and *thersites*) there are variations of SWPs that resemble conchologically extreme DWPs. The existence of intermediate individuals or even populations is indeed an interesting phenomenon in the genus *Zoila*, but not a proof that most of its populations are basically all the same species. The clue to a systematic treatment giving credit to the above–mentioned thoughts may be found by also considering two facts:

1) Evolution (and the process of speciation) is proceeding at a different rate in the various depths and localities along the Australian coast. Populations develop into conchological extremes (or: separate species) at the geographic or bathymetric extremes of their distributions. While in–between, their process of speciation is in an intermediate phase, whose product is intermediate phenotypes (see also WAKE, YANEV & FRELOW 1989 and SIEWING, 1982).

2) When evaluating the intermediate character of a population, taxonomists' arguments were usually based on conchological features only. Many of the so–called intermediates are not intermediate at all as soon as all of their conchological features, their geographic, ecological and bathymetric origin are taken into account: if any of these factors are not intermediate as well, then the status as a link no longer has any standing. Many shells appear to be intermediates only when placed into an artificially selected sequence (as described above for *decipiens*). In the genus *Zoila*, the vast variety of shapes and color variations offers a wide range of shells serving as potential candidates for such an arbitrary array of "intergrades".

2.5. Terminology of a *Zoila*–shell

The general shell features of a *Zoila* correspond to those of other cowries. There are, however, certain characteristics of particular interest for recognition of species (see text fig. 9). The formation of the extremities is one of those. In some species, the margins of the extremities may be very fragile and sharp (*marginata*, *friendii*), whereas in other species they are callused and rounded (*decipiens*, *venusta*). The shape of the spire is another important aspect. In some species the spire is pointed (*friendii*), in some it is hidden (*ketyana* f. "*hypermarginata*"), but it may also be flat and conspicuous (*venusta roseopunctata*). Also the presence (*jeaniana*) or absence (*venusta*) of the columellar teeth are important features. Even subtle differences in the shape of the base may be of great importance (e.g. in the separation of *eludens* [rounded and convex] from *perlae* [concave]). A minute but interesting feature observed in some species, is an iridescent callus often present near the posterior extremity (e.g. in *j. jeaniana* and *j. aurata*).

On the other hand, some features highlighted in the characterization of species of other cowry genera (e.g. the fossula and the columellar peristome) may be omitted in the description of a *Zoila*, as they are either absent or uniform.

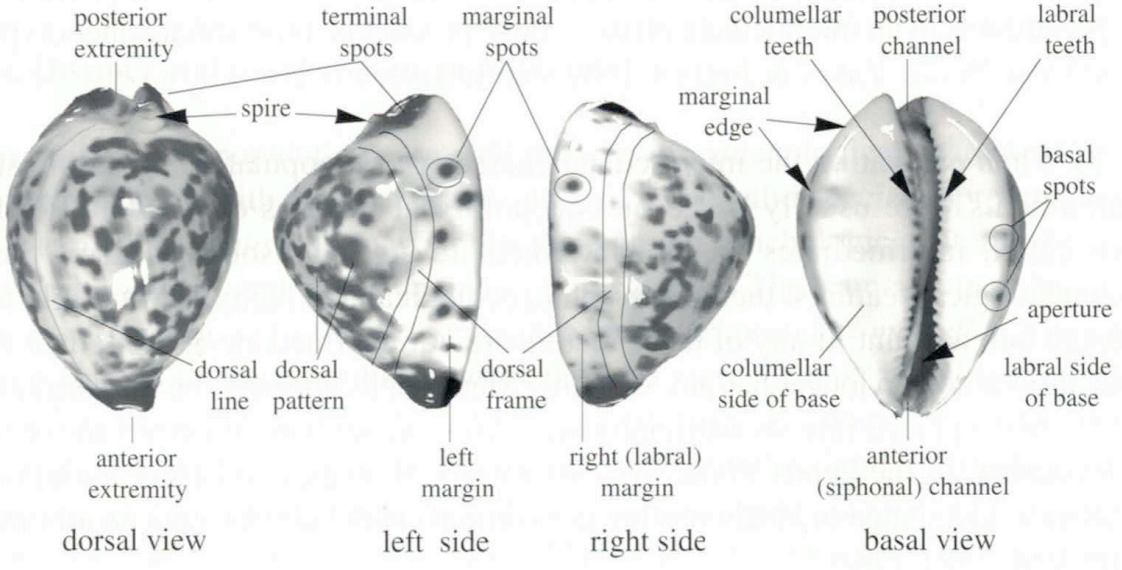


Fig. 9: Terminology of a *Zoila* shell (*Zoila perlae*)

2.6. Definitions of taxonomic terms

For a systematic subdivision of the genus *Zoila*, the following terms and definitions are used herein:

• **Genus**, as a unit of related species separable from all other groups of species by at least one unique characteristic. A subdivision of the living species on a subgeneric level seems not possible at this stage, and with the relatively small number of species, it seems unnecessary. Yet, the species can be placed into five distinctive groups of shells where no intergrading forms or close resemblance can be observed("species–groups").

• **Species** are "tools that are fashioned for characterizing organic diversity (...) Practicing taxonomists and other biologists need to be able to reliably identify species (...) operational species definitions serve a practical purpose that does not necessarily correspond to theoretical species concepts, and theoretical species concepts are often impractical." (Endler in Otte & Endler 1989). I use a biological concept defining a species as a reproductive community separated from other similar communities by intrinsic isolating barriers (Mayr 1967, Templeton 1989). These barriers (criteria) are for instance of geographical, bathymetric or ecological nature, but also, of conchological nature: two phenotypically different specimens do not recognize each other as mating partners (Recognition Species Concept, Ghiselin 1974). This definition takes into account the fact that a species occupies a specific ecological niche not occupied by another species. It gives credit to the fact that well–established species of numerous phyla repeatedly produce hybrids. In the malacological world, the example of *Cypraeovula amphithales* (Melvill1888) as a product of interbreeding between *edentula* (Gray 1825) and *capensis* (Gray 1828) is famous, especially because the fertility of the hybrid forms could be proven (Liltved 1989). To come back to the above statement on intermediates, the occurrence of intermediate stages must not be taken as proof that two conchologically separable populations belong to the same species.

In separate, closely related species, there may be distribution overlaps ("hybrid zones"). The hybrids that may occur in those zones show intermediate characteristics but have a lower viability and/or reduced fertility compared to their respective parent–species. As a consequence, they are relatively rarer than their parent species (postzygotic isolation).

• **Subspecies** is a term used to characterize separable sub–units of a species. The systematic assignment as subspecies is given to those geographically definable populations showing intermediate stages in intermediate geographical or bathymetric zones, as well as to those populations whose conchological features are not consistent in a majority of the individuals. Those populations that are conchologically distinct within geographically or ecologically defined boundaries should be interpreted as valid species, provided that the number of hybrids is low.

• **Forma** is not a taxonomical unit, but is sometimes useful to describe individual variations (alleles) that repeatedly occur within populations. In some cases, a forma name describes isolated micropopulations or localized segments of populations (demes), or those geographical variations whose conchological features are not consistent enough for the subspecies level.

The evaluation of the status "forma" versus subspecies may in some instances be difficult and, in some cases, is admittedly arbitrary. In the taxonomy of the Cypraeidae, numerous "forms" have later proved to be of valid species rank[8]. This is one reason why the category is maintained in this book, although names explicitly introduced or cited as "forma" or "variation" have no taxonomic validity[9]. Further names, not separately highlighted, will be explained whenever possible and they will be used also in the plate captions, to enable a correct assignment of these names by anyone who chooses to use them.

[8] For instance, *Cypraeovula edentula* (Gray 1825), *Cribrarula fallax* (Smith 1881), and *Umbilia armeniaca* (Verco 1912) were originally described as forms of other species.

[9] According to articles 45.5 and 45.6 of the ICZN (International Code of Zoological Nomenclature, see Kraus 2000).

3. Systematic part

In this chapter, the species groups and their members will be characterized and discussed. The shell formula is derived from measurements taken from all available adult and normally formed specimens. It consists of the following elements: L (W – H) X : Y. (#) denotes that the teeth are partly absent on columellar side. This formula has proven a reliable tool for characterizing populations numerically. It is stated in angular brackets at the end of the shell descriptions. L: average length (mm); W: average width/length ratio in %; H: average height/length ratio in %; X: normalized number of labral teeth; Y: normalized number of columellar teeth, following the formula proposed by SCHILDER & SCHILDER 1938[10], 1952. The size ranges list the smallest and largest specimens known to me.

Mollusca: Gastropoda: Cypraeidae, subfamily BERNAYINAE

Genus *Zoila* JOUSSEAUME 1884

(Type species of the genus is *Cypraea scottii* BRODERIP 1831, a synonym of the living species *Zoila friendii* GRAY 1831).

Definition from LORENZ & HUBERT 1993, modified: Large, inflated shells with conspicuous spire, narrow aperture and produced, often sharp and rostrate extremities. Margins sometimes flaring. Base usually rather flat. Columellar teeth mostly indistinct midway. Variable and bright coloration. The species of *Zoila* have intracapsular development. The mantle is thick, rather translucent. Some species have simple, wart–like papillae. Twelve living species of *Zoila*[11] are recognized herein (*decipiens, eludens, friendii, jeaniana, ketyana, marginata, mariellae, orientalis, perlae, rosselli, thersites, venusta*; endemics of South and West Australia) and innumerable conchological variations, often making identification difficult. The living members of the genus are here subdivided into five groups of conchologically related species: *decipiens*–, *venusta*–, *marginata*–, *rosselli*–, and *friendii*–group.

[10] $r = 7 + \left((c-7)\sqrt{\frac{25}{L}} \right)$ r = normalized number of teeth, c = teeth counted, L = shell's length.

[11] LORENZ & HUBERT did not recognize *eludens*, *ketyana* and *orientalis* as valid).

3.1. The *decipiens* – group

Characteristic features:
Globular shells with short, rounded extremities. Teeth distinct on both sides. Spire slightly pointed. No embryonic banding[12]. Close conchological resemblance to species of *Cypraeorbis*, therefore considered the most archaic group. Four living species recognized by many authors and also herein: *decipiens, eludens, mariellae, perlae.*

3.1.1. ***decipiens*** (SMITH 1880)
Deceptive Cowry[13] Pl. 1 – 2; map 2 common

Reference: *Cypraea decipiens* E. A. SMITH (1880) Proc. Zool. Soc. London: 482–483
Holotype shown in text fig. 10, depository not known to me. Type locality: North Australia.
Synonym: *atrata* SULLIOTI 1924

Shell:
Inflated, heavy. Dorsum distinctly humped. Spire only slightly projecting, partly covered by callus. Extremities short and blunt. Teeth short, present on both lips, less prominent on columellar side. Dorsum showing more or less dense mottling and often a characteristic "malleated" surface. Uniform dark brown to black base and margins. [52(68)16:14]

Distribution and habitat:
Cape Leveque to Eighty Mile Beach, and around Onslow, Western Australia. Collected by divers from 5 – 35 m in crevices and on sponges.

Size Range (mm): **41 – 70** Compare with: *eludens, mariellae, perlae*

A common, easily recognizable member of the genus. It is usually found by pearl fishermen operating off Broome. Very few trawled samples from deeper waters are known (Pl. 2 fig. 4). These are larger and more rostrate than their shallow water relatives. No conchologically intermediate stages to another species are known, the dark basal and marginal color safely distinguish *decipiens* from *perlae* and *eludens,* in which the base is pale brown to cream and the margins are pale with darker spotting. Subadult shells already show the dark tinting of the base, whereas the margins can still be whitish.

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[12] Before the adult pattern forms, the juvenile shell of many Cypraeids displays a wavy zigzag pattern or straight, regular transverse bands. This embryonic banding is an important systematic feature (see LORENZ & HUBERT 1993, 2000).

[13] The eroded holotype resembling *thersites*.

So–called golden forms have been produced by baking (see LOBETTI–BODONI 1992). The larger and often more callused shells of the uncommon "Onslow population" [59(68)17:14](Pl. 2 fig. 1–3) have not been given a subspecific name, although their isolation from the nominate "Broome population" suggests that a certain degree of genetic separation might exist.

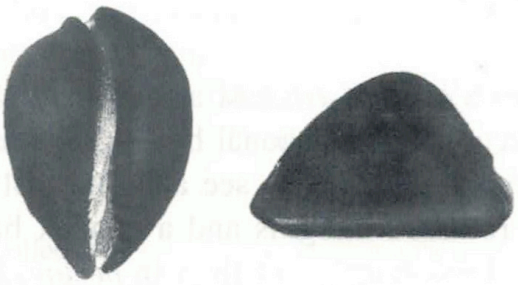


Fig. 10: Original figure of the holotype of *decipiens,* "North Australia"

3.1.2. ***eludens*** RAYBAUDI 1991
Elusive Cowry Pl. 3 – 4; map 2 rare (formerly uncommon)

Reference: *Zoila (Zoila) eludens* L. RAYBAUDI MASSILIA (1991) La Conchiglia 260: 8–15
The holotype of *eludens* is shown in text fig. 11, coll. RAYBAUDI. Type locality: "kept secret".

Shell:

Very heavy, solid. Dorsum humped. Base slightly convex, callused. Margins rounded, sometimes very callused. Extremities rounded and short. Spire hardly projecting, covered with callus. Teeth rounded and short, well produced throughout on both sides. Base cream, blotched with darker orange to brown. Margins cream, coarsely spotted, distinctly iridescent, often with a bluish dorsal frame. Dorsum densely mottled with brown and black. Black terminal spots. [64(66)15:14]

Distribution, habitat and collecting:

Exmouth area, Western Australia. Lives on sponges in depths of 28 to 45 m, the variety *delicatura* to 70 m. Large numbers of this distinctive *Zoila* have been collected by divers; hurricanes devastating vast areas around Exmouth Gulf have depleted the host sponges. Shortly after its discovery the beautiful *eludens* has become very rare.

Size Range (mm): **43 – 74** Compare with: *decipiens, jeaniana*

Geographic variation:

• ***eludens*** forma ***delicatura*** CHANDLER & DUROSS 1997

Delicate *eludens* Pl. 3; map 3 very rare

Zoila delicatura J. CHANDLER & C. DUROSS 1997, World Shells 20: 65–67

From the northern limit of the distribution, 35 to 70 m depth. Smaller and less callused, usually more elongate shells. Margins less callused and less densely spotted. [49(66)15:13]

The placement of the SWP's of *eludens* as subspecies of *perlae* has been a debated subject on account of occasional heavy, large–shelled individuals of *perlae* (LORENZ & HUBERT 1993, 2000, see also plate 5 fig. 5). The shells of *eludens* always have rounded margins and a convex base stained orange to brown. The teeth are less sharply cut than in *perlae*, the dorsal spotting is much coarser and more confluent. Finally, the spire in *eludens* is covered with callus whereas in *perlae* it is usually partly exposed. The spectacular *eludens* is known from only two populations, the nominate Exmouth form and a smaller–shelled one, supposedly from the northern range limit, which was named *delicatura.* Herein *delicatura* is listed as a variation only, as too little is known about its range and habitat. Despite smaller size and a certain tendency to be less densely spotted, no consistent conchological features seem to exist that would justify a separation at higher rank.

There is a resemblance of the general color of *eludens* to SWPs of *jeaniana.* The fragile, angular extremities of *jeaniana* safely distinguish the two.

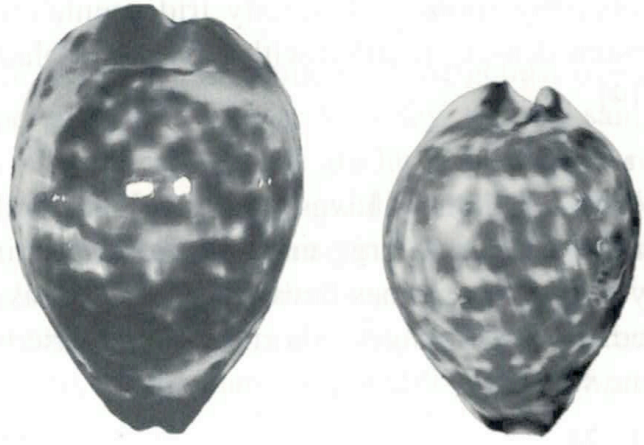


Fig. 11: a) left: Holotype of *eludens* RAYBAUDI, coll. RAYBAUDI, b) right: Holotype of *delicatura* CHANDLER & DU ROSS, coll. Perth Museum.

3.1.3. ***perlae*** LOPEZ & CHIANG 1975

In honor of Mrs. PERLA CHIANG Pl. 5; map 2 extremely rare

Reference: *Zoila perlae* A. LOPEZ & C. S. CHIANG (1975) The Veliger, Vol. 18: 84–85 Holotype shown on text fig. 12., coll. Los Angeles County Museum. Type locality: North West Cape.

Shell:

Distinctly humped dorsum with darker spotting. Spire short, slightly projecting, seldom covered with callus. Cream–colored margins distinctly spotted. Dark, rather blunt rounded extremities. Margins hardly callused, straight. Base concave, cream to orange brown. Teeth distinct on both sides and rather numerous. [41(71)17:15]

Distribution, habitat and collecting:

Off northwestern Australia, exact range unknown. A deep water species. Reported to be trawled from approximately 150–280 m, far offshore. This beautiful and distinctive cowry was available only during a relatively short period between the late seventies and the late eighties from Taiwanese trawlers operating off the Australian coast. In recent years no more specimens have been found and therefore *perlae* is one of the great rarities attaining a premium price in almost any condition.

Size Range (mm): **35 – 62** Compare with: *decipiens, eludens, mariellae, jeaniana*

The holotype of *perlae* corresponds to the small, sparsely spotted specimens found by Taiwanese trawlers, the type depth and locality were listed as "182 to 274 meters of water, mud bottom, 18° to 25° S, paralleling the offshore coast of North West Cape, Western Australia [approximately 21°00' S; 114°10' W]". The species differs from other members of the complex by the pale, dark–spotted, angular margins with a distinctly concave base, which is pure white to faint orange.

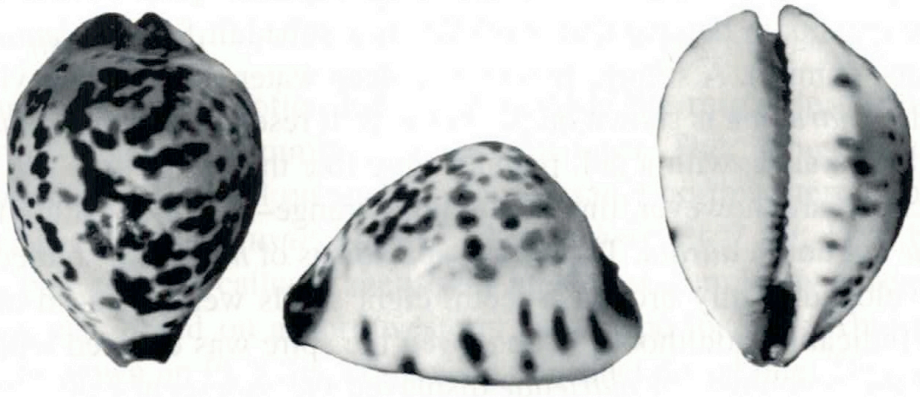


Fig. 12: The holotype of *perlae* (39 mm), from The Veliger Vol. 18.

A few larger (around 50 mm), heavy shelled specimens resembling *eludens* are known. In those, the dorsal spotting is dense but finer than in *eludens*, and the base is concave and whitish, clearly identifying these shells as extreme individuals of *perlae*. The first specimens of *eludens* that reached Europe were interpreted as a shallow water subspecies of *perlae* by LORENZ & HUBERT 1993 because of the existence of those large and heavy *perlae*. With the reasonable number of *eludens* available now, one may conclude that the characteristics of the basal shape and color are constant separating features.

3.1.4. ***mariellae*** RAYBAUDI 1983
In honor of Mrs. MARIA RAYBAUDI Pl. 6, 39; map 2 extremely rare

Reference: *Zoila* (Z.) *mariellae* L. RAYBAUDI MASS. (1983) La Conchiglia 176–177: 11–14
The holotype is reproduced on Pl. 6 fig. 1, coll. RAYBAUDI. Type locality unknown.

Shell:
Pyriform, inflated, with slightly rostrate extremities. Dorsum distinctly humped in the posterior third. Spire short, pointed, and exposed. Base flattened, aperture distinctly curved posteriorly. Teeth distinct on both sides, faintly tinted with brown. Unspotted dorsum with a grayish or olive–green hue. Orange to brown extremities and base. Occasionally with faint marginal spots. [58(71)17:15]

Distribution and habitat:
Exact range unknown, somewhere off northwest Australia, trawled from deep water by Taiwanese trawlers. Perhaps less than fifty specimens have been found, and today a well–preserved specimen of *mariellae* is one of the most highly prized malacological items.

Size Range (mm): **52 – 65** Compare with: *decipiens, perlae*

This rare, distinctive *Zoila* varies little (see RAYBAUDI 1992c). An important conchological feature apart from color is the exposed spire. This feature has led some experts to believe that *mariellae* is a subadult form of *jeaniana* (G. POPPE, pers. comm.). A strange plain white deep water specimen provisionally assigned to *mariellae* is shown on pl. 39 fig. 3. It resembles *jeaniana aurata* in general appearance, with a tall, pointed spire like that of *aurata*. The teeth of this specimen are, however, tinted with faint orange–brown, a feature found in *mariellae* but not in *aurata*. The twelve specimens of *mariellae* studied all had well–developed faintly brownish teeth, eight shells were callused along the margins indicating adulthood, in one, even the spire was covered with callus. None of the specimens of *mariellae* displayed the iridescent callus, which is always present in *jeaniana*, even in subadult specimens.

3.2. The *venusta* – group:

Characteristic features:

Large, heavy shells. Spire flattened. Columellar teeth reduced to absent midway. Posterior extremity massive and rounded. Straight indistinct embryonic banding. Shell showing reddish fluorescence under UV light. Similar to some members of the ancient *Cypraeorbis*. One living species universally recognized by authors: *venusta.*

3.2.1.a ***venusta venusta*** (SOWERBY 1846)
Delightful Cowry Pl. 7 – 8; map 3 uncommon

Reference: *Cypraea venusta* G. B. SOWERBY (1847) Proceedings of the Linnean Society London, Vol. 1: 314
Holotype reproduced on Pl. 7, fig. 2, coll. Cambridge University Museum. Type locality: "Port Adelaide, South Australia", West Australia by designation (see IREDALE 1935).
Synonyms: *thatcheri* COX 1869 (Holotype see Pl. 7, fig. 1), *catei* SCHILDER 1963 (Holotype see Pl. 8, fig. 1)

Shell:

Elongate–oval, often rather massive. Extremities callused and rounded, produced posteriorly. Columellar teeth absent midway. Spire flat, often conspicuous. The nominate form is rather large, very heavy, and callused; the spire is mostly hidden by the callus. Dorsal pattern sparse and pale, often beautifully orange. [70(67)16:11]

Distribution, habitat and collecting:

Western Australia, from the Abrolhos Islands to the Cervates area. Lives on different species of sponge at depth ranging from 5 to 45 m. The true western *venusta* is a rare shell and is usually offered under the name *venusta thatcheri.* Well–preserved specimen with typical orange spotting are sought after, as well as specimens from the Abrolhos Islands.

Size Range (mm): **56 – 91** Compare with: *thersites, decipiens*

The name *thatcheri* is often used to subdivide the rare pale northwestern shells from the more common southeastern ones. The names *venusta* and *thatcheri* were both based on shells from the same northwestern population, however. The types (*venusta*: Pl. 7 fig. 2, *thatcheri:* Pl. 7 fig. 1) of both are elongate, pale colored, callused shells with an almost completely covered spire. Also *catei* was based on a northwestern shell (type locality: Abrolhos, the holotype is shown on Pl. 8 fig. 1) showing a distinct dorsal line. This feature is found in other populations and has no taxonomic value. The nomenclature of these names was discussed by CATE (1962) and WILSON & MCCOMB (1967).

3.2.1.b ***venusta roseopunctata*** (RAYBAUDI 1985)
Rose–spotted *venusta* Pl. 12 – 17; map 3 moderately common

Reference: *Zoila (Zoila) venusta roseopunctata* L. RAYBAUDI MASSILIA (1985b) The Connoisseur of Seashells 2: 7 fig. 12C
Lectotype see text fig. 13, designated here, coll. RAYBAUDI. Type locality: Esperance.
Synonyms: *bakeri* GATLIFF 1916 (holotype see text fig. 14), *orientalis* RAYBAUDI 1990, *roseimmaculata* RAYBAUDI 1985b, *roseopunctata* MELVILL 1888 (nomen nudum)

Shell:

Large, inflated. Spire partly exposed, usually rather conspicuous. Dorsal ornamentation varies from sparse spotting to mottled blotching, occasionally melanistic, or completely immaculate (var. *roseimmaculata*). Margins usually rather pale and faintly spotted. Deep water specimens (var. *profunda*) are cream, with reduced to absent dorsal pattern and coarser, thickened labral teeth. [72(69)16:13]

Distribution, habitat and collecting:

West of Denmark to Esperance, southwestern Australia, in deeper water farther east beyond Cape Recherche. Taken by divers from 2 to over 50 m, usually in caves or under ledges, in association with different types of sponge. The eastern deep water variation *profunda* is found by trawlers from 80 to 150 m. Typical, well–preserved specimens with average dorsal pattern have become readily available due to the activities of divers in the Albany to Esperance area. Immaculate, as well as exceptionally colored shells are highly prized items, as well as specimens of forma *profunda*.

Size Range (mm): **50 – 86** Compare with: *thersites, decipiens*

Important geographical variation:

• ***venusta roseopunctata*** forma ***profunda*** RAYBAUDI 1990
Deep–water *venusta* Pl. 8; map 3 rare

Zoila venusta roseopunctata forma *profunda* L. RAYBAUDI MASSILIA (1990d) The Connoisseur of Seashells 23: 26–27
Original figure shown on text fig. 15, courtesy RAYBAUDI

Cape Recherche to Great Australian Bight, southern Australia, deep water. Inflated, extremities rather rostrate. Dorsum with a malleated surface, cream, reduced to absent pattern. Labral teeth very strong, less numerous. [75(71)14:12]

Color variation:

• ***venusta roseopunctata*** forma ***roseoimmaculata*** RAYBAUDI 1985
Rose–colored immaculate *venusta* Pl. 7 rare (good specimens)

Zoila venusta var. *roseoimmaculata* L. RAYBAUDI MASSILIA (1985b) The Connoisseur of Seashells, No. 2: 6

Albany to Esperance, southwestern Australia; Specimens without any darker pattern found alongside typical darker mottled shells. [75(69)16:13]

Lorenz & Hubert (1993, 2000) subdivided *venusta* into two subspecies, *venusta* and *episema*. The distribution maps given for these were highly inaccurate, as *episema* is not restricted to the northwestern limit of the species' range but inhabits an area between the paler colored populations assigned to *venusta venusta.*

The name *roseopunctata* (Melvill 1888, nomen nudum) was chosen to subdivide the southern *venusta* at the level of a forma. However, the name *roseopunctata* was validly introduced by trinominal use by Raybaudi 1985. The usage of *roseopunctata* is admittedly unfortunate because it refers to a color feature, which is highly variable in this particular subspecies. No description was given, but it is the earliest name for a shell of the southern population. Raybaudi (1995d) informally proposed the name *albanyca* as a subspecies name for the same population. Further names are listed in the same article, most of which give credit to the outstanding variability of the dorsal pattern in the southern shells here all called *roseopunctata.*

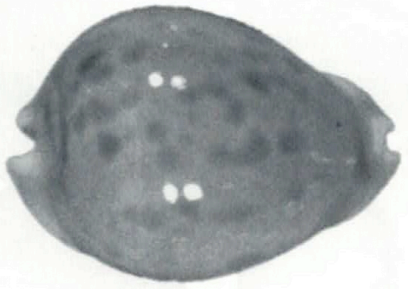


Fig. 13: Lectotype of *roseopunctata* Raybaudi 1985

The name *bakeri* was based on an unspotted, very rostrate shell with marked teeth on both sides of the aperture, with a large, exposed spire, probably trawled from deeper water. The type locality was given as "Western Australia". According to Wilson (1993), this shell resembles a *venusta* population from Esperance, despite being distinctly denticulate on both sides of the aperture, and having rostrated extremities and a rather pointed spire. The true identity of *bakeri* remains uncertain as no further similar shells have been found.

The eastern deep water population was first mentioned by Summers (1961) who reported a specimen from the Great Australian Bight in an Australian collection, and later by Wilson & McComb (1967). Its taxonomic history is a little bit complicated. Raybaudi (1985b) first mentioned *Zoila venusta roseopunctata* forma *profunda* from the Great Australian Bight without

illustrating a specimen. In 1990d he used that name again and illustrated two specimens along with a short description. In the same year, he introduced *Zoila venusta orientalis* as a subspecies (1990a), basing his description on the same specimens previously illustrated as forma *orientalis*. This name, however, is preoccupied by *Zoila marginata orientalis* RAYBAUDI (1985a, see below for a detailed discussion).

The types are unspotted, callused shells, one of which shows the coarser labral dentition characteristic of this eastern deep water form, the other having teeth that are abnormally split and therefore very fine. Another specimen of *profunda* with sparse dorsal spotting is shown and discussed by WILSON & MCCOMB (1967) p. 475 fig. 338; a detailed analysis on this variety was given by HART (1997), another specimen is illustrated in LORENZ & HUBERT (2000: 500 fig. 1–3).

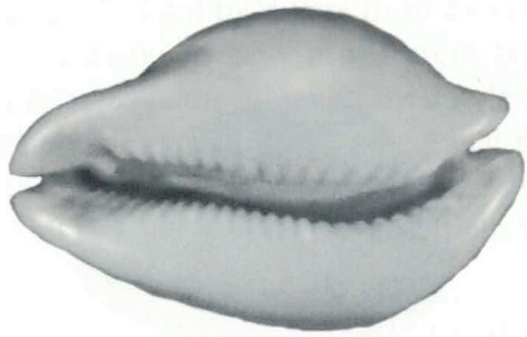


Fig. 14: Holotype of *bakeri* GATLIFF 1916, after WILSON & MCCOMB 1967

3.2.1.c ***venusta episema*** IREDALE 1939
Official *venusta* Pl. 9 – 11; map 3 common

Reference: *Zoila episema* T. IREDALE (1939) Australian Zoologist, Vol. 9: 300–301
Holotype shown on Pl. 10, fig. 1, coll. South Australian Museum. Type locality: Cape Naturaliste.

Shell:

Elongate, sometimes rather depressed. Spire partly covered by callus. Base rather concave. Dorsum with dark mottling and spotting, margins usually dark brown. Often there is a bluish to whitish dorsal frame. [71(66)16:11]

Distribution, habitat and collecting:

Lancelin Island to Augusta, Western Australia; Lives on sponges, often in caves and under ledges, from 2 to 50 m. The smaller *sorrentensis* is among the

more common *Zoila*. Typical *episema* often have natural flaws such as irregularities in the nacre. Perfect specimens of more than 70 mm are seldom available.

Size Range (mm): **38 – 85** Compare with: *decipiens*

Geographic variation:

• ***venusta episema*** forma ***sorrentensis*** SCHILDER 1963

venusta from Sorrento Bay Pl. 11; map 3 common

Zoila venusta sorrentensis F. A. SCHILDER (1963a) The Veliger, Vol. 5: 125–128

Sorrento Bay to Mandurah, Western Australia; smaller, depressed. More elongate. [56(65)17:11]

The population universe of *Zoila venusta* makes a subspecific subdivision as done in other species of the genus difficult. The darker *episema* population occurs between two areas inhabited by paler–shelled populations, the smaller *sorrentensis* is not confined to a particular area, the southern *roseopunctata* is occasionally not separable conchologically from either the northwestern *venusta* or even *episema*. The eastern *profunda* is known to me only from about fifty specimens, and the features of dentition are not consistent. WILSON & SUMMMERS (1985) interpret such phenomena as an indication for taxonomically insignificant "demes" (local variation without geographic pattern).

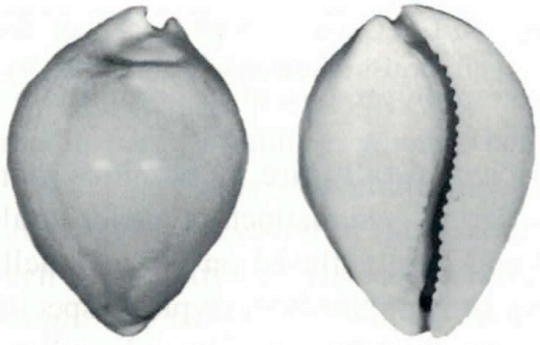


Fig. 15: Original specimen on which the names *profunda* RAYBAUDI 1990d and *orientalis* RAYBAUDI 1990a were based.

CATE 1962, in a comprehensive treatise of the group, concludes that *episema* deserves the rank of a valid species because of morphological differences. This standpoint was revised by SCHILDER 1963a, who considered *episema* as a subspecies of *venusta*. WILSON (1993) treats *episema* as synonym of *venusta*, but acknowledged morphological differences (see also SUMMERS 1961).

To summarize, there are four distinguishable groups of *venusta*:
1) a northwestern, large, pale, and heavy shelled population with a small, almost completely covered spire: *venusta venusta*
2) a darker–shelled, southwestern population: *venusta episema*, (including the smaller shelled forma *sorrentensis*)
3) an inflated, vividly colored southern population with a rather exposed large spire: *venusta roseopunctata*
4) an inflated, pale, coarsely toothed deep water eastern population: *venusta roseopunctata* forma *profunda*, which might deserve the rank of a subspecies.

3.3. The *marginata* – group

Characteristic features:
Medium sized to small shells with flaring margins and fragile, rostrate extremities. Spire pointed. Teeth equally distinct on both sides. No embryonic banding. Three species recognized herein (*marginata*, *ketyana*, *orientalis*), of which only *marginata* is recognized as valid by other authors.

3.3.1.a **_marginata marginata_** (GASKOIN 1849)
Broad–margined Cowry Pl. 18 – 21; map 4 – 5 moderately common

Reference: *Cypraea marginata* J. S. GASKOIN (1849) Proc. Zool. Soc. London 1848: 91–92
Holotype see Pl. 19, fig. 1, coll. British Museum of Natural History. Type locality unknown.

Shell:
Elongate, with a conspicuous tall spire. Extremities sharply rostrate and bent up. Margins angular, flaring, and distinctly developed along both sides of the shell. Base flattened and little callused on the columellar side. Margins and base spotted with dark brown. Northern (typical) specimens are rather heavy shelled, with reduced marginal flanges. The columellar teeth are rather short midway, the dorsal pattern is reduced to absent [54(61)19:16].
The southern variety *consueta* is more elongate, with flaring, fragile margins and extremities and a colorful dorsal pattern.

Distribution, habitat and collecting:
Abrolhos Islands southwards to Augusta, Western Australia; Lives in caves and crevices, mostly on sponges at depths ranging from 5 to 50 m. The variety *consueta* is rather commonly found in all shades of color. The northern typical form is rather rare.

Size Range (mm): **46 – 77** Compare with: *ketyana, orientalis*

Geographic variation:

• ***marginata marginata*** forma ***consueta*** BIRAGHI 1993

Common *marginata* Pl. 19 – 21; map 5 common

Zoila marginata consueta G. BIRAGHI (1993) La Conchiglia 25 (266): 39–42

Perth area, Western Australia; Elongate, with rostrated extremities and flaring margins. Dark mottled dorsum. The most common form. [61(56)19:17]

The holotype of *marginata* (Pl. 19 fig. 1) has been subject of a debate raised by BIRAGHI (1993a,b, 1994). He tried to assign the holotype of *marginata* to the southeastern *orientalis* (then known as *raybaudii*), and introduced *consueta* as new name for *marginata* (see also TAYLOR & WALLS 1975 p. 223: the illustration shows a color photograph of GASKOIN's holotype).

Following the conchological analysis by HUBERT (1994) and RAYBAUDI (1994e), the holotype of *marginata* belongs to a western population of *marginata* in the classic sense. The prominent angular margin also on the left side of the shell (absent in *orientalis*), the slender, pyriform shape (rounded and more inflated in *orientalis*), and the dorsal freckling of the holotype resemble some shells from the western population of *m. marginata* very closely (compare pl. 19 fig. 1 with fig. 2), whereas I have not seen any specimens of *orientalis* that resemble the holotype of *marginata* other than by the pale color and the relatively sparse dorsal pattern.

To the south of the distribution of *marginata marginata*, lightweight, long, thin, and extremely variable forms dominate, whereas heavier, sparsely spotted shells are found in the north (Cervantes – Geraldton area). Those were formerly called *intermedians* LOBETTI. For a revision of this taxon, see below. GASKOIN's holotype lies in between these extremes. BIRAGHI's *consueta* is here placed in synonymy with *marginata*. The usage of this name on the level of a forma is proposed here to specify the variable, densely blotched southwestern variation, in accordance with other authors (e.g. WILSON 1993, who notes that within the *consueta* range, broad sparsely spotted forms also occur; those resemble *m. marginata* in the strict sense (e.g. at Rottnest Island).

3.3.1. b ***marginata albanyensis*** RAYBAUDI 1985
marginata from Albany Pl. 21 – 22; map 5 moderately common

Reference: *Zoila (Zoila) marginata albanyensis* L. RAYBAUDI MASSILIA (1985a) The Connoisseur of Seashells, No. 1: 8–9 fig. 7A.

Lectotype see text fig. 16 designated here[14], coll. RAYBAUDI. Type locality: Albany.

Shell:

Elongate, inflated. All white or covered with faint, irregular dashes of brown dorsally. Marginal spots inconspicuous in the dorsal view. [63(60)19:16]

Distribution, habitat and collecting:

Albany to Esperance, southwestern Australia; Feeds on sponges in 5 – 45 m, often found in caves. A common variety which is regularly collected by divers. Perfect specimens without any irregularity or damage are, however, rare.

Size Range (mm): **40–77** Compare with: *ketyana, orientalis*

Color variation:

• ***marginata albanyensis*** forma ***nimbosa*** RAYBAUDI 1994
Cloudy *marginata* Pl. 22 moderately common

Zoila marginata albanyensis var. *nimbosa* L. RAYBAUDI MASS. (1994b) World Shells 9: 23

Dorsum covered with diffuse cloudy patches of brown. [61(62)19:15]



Fig. 16: Lectotype of *albanyensis*, coll. RAYBAUDI, from The Connoisseur 1: 8 fig. 7A

There is universal agreement on the status of *albanyensis* as a color variant eastern population of *marginata*, which ranges from pure white to fawn–mottled shells. The name *nimbosa* was introduced for such cloudy or mottled individuals of *albanyensis*. There is a trinominal description of the name *albanyensis* in the publication listed as original reference, and RAYBAUDI later supplied a comprehensive analysis (e.g. in WS 9, 1994b: 21) so that I accept the name as properly introduced (in accordance with WILSON 1993 and LORENZ & HUBERT 1993, see also the discussion of *orientalis*).

[14] In the descriptions of *albanyensis* and other taxa, RAYBAUDI did not designate holotypes. Herein, the first specimen illustrated in the descriptions is chosen as lectotype.

Specimens of *m. marginata* with a completely white dorsum and sparse marginal spots are also known from Dongara at the northwestern range limit of the species. They differ from southeastern *albanyensis* by the reduced marginal flanges and shorter columellar teeth.

3.3.2.a **ketyana ketyana** RAYBAUDI 1978
In honor of Mrs. Kety Nicolay[15] Pl. 26; map 4 – 5 very rare

Reference: *Cypraea (Zoila) marginata ketyana* L. RAYBAUDI MASSILIA (1978) La Conchiglia 106: 11–14

Lectotype designated here, see text fig. 17, coll. RAYBAUDI. Type locality unknown.

Shell:

Oval to elongate–oval, very callused and heavy. Base convex, margins produced, surrounding the shell. Teeth strong and rather long on both sides. Spire pointed, usually covered by callus. Base and margins distinctly spotted and striped. Marginal spots form depressions, giving the shell an irregular outline. Dorsum with fine brown spots or unspotted white. [45(66)20:16]
Specimens from shallow water (25 – 50 m) are larger, with more expanded margins and dark dorsal spotting. [50(70)18:16]

Distribution, habitat and collecting:

Offshore Dampier to Shark Bay area, Western Australia, exact distribution unknown. Lives on *Geodea* sponges in depths ranging from 25 to over 200 m. The nominate population was trawled from 80 – 200 m off northwestern Australia, recent findings were made by divers in 25 – 45 m. The typical *ketyana* from deep water has not been collected recently, but a considerable number was trawled by Taiwanese.

Size Range (mm): **27 – 56** Compare with: *m. albanyensis*

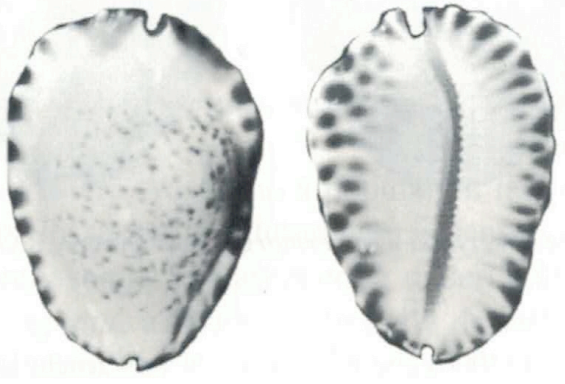


Fig. 17: Lectotype of *ketyana,* collection RAYBAUDI

[15] Italian collector and former editor of La Conchylia.

Important local variations:

• ***ketyana ketyana*** forma ***hypermarginata*** RAYBAUDI 1993

Hyper–margined *ketyana* Pl. 25; map 5 moderately rare

Zoila marginata ketyana f. *hypermarginata* L. RAYBAUDI MASSILIA (1993b) World Shells 7: 3–14[16]. Original figure see text fig. 18

Bernier Is., Western Australia. Large, heavy. Margins expanded. Dorsum white, hardly spotted. [50(70)18:15]

• ***ketyana ketyana*** forma ***lutea*** RAYBAUDI 1993

Light colored *ketyana* Pl. 25; map 5 very rare

Zoila marginata ketyana f. *lutea* L. RAYBAUDI MASSILIA (1993b) World Shells 7: 3–14 Original figure see text fig. 19

Southern end of Dirk Hartog Is., Western Australia. Elongate, heavy. Aperture narrow, teeth dense. Dorsum white, base orange. [55(65)20:17]

The northernmost populations of *marginata marginata* are known from Dongara, Geraldton, and the south of the Abrolhos Islands. These shells resemble pale, sparsely spotted specimens of *ketyana* from northern localities and for a long time were interpreted as intermediate stages. However, between the geographic ranges of these taxa, the recently discovered *k. bataviensis* (described below) is found. This southernmost subspecies of *ketyana* seems to border on the geographic area of the northernmost *marginata* populations and contrasts conchologically with them (for a detailed differentiation see plates).

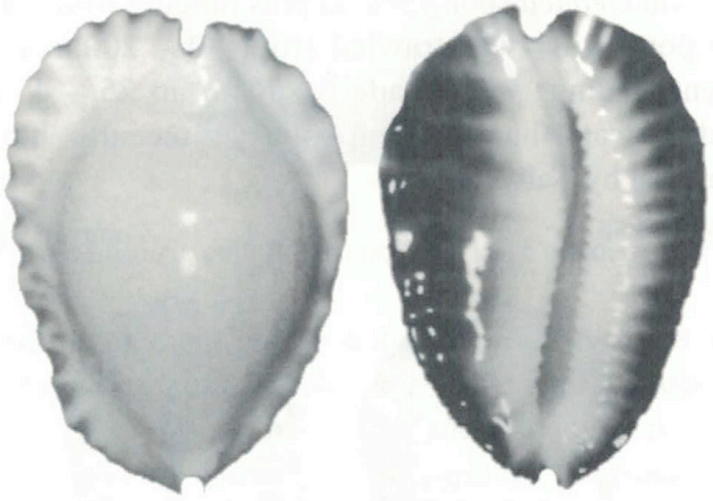


Fig. 18: Original figures of *ketyana* f. *hypermarginata*, courtesy RAYBAUDI

[16] LORENZ & HUBERT (2000) cite the authors of this article as "RAYBAUDI, EDINGER & CLARKSON". However, RAYBAUDI intended to be the sole author. Listing A. EDINGER and P. CLARKSON below the headline of the paper was intended as an acknowledgement of their collaboration only.

By definition, *ketyana* deserves the status of a valid species as no true intermediate populations are known. *Zoila ketyana* and its subspecies are only found in association with one host, the large, solitary *Geodea* sponge. Typical *marginata* are not host–specific but feed on several types of sponges.

In *ketyana* we are facing a distribution type that is best described as scattered micropopulations. Each of these has different consistent conchological characters. The DWPs of *ketyana* vary considerably in shape, color, and size: as long as no exact locality and depth data is available, one cannot draw any further conclusions on the status of the variations shown on plate 23.

At Gnaraloo Station, Western Australia, a population resembling the classic deep water *ketyana* is found in moderately shallow water (38 – 45 m)[17]. In my opinion, it represents a shallow water population of the typical deep water *ketyana*. It differs by its larger size, still more callused margins which are bent up laterally, and a more convex base. The dark and dense dorsal pigmentation separate it from the adjacent *hypermarginata* and *lutea*. Transitional forms to the classic *ketyana* in deeper water of adjacent areas are not known.

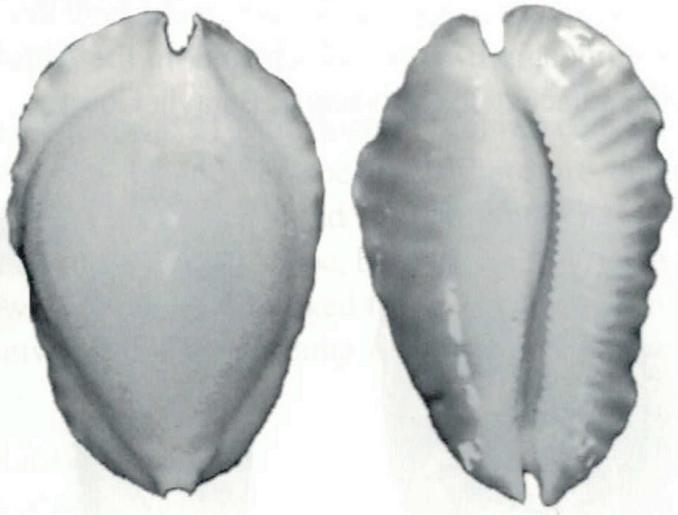


Fig. 19: Original figures of *ketyana* f. *lutea*, courtesy RAYBAUDI

At Bernier Island, Western Australia, a population lacking the conspicuous dorsal spotting occurs. Its strongly callused base is densely spotted and streaked with orange only, rarely shades of darker color underlie the spots. This variety was named *hypermarginata*, a forma name aptly describing the character of this remarkable population.

[17] It has been called "forma *superba*" by shell–dealers, but this name was never published as far as I know.

Along the southwestern side of Dirk Hartog Island, Western Australia, a more elongate, densely toothed form of *ketyana* is found. The population is very small and few specimens have so far been found. Those fill the ecological role of *ketyana*: they live in the 38 – 45 m range, exclusively on *Geodea* sponges. They represent the largest and heaviest form of *ketyana*. Referring to its pale, almost always unspotted dorsum, and the bright orange basal ornamentation, it was named *lutea* RAYBAUDI, a name here adopted: as the author explicitly introduced *lutea* under the genus *Zoila*, synonymy conflict with the earlier *Cypraea lutea* LINNÉ 1758 (now accommodated in the subfamily CYPRAEOVULINAE, genus *Palmadusta*) is not the case, even if future authors decide to lift the taxonomically invalid forma name to subspecies rank.

The above–mentioned populations of *ketyana* have a common feature: the shell's maximum width is in the posterior third, giving them a common general shape. Recently, another population was discovered by HUGH MORRISON and his diving partners in the Abrolhos Islands. These shells show a variety of interesting, characteristic conchological features beyond the level of mere color variation. Their life as specialized ectoparasites on *Geodea* characterize them further as a new *ketyana.* This southern subspecies of *ketyana* is here described and named after the Dutch sailing ship BATAVIA, which sunk in the Abrolhos Island group in 1629, giving the adjacent coast its name, Batavia Coast.

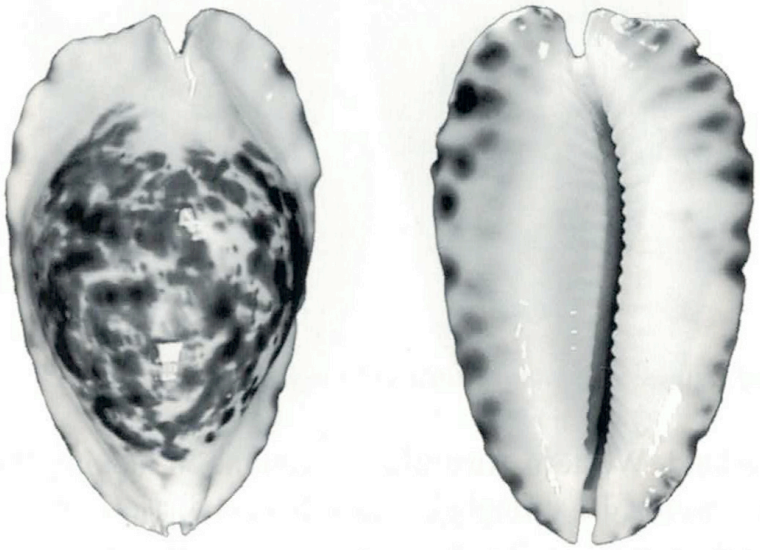


Fig. 20: Holotype of *ketyana bataviensis* ssp. nov., coll. South Australian Museum

3.3.2. b **_ketyana bataviensis_** ssp. nov.

by Felix Lorenz and Hugh Morrison

ketyana from the Batavia Coast Pl. 23 – 25; map 4 – 5 very rare

Material: fourteen specimens collected by divers at depths between 38 and 45 m in the Abrolhos Island group, Western Australia, have been studied by the second author:

Holotype (text fig. 20):	56.2 x 34.3 x 26.1	(South Australian Museum)
Paratype 1:	55.6 x 31.1 x 23.9	(collection Lorenz)
Paratype 2:	57.1 x 33.1 x 26.5	(collection Lorenz)

(enumerated: length x width x height in mm)

Description:

Elongate, cylindrical, with flaring margins bordering the posterior extremity. The marginal callus is hardly developed midway but still borders the entire shell. On the posterior end, the margins are expanded and flaring. The dorsum is depressed. The base is extremely callused and convex, grooves are formed posteriorly towards the marginal edges. The aperture is very narrow and straight. The teeth are short, coarse and numerous. The marginal spotting is large, forming deep depressions, whereas the edges of the margins are hardly corrugated. Basally, there are shades of orange from the margins towards the aperture. The dorsum is broadly framed with whitish–cream, the dorsal dome is densely mottled with brown. [56(58)20:15]

Variability:

In the paratypes (see text fig. 21), the dorsum is either densely mottled, almost black in one specimen, in another specimen there are distinct large black spots. Some specimens are rather broad and extremely heavy, resembling the Gnaraloo population of *ketyana* in shape, but differing by being densely mottled dorsally with brown and black. A marked feature of all *k. bataviensis* examined is the contrast between the wide frame of cream–white encircling the dark mottled dorsum.

Distribution, habitat and collecting:

A total of 14 specimens was taken by divers during 250 dives carried out in various spots of the Abrolhos Island group in 1999. All specimens were found at depths of 33 to 40 m on and under *Geodea* sponges scattered throughout the Abrolhos Island group, 75 km west of Geraldton, central coast of Western Australia. Paratype 2 was found in a fish trap at unknown depth off Geraldton in the late eighties.

Discussion:
This most southern population of *ketyana* differs from typical northern *marginata marginata* by its extreme weight and callosity of the shells, the marginal spotting forming distinct depressions, the callused, convex base and the narrow aperture (resembling the *lutea* population from further north). Its ectoparasitic life on *Geodea* sponges ecologically classifies it as a population related to *ketyana.* Some specimens illustrated as *marginata* in the literature (Wilson & McComb (1967) pl. 335 fig. 7–8, Burgess (1970) pl. 38 fig. D,D1, Raybaudi (1994a): 16 fig. 72–78 and Lorenz & Hubert (1993) pl. 8, fig. 16–17) have the typical white dorsal frame, a narrow aperture, and the characteristic convex base of *k. bataviensis* and should be assigned to this new taxon rather than to *marginata.*

In the late sixties, a small number of shells resembling typical (northern) *marginata* and the types of *k. bataviensis* in certain features, were collected from a fish trap off Abrolhos Is. (Gurr 1981a). These are heavy, rather narrow, with a whitish dorsum showing small, scattered spots and a flattened callused base with dense blotching of dark brown to black [53(61)20:16](Pl. 18, fig. 5–6). The shape of the base resembles *marginata*, whereas the dark basal color is closer to *ketyana bataviensis*. The characteristic white frame encircling the dorsum (see above) is missing. There are few known specimens of this variety, some of which were illustrated also by Raybaudi (WS 6, 1993a: 11 fig. 28–30 and WS 8, 1994a: 18 fig. 85).

The correct systematic position of these extreme shells is unclear; they are here assigned to *marginata* with a question mark. They may, in fact, be interpreted as a link between the northernmost populations of *marginata* and the southern subspecies of *ketyana* (here named *bataviensis*). Hopefully, intensified research in the Abrolhos Island group will produce more specimens and deeper insights.

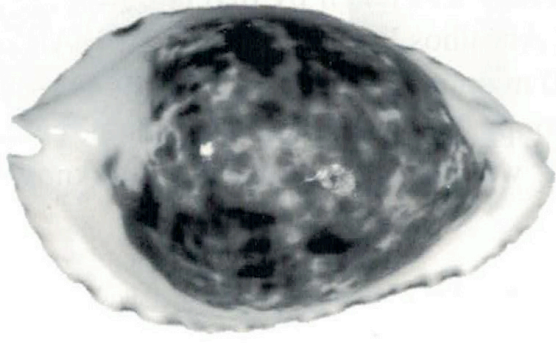


Fig. 21: Z. *ketyana bataviensis*, paratype from collection Beals, 58,0 mm

3.3.3. ***orientalis*** RAYBAUDI 1985

Eastern *marginata*[18] Pl. 27; map 4 uncommon

Reference: *Zoila marginata orientalis* L. RAYBAUDI MASSILIA (1985) The Connoisseur of Seashells, No. 1: 8–9. Lectotype see text fig. 22, designated herein, coll. RAYBAUDI. Type locality: South Australia.

Synonyms: *intermedians* (LOBETTI–BODONI 1986), syn. nov., *raybaudii* LORENZ 1992, syn. nov. Invalid names: *extrema* RAYBAUDI 1992d, *meridionalis* RAYBAUDI 1993a[19]

Shell:

Oval, rather inflated. Only the labral margin is produced and rather angular, with regular corrugations formed by the marginal spots. There is no distinct margin midway on left side. Spire distinctly projecting. Aperture wide. White to pinkish, with regular dorsal spotting, resembling a bird's egg. [58(65)19:15]

Distribution, habitat and collecting:

Ceduna to Kangaroo Island, South Australia. Feeds on red *Trachycladus* sponges and hides in ledges of rocks, among seaweed, at depth between 12 and 45 m.

Size range (mm): **42 – 65** Compare with: *marginata*, *ketyana*

This species has a long taxonomic history. The magazine "The Connoisseur of Seashells" has been accepted as a publication meeting the standards of the ICZN and at least some of the names introduced there are taxonomically valid (see COSSIGNANI & PASSAMONTI 1991, WILSON 1993, LORENZ & HUBERT 1993, GROVES 1994). In many cases, names were merely listed as forms and therefore have no taxonomic value. In the Issues 1 and 2 (1985a, b), however, several *Zoila* were described in a correct trinominal way, which means, as subspecies. Among these is *albanyensis*, which was accepted as taxonomically valid by later authors (e.g. COSSIGNANI & PASSAMONTI 1991, WILSON 1993, LORENZ & HUBERT 1993). The name *orientalis* was described on the same page as *albanyensis*, in exactly the same manner: with a well–recognizable specimen with its origin ("S. Australia"). Strangely, this name was neglected by everyone (RAYBAUDI 1992e, WILSON 1993, and also by myself, when describing *raybaudii* LORENZ 1992).



Fig. 22: Lectotype of *Zoila orientalis*, from The Connoisseur 2: 8 fig. 7C

[18] Originally described as subspecies of *marginata*.

[19] RAYBAUDI (1985b) cited "1980" as date of description of *meridionalis*, but there is no such publication. The earliest citation of the name along with a photograph is RAYBAUDI (1993b).

Also the name *intermedians* is a synonym of *orientalis*. The type figures of *intermedians*, claimed by LOBETTI (1986) to come from the west coast, unmistakably show southeastern shells (text fig. 23): The large dorsal spotting, the irregular margins, the formation of the extremities, and in particular, the absence of a distinct columellar lateral flange identify all three types of *intermedians* as the southeastern population later named *raybaudii*. Also the comparative text given by LOBETTI reveals that he was studying southeastern shells (which were probably sold to him with incorrect locality data). Although in the beginning of the article, LOBETTI (1986) introduced a "forma *intermedians*", in his comparative table the taxonomy is trinominal ("*Zoila marginata intermedians*").



Fig. 23: Syntypes of *intermedians* LOBETTI, all coll. RAYBAUDI

Since the populations of *orientalis* are conchologically distinct and geographically isolated from *marginata*, the rank of *orientalis* as a valid species is proposed here. This step is a consequence of the treatment of other species in the genus in which the situation is similar (*thersites*, *jeaniana*).

3.4. The *rosselli* – group

Characteristic features:
Medium–sized to small, with flaring margins and fragile, rostrate extremities. Spire pointed. Teeth equally distinct on both sides. No embryonic banding. Similar to *marginata* in general shape, but differs by the uniform color of the base and margins and the absence of dorsal spotting. Anatomical differences of radula, female genital system (no bursa copulatrix), and the mantle suggest a distinction from the other species of *Zoila* (WILSON & MCCOMB 1967). One species (*rosselli*).

3.4.1. ***rosselli*** COTTON 1948

In honor of HAROLD ROSSELL[20] Pl. 28 – 31; map 6 uncommon

Reference: *Zoila rosselli* B. C. COTTON (1948) Transactions of the Royal Society of Southern Australia, Vol. 72: 30–31

Holotype see text fig. 24, South Australian Museum. Type locality: Fremantle.

Synonyms: *albolutea* RAYBAUDI 1994d, *lobettiana* RAYBAUDI 1995a

Shell:

Sharp extremities. Dorsum distinctly humped, usually exposing a white window in the black coating. Base and margins very dark, spotted in southeastern specimens, tinted with paler brown in northwestern ones (var. *satiata*). Dental interstices usually lighter. [50(68)19:15]

Distribution, habitat and collecting:

Point Quobba area to Cape Recherche, Western Australia. This species starts to occur in 2 – 3 m but is most common at depths between 25 and 45 m. Few specimens have been trawled at greater depths.

Size range (mm): **30 – 74** Compare with: *marginata*

Rare local color variation:

• ***rosselli*** forma ***edingeri*** RAYBAUDI 1990

In honor of ANDREW EDINGER[21] Pl. 31; map 6 extremely rare

Reference: *Zoila* (*Zoila*) *rosselli edingeri* L. RAYBAUDI MASSILIA (1990b) La Conchiglia, No. 256: 26–30

Holotype see Pl. 31, fig. 2, courtesy RAYBAUDI

Point Quobba area, Western Australia. Entire dorsum golden brown, base somewhat darker reddish. A very rare variation known only from the northwestern population ("*satiata*").

Important geographic variation:

• ***rosselli*** forma ***satiata*** LORENZ & HUBERT 2000

Saturate *rosselli* Pl. 30; map 6 uncommon

Zoila rosselli forma *satiata* F. LORENZ & A. HUBERT (2000) A Guide to Worldwide Cowries, Pl. 125, fig. 11–12

Pt. Quobba to Abrolhos Is., Western Australia. Short, heavy. Dorsum dark red to all black, base paler, often with a tint of orange. Strong, darker teeth, somewhat extending on the columellar side. [52(68)18:17]

[20] Collector of Fremantle, W. Australia, who found the first specimens.

[21] Australian diver and discoverer of this variety.

The beautiful *rosselli* was formerly a rarity treasured by collectors. Intensive collecting by divers along the southwestern coast of Australia has yielded many hundreds of fine specimens. The northern *satiata* is moderately rare.

Only a few specimens of the golden *edingeri* have ever been found, and after the depletion of the *rosselli* populations by divers, and the devastation of the habitat by hurricanes, no more might ever be found. The golden form of *rosselli* is among the highest–priced seashells.

All important aspects of the holotype of *rosselli* are illustrated in the original description. Although it is a decorticated eroded shell lacking the dorsal pigmentation, the assignment to the southwestern population can be ascertained. The population from the northern range limit are heavier, darker, with different dentition, and less flaring extremities. It was named *satiata* at the level of a forma in the second edition of LORENZ & HUBERT's "Guide to Worldwide Cowries".

Spectacular large specimens of *rosselli* are found in the Abrolhos area [62(63)20:17].

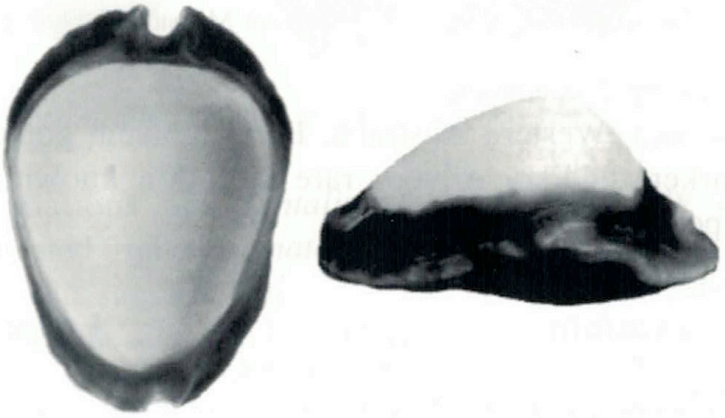


Fig. 24: Holotype of *rosselli* COTTON, courtesy RAYBAUDI

The golden colored *edingeri* occurs within certain *satiata* populations in the north of the range. In agreement with WILSON (1993), BEALS (1997) and LORENZ & HUBERT (2000) it should be regarded as an individual form. A single specimen was collected in which the anterior third was of golden color whereas the rest of the shell was typically dark (Pl. 31, fig. 3, coll. F. HUBER). Spectacular golden individuals are occasionally found in all species of the genus.

In the southeastern part of the range, *rosselli* larger, with a wider aperture, a wide irregular mottled dorsal window, and wide flanged margins. The teeth

are often longer labrally. The base is less callused and shows distinct darker spotting [60(64)19:16]. On a pricelist, such shells were called forma *latistoma*, but no official description seems to exist for this rather distinct population.

There is one report of a variant with orange margins and a white dorsum described and illustrated by BOARD (1979) and reproduced here with reconstructed colors on Pl. 31, fig. 4. Artificially coated and air–brushed imitations of this particular form have been named *albolutea* (see RAYBAUDI 1994e) and *lobettiana* RAYBAUDI 1995 (Pl. 31, fig. 5), both names have no systematic but merely entertainment value.

3.5. The *friendii* – group

Characteristic features:
Small, globular to large elongate shells. Columellar teeth usually reduced midway. Spire pointed. Extremities sharply margined. Margins not flaring. Wavy embryonic banding, spotted margins. Certain resemblance to younger fossils from Indonesia. Three species recognized as valid herein: *friendii*, *jeaniana*, *thersites*.

3.5.1. a **_jeaniana jeaniana_** CATE 1968
In honour of Mrs. JEAN CATE[22] PL. 32 – 36; map 7 moderately rare
Reference: *Zoila friendii jeaniana* C. N. CATE (1968) The Veliger, Vol. 10: 222–224. Holotype deposited in the West Australian Museum. Type locality: Koks Island.

Shell:
Elongate–oval, heavy. Dorsum slightly humped. Base distinctly flattened, margins rather angular. Dentition on columellar side rather distinct. Sharp extremities. Variable coloration from white to very dark dorsally, margins spotted with dark. Base varies from dark brown to black. [72(65)19:17]

Distribution, habitat and collecting:
Montebello Islands to Abrolhos Islands, Western Australia. Found by divers from 35 to 60 m, or trawled from deeper water to 150 m. The dark shallow water *sherylae* has recently been found in large numbers, but divers report a drastic decline of the populations.

Size Range (mm): **30 – 101** Compare with: *friendii, perlae*

[22] Malacologist and wife of CRAWFORD N. CATE.

Local variation:

• *jeaniana* forma *sherylae* RAYBAUDI 1990

In honor of SHERYL EDINGER Pl. 35; map 7 uncommon

Zoila (Zoila) jeaniana sherylae L. RAYBAUDI MASS. (1990c) La Conchiglia, 253–255: 24–27

Point Quobba area, Western Australia. Smaller, with darker tips. Base black. Columellar teeth often less distinct. [66(66)19:18]

The SWPs of *jeaniana* do not differ significantly from DWPs, or better known as "Taiwanese trawled variety". There are several variations in color, of which the "snowy white margined form" is the most spectacular. It has a dense and dark dorsal mottling and white, sparsely spotted margins, separated from the dorsum by a bluish frame (see pl. 34). Such shells have been found by divers at Bernier Island, but have also been trawled. The forma name *sherylae* was proposed for dark pigmented shallow water shells.



Fig. 25: Lectotype of *aurata* RAYBAUDI, from La Conchiglia 120–121: 13

3.5.1.b ***jeaniana aurata*** RAYBAUDI 1979

Golden *jeaniana* Pl. 37 – 39; map 7 rare

Zoila (Zoila) jeaniana aurata L. RAYBAUDI MASSILIA (1979) La Conchiglia 120–121: 11–14

Lectotype see text fig. 25, designated here, coll. RAYBAUDI. Type locality unknown.

Shell:

Oval to rhomboidal. Inflated, often humped. Flattened orange to white base. Dorsal spotting pale, sparse, sometimes absent. Margins rather angular, pale, sparsely spotted. Columellar teeth rather distinct. [78(69)19:17]

Distribution, habitat and collecting:

Somewhere between Dampier and Geraldton, W. Australia, exact range unknown. Trawled from 150 – 250 m. About twenty years ago, this was one of the more readily available *Zoila*. Since the Taiwanese stopped trawling off Western Australia, hardly any specimens have been found.

Size range (mm): **33 – 104** Compare with: *thersites contraria*

The wider shape and the dorsal and marginal pattern distinguish the DWPs of *aurata* from typical *jeaniana*. This taxon is here considered a bathymetrically defined subspecies of *jeaniana*, most common at depths from 100 to 250 m. As in the case of *perlae* and *eludens*, differences in coloration and shell morphology occur at different depths, but in the case of *aurata* there are conchologically intermediate populations from intermediate depths of 70 to 120 m. Specimens of those are shown and discussed on plate 36.

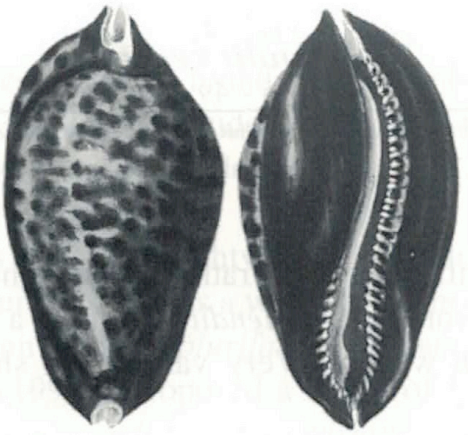


Fig. 26: *Zoila friendii friendii*, illustration from SOWERBY's Thesaurus (1870)

3.5.2.a ***friendii friendii*** (GRAY 1831)

In honor of Capt. FRIEND, F.R.S. Pl. 40 – 44; map 8 common

Reference: *Cypraea friendii* J. E. GRAY (1831) The Zoological Misc. (London), Vol. 1: 35 The holotype is possibly the shell illustrated by SOWERBY II (1870), see text fig. 26. Type locality: Swan River (Perth).

Synonym: *scottii* BRODERIP 1831

Shell:

Elongate, often rather slender, with sharply rostrate extremities. Margins rounded. Columellar teeth absent midway. Base usually dark. Spire conspicuously projecting. Dorsum bluish, with distinct embryonic banding, densely spotted and mottled with brown to black. [74(53)16:#]

Distribution, habitat and collecting:

Abrolhos Islands to Cape Leeuwin (type locality: Swan River, Perth). Ranges in depth between 2 and 100 m. Most common around 15 m on sponges. A pale deep water variation has been trawled off Perth. Perhaps the most popular species, available in various shapes and colors. Once the shells exceed 100 mm, premium prices are paid. The pale deep water form is extremely rare.

Size range (mm): **43 – 109** Compare with: *thersites, jeaniana*

There is a DWP of *friendii* found off the Perth area: slender, with a white base and orange dorsal spotting and distinct columellar teeth, [73(62)21:16]. No name has been introduced so far due to the scarcity of such shells. The dwarf population from the Dunsborough area has not been named separately, while smaller bluish shallow water specimens [50(56)14:#] from the southwestern part of the distribution, from Busselton to Bunbury, resemble the syntypes of *scottii* (Broderip 1831).

3.5.2.b ***friendii vercoi*** Schilder 1930
In honor of J. C. Verco[23] Pl. 45 – 49; map 8 moderately common

Reference: *Zoila friendii vercoi* F. A. Schilder (1930) Zool. Anzeiger, Vol. 92: 74–75
Holotype see Pl. 45, fig. 4, coll. South Australian Museum. Type locality: Esperance.

Shell:
Elongate to globular–inflated, mostly rather lightweight. Middle of base mostly without callus. Differs from typical *friendii friendii* by a relatively wider aperture, broadly bordered with whitish. Very variable in shape and color pattern. [81(66)17:#]

Distribution, habitat and collecting:
Augusta to Cape Recherche, southwestern Australia, farther east in deep water. Known from 5 to 150 m, on various types of sponge, rarely trawled from deeper water. In recent years, this once highly treasured subspecies has been found in fairly large numbers.

Size Range (mm) **60–96** Compare with: *thersites*

color variation:
• ***friendii vercoi*** forma ***candida*** Raybaudi 1996
Shiny white *vercoi* Pl. 49; map 8 moderately rare

Zoila friendii vercoi var. *candida* L. Raybaudi (1996a) World Shells 16: 23
Grayish–yellow shells with no pattern and often conspicuous banding. [73(69)20:#]. For light colored specimens with very sparse pattern, Raybaudi proposed the name *lentiginosa* in the same article.

The name *vercoi* was introduced for the southern population of *friendii*, which tends to be more inflated, with a wider aperture. The holotype of *vercoi* is illustrated in WS 16: 23, fig. 6–8. It shows a comparatively slender southern shell that can still be assigned to *vercoi* in the common usage.

[23] Australian malacologist 1851–1933.

The name *insulata* was given to slender shells found in the area around Hopetoun and Cape Le Grande. The shells are similar to *friendii* because of their narrower shape and greater weight. The introduction of *insulata* was not accompanied by sufficient illustrations. Only a barely recognizable photo showing a dorsal aspect was provided along with the name, but no discussion or comparison. The resemblance of the specimen illustrated as *insulata* to the holotype of *vercoi*, and the existence of other such populations shows that within the range of *vercoi* several more or less slender–shelled populations occur. The name *insulata* does not describe a phylogenetically intermediate form, as could be claimed if it were found in the area between the *friendii* and the *vercoi* ranges, or if somebody decided to set up a row of "intermediates" (see chapter 2.4).

Within all populations of *vercoi*, lightweight individuals lacking any darker pigmentation may be found, as well as a wide spectrum of densely and sparsely spotted, mottled, or even striped (*plurifasciata* Lobetti 1993) stages. In his 1996 article, Raybaudi (1996b) proposed a series of Latin terms for most of these: *albabasis*, *albicans*, *candida*, *griseovirgata*, *lentiginosa*, *pallida*. As mentioned above, these individual variations of *vercoi* must not be confused with the heavy shelled, pale to all–white DWPs from the Great Australian Bight, for which the name *contraria* is to be used according to the original intention of its author (see below).

3.5.3.a ***thersites thersites*** (Gaskoin 1849)
Humpbacked Cowry Pl. 53 – 54; map 9 common

Reference: *Cypraea Thersites* J. S. Gaskoin (1849) Proc. Zool. Soc. London 1848: 90–91
The figure in Sowerby (1870), see text fig. 27, probably shows the holotype. Type locality unknown.

Synonym: *atrata* Sulliotti 1924

Shell:

Heavy, inflated, with slightly rostrate, sharp extremities. Narrow aperture. Columellar teeth absent midway. Spire pointed but covered with callus and hidden by the posterior extremity. Base callused, dark brown to black, becoming white toward the aperture. [77(66)17:12]

Distribution, habitat and collecting:

Ceduna area to west of Cape Jaffa, South Australia. Lives on sponges, often among seaweed at depth ranging from 2 to 45 m, often trawled from 40 – 80 m. A common species. Very dark shells in perfect condition are rare, and

specimens over 95 mm are highly prized. The whitish color variation *eburnea* is extremely rare and seldom seen in collections.

Size range (mm): **60 – 116** Compare with: *friendii*

color variation:

• ***thersites*** forma ***eburnea*** RAYBAUDI 1985

White *thersites* Pl. 51; map 9 extremely rare

Zoila (Zoila) thersites eburnea L. RAYBAUDI MASSILIA (1985b) The Conn. of Seashells 2: 6
Original figure see Pl. 51, fig. 1

Kangaroo Is., South Australia, shallow water. Cream base and margins. Dorsal pattern reduced to absent. Resembling the deep water *contraria*. A rare aberrant color form occurring alongside typical dark shells.

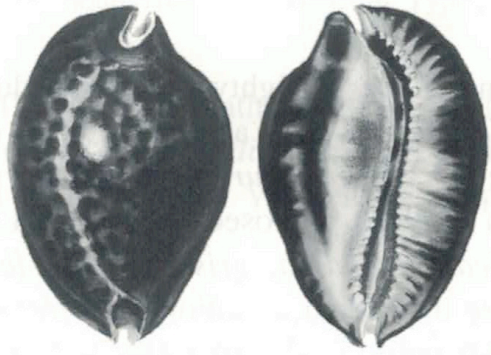


Fig. 27: *Zoila thersites thersites*, illustration from SOWERBY's Thesaurus (1870).

The status of *thersites* as a valid species is agreed upon by most authors. The conchological features of the narrow aperture framed with a wide whitish area, the inflated shell, and the short, mostly hidden spire are consistent; the geographical gap between the SWPs of *vercoi* and the *thersites* range support the evaluation as a valid species.

3.5.3.b ***thersites contraria*** IREDALE 1935

Contrary *thersites* Pl. 50 – 52; map 9 very rare

Reference: *Zoila thersites contraria* T. IREDALE (1935) Austr. Zoologist, Vol. 8: 107
Lectotype see Pl. 53, fig. 2, coll. Australian Museum, Sydney

Shell:

Heavy and inflated. Extremities often rather rostrate. Columellar teeth absent midway. Base plain white, unspotted, slightly convex, callused. Dorsum whitish, with indistinct embryonic bands. Dorsal pattern sparse, pale, or absent. [71(69)17:#]

Distribution, habitat and collecting:
South Australia, between Eucla and the Cape Jaffa area. Trawled from 100 m to 300 m. A rare taxon; perfect shells are much sought after.

Size range (mm): **62 – 96** Compare with: *f. vercoi* forma *candida*

There is some confusion about the usage of *contraria*. IREDALE (1935) described a pale, lightweight shell similar to *thersites* (this type is lost), but gave no illustration or any other precise details. The lectotype (Pl. 52 fig. 2) chosen by WILSON (1993) is a somewhat subadult specimen of a DWP morphologically intermediate between *vercoi* and *thersites*, with a whitish base and sparse or absent dorsal pigmentation.

An essay of these deep water shells was published by RAYBAUDI (WS 17, 1996b). In that paper, the traditional usage of *contraria* as a form of *vercoi* is revised; *contraria* was recognized as being a DWP related to *thersites*, with close resemblance to occasional pale color forms of *vercoi*, for which IREDALE's name was incorrectly used for decades (e.g. LORENZ & HUBERT 1993). RAYBAUDI challenges the correct choice of a subadult lectotype as done by WILSON. The name *profundicola* RAYBAUDI 1996 was introduced and placed in synonymy with *contraria* at the same time: fig. 48 ("*profundicola*") on p. 10 is the same shell as fig. 61 ("*thersites contraria*") on p. 12, and fig. 51 ("*profundicola*") on p. 48 is fig. 53 on p. 11 ("*thersites contraria*").

There are also pale colored shallow water individuals of *thersites* for which the varietal name *eburnea* is in common use. These rare, very beautiful variants are conchologically inseparable from some deep water specimens. To summarize the problematic situation, there are three types of conchologically similar shells:

1) A pale grayish–banded variation of *vercoi* from the Albany – Esperance area, found at 5 to approximately 80 m, alongside typical dark pigmented *vercoi.*

2) A pale orange–mottled to all–white variety of *thersites* found in moderately shallow water alongside typical *thersites* (= forma *eburnea*).

3) The "true" *contraria* from deep water, found offshore along an area between Cape Recherche and Ceduna. Neither *vercoi* nor *thersites* are found in the area inhabited by these DWPs. I consider *contraria* a deep water subspecies of *thersites* with a distribution reaching far west in deep water.

A common error in the literature is to declare all pale–shelled individuals of either *vercoi* or *thersites* as "ecological variations" – no difference in the ecology of dark–shelled and pale–shelled individuals exists in the areas where they occur side by side.

But what exactly causes the variability? WILSON (1993) interprets the formation of patterns a "phenotypic response without a genetic basis". If this were the case, then why do two individuals living together respond differently to the same ecological factors? Individual genetic variability influences the formation of color and pattern, and the higher the genetic variability, the greater the spectrum of conchological variability under identical ecological conditions.

The genetic potential to produce this phenotypical variability is not constant. The slender–shelled *vercoi* population from the Hopetoun area, for instance, hardly ever produces patternless variants, nor does *friendii friendii* from the west coast. In *thersites*, the shallow water forma *eburnea* exists almost exclusively in a small area off Kangaroo Island.

Phylogenetically, *contraria* may be considered an archaic member of the genus to which the shallow water *thersites* and *vercoi* are closely related: both still bear conchologically extreme "off–color"[24] alleles within (some of) their populations. In *vercoi*, those become more common with depth, and we here face an example of true intermediate forms. One consequence of this phenomenon, as proposed by WILSON (1993), is to consider *vercoi* and *thersites* subspecies of *friendii*, and the wide range of DWPs as "forms". Geographically and conchologically, the SWPs of *vercoi* and *thersites* (including their pale variations) are distinct. The DWPs of *contraria* connect them conchologically, or to be more precise, their rare pale color variants.

The geographic distance between *vercoi* and *thersites* has supported a considerable degree of genetic separation, as phenotypical *thersites* are never found among *vercoi* populations and vice–versa. The possibility of genetic exchange between these SWPs over a distance of almost one thousand kilometers is very unlikely. The rising percentage of pale–shelled individuals of *vercoi* at greater depth is an interesting phenomenon that might be interpreted as a visible result of a gradual speciation process, but other interpretations may as well be correct, e.g. that of WILSON 1993.

[24] or patternless, not to confuse with the extremely rare "golden forms".

My proposal is to distinguish between the extremes and to treat conchological intermediates individually, as either pale forms of *vercoi* or *thersites*, depending on the locality, depth, and community they originate from.

The first task[25] of a taxonomist is to provide names for biological units and sub–units (see also SCHILDER 1966a). It makes little sense to unite the entire *friendii* group because of the difficulties one might have with assigning certain shells to either of the names taxonomists have provided. Hopefully the treatment of the *friendii*–group as proposed here will facilitate communication about its diversity .

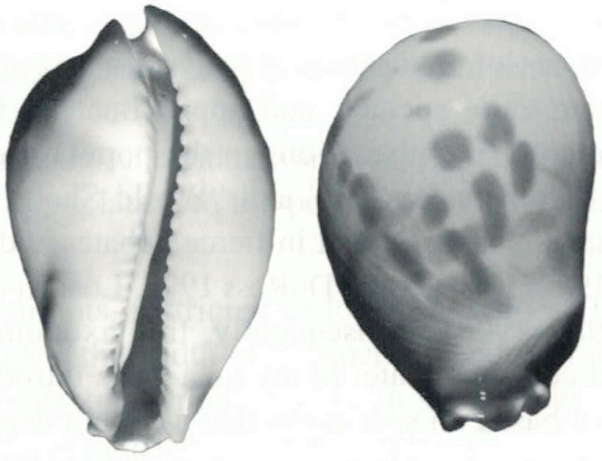


Fig. 28: The famous "two headed *venusta*": *Zoila venusta roseopunctata*, an abnormal specimen with two siphonal canals, approx. 80 mm, coll. STACEY. The diver who found it reported that the shell had a split siphon but only one head (G. SMITH 1982).

[25] The second task of the taxonomist, to give clear definitions and decent illustrations along with the names, has not been fulfilled by some authors.

4. Discussion

The genus *Zoila* has always attracted both, amateur collectors and professional malacologists. New findings, interesting specimens (see text fig. 28) or range extensions have always been incidents of high interest (e.g. Board 1979, Gurr 1981a, 1981b, Laws 1966, Leehman 1978–1980, Schilder 1966d, 1966e, Smith 1982). On the other hand, the genus has a relatively short history of scientific research (Iredale 1935, 1939, Cate 1962, 1964, 1968, Laws 1966, Schilder 1963b, 1966c, Summers 1961, Wilson & Summers 1966 and Wilson & McComb 1967). In the late seventies and early eighties, many new discoveries were made, first because of extensive trawling conducted by the Taiwanese fishing fleet off the Western Australia coast, and secondly, because of the activities of scuba divers.

The dramatic situation concerning taxonomy of the genus started in the late seventies, when Luigi Raybaudi Massilia of Rome started comprehensive conchological analysis of thousands of specimens, resulting in three new subspecies and three valid species, and approximately 30 forms (Raybaudi 1978 – 1996). The colorful publications in the popular–scientific magazines "La Conchiglia", "The Connoisseur" and "World Shells" triggered a lot of interest among amateurs and resulted in fierce debates and many descriptions (Biraghi 1993a,b, 1994, Chandler & DuRoss 1997, Lobetti–Bodoni 1986, 1992, 1993, Raybaudi 1985–1996). Consequently, the taxonomic situation of the genus *Zoila* is in a confused state. Many taxa were introduced in a careless, awkward way, often based on specimens that were not deposited in museums. Some names are commonly used in a way not supported by the type material. I have tried to locate illustrations of all the important type specimens and to review the original descriptions in order to find the earliest name for each taxon which was introduced in a relatively sensible way. Only descriptions which met the following criteria were taken into account for subspecies– and species–names in accordance with articles 45.5 and 45.6 of the ICZN (International Code of Zoological Nomenclature, see Kraus 2000):

- Defined authorship in a recognized publication
- Recognizable illustration of type specimens
- A discussion in written form supported by the illustrated type
- A trinominal usage of the name

Descriptions meeting those criteria are marked with (!). Those synonyms considered useful for the distinction of a definable variation have been marked (*), invalid names are indicated with §, whenever one or more of the above

criteria were not met by the descriptions. In table 2 (at the end of this chapter), the result of this evaluation is shown. Sixty–four names for living *Zoila* were found in the literature, forma names that were given several times to different species (e.g. *nigerrima*, *nana*, ect.) are excluded. Twelve species are recognized as valid following the above–listed definition of species(see chapter 3.2), seven taxa are geographically defined subspecies in good standing. Fourteen synonyms were chosen as forma names for reasonably consistent individual or local variations.

Wilson & Summers (1966) gave a detailed comparison of *Zoila friendii, vercoi* and *thersites*. They postulated that "Diagnostic characters used to separate subspecies or closely related species must be relatively consistent and characteristic of a geographical region not just a local population. They should be discontinuous. Clinal characters are useful in few circumstances, while eco–phenotypic and genetic variants restricted to local populations, or demes, are unacceptable as systematic characters." In their work, a distinction is made between the following "variant categories" for *Zoila friendii*:

1: "Intra–locality variants": individual variations, e.g. position of dorsal blotches, position of the spire in relation to the posterior extremity (compare e.g. Pl. 43 fig. 7 and 8).

2: "Inter–locality variants, restricted to localized demes (i. e. no geographic pattern)": As examples, the width of the aperture and overall size are listed. In this work, the category of "forma" applies in some cases, e.g. *rosselli* forma "*edingeri*", *marginata albanyensis* forma "*nimbosa*".

3: "Geographically continuous variants, i. e., clinal characters": examples given are the relative width of the shell and the aperture. In this work, the term subspecies applies, e. g. *friendii friendii* and *friendii vercoi*, *jeaniana jeaniana* and *jeaniana aurata.*

4: "Geographically discontinuous variants": presence or absence of columellar teeth are given as example with reference to the northwestern "variant" of *friendii* that was later described as *jeaniana*[26]. In this book, the term species applies in such cases, e.g. in the separation of *friendii* from *thersites* and *jeaniana.*

[26] Wilson 1993 considers *jeaniana* a subspecies of *friendii*, along with *thersites* and *vercoi.*

The integral approach of their work, in my opinion, does not give credit to the modern taxonomist's approach to biodiversity. Evolutionists have identified local populations (demes) as a first step in a speciation process (SIEWING 1982); particular attention must be paid to them. Modern taxonomists tend to choose a differential approach by subdividing local populations with consistent features.

Claiming that "local variants" had no "geographic pattern" makes little sense considering the vast ranges of *Zoila*, stretching across hundreds of kilometers of coastline. It is true that most of the category 2 demes (isolated populations encircled within the wide range of some taxa, e.g. the "*nimbosa*" forms of *marginata albanyensis*), might have little importance in the systematic taxonomy of the species. But as such demes do exist, the communication among taxonomists is facilitated when a forma name ("without taxonomic value") is at hand. At long last, in the evaluation of the taxonomically significant populations discussed in this work, none belongs to either category 1 or 2 of WILSON & SUMMERS (1966).

Defining a species as the sum of those populations retaining the hypothetical potential to interbreed successfully, implies that geographically and/or ecologically isolated populations bear the problem that, in practise, we cannot disprove validity unless we induce successful copulation of two candidates breed successfully over multiple generations to realize effects of reduced fertility or viability on the offspring generations.

Especially in those cases where a wide geographic or bathymetric distance between conchologically differing populations inhibits genetic exchange, the species rank appears a more appropriate solution in systematic taxonomy rather than "geographically discontinuous variants". In the relatively fewer cases with clinal characters (category 3 of WILSON & SUMMERS 1966), the status of a subspecies was chosen herein.

The debate about the number of valid species and the status of certain taxa is especially fierce in the genus *Zoila*. I would agree to almost any proposal as long as it is applied in a consistent way and gives reasonable credit to the fact that e.g. *thersites* and *jeaniana* are not synonymous. WILSON (1993), for instance, recognizes *perlae, eludens, mariellae* and *decipiens* as valid species, but on the other hand, he lumps *jeaniana* with *friendii*; BURGESS (1985) treats those groups in the opposite way. This, in my opinion, is not consistent because the geographic separation and the conchological differences between all of these

taxa are of a comparable qualitative nature (see chapter 2.3). Table 1 (at the end of this chapter) compares the assignments of taxa made here with those of the works of BURGESS (1985), WILSON (1993), RAYBAUDI (1996), and LORENZ & HUBERT (2000).

Herein, the systematic arrangement and evaluation of *Zoila* populations is done on the basis of shells, their bathymetric and geographic origin, and their hosts. All taxa were described based on this. Little could be derived from anatomic studies as far as I have been able to learn. WILSON & MCCOMB (1967) studied the anatomy of several species of *Zoila* and found *rosselli* to differ from all others by the absence of a bursa copulatrix. This part of the female reproductive system has been subject of intense study in the Cypraeidae (KAY 1960, GOSLINER & LILTVED 1985) and was given high systematic importance. Even within a single species organ complexes may vary (RAU 1934, LORENZ 2000); comprehensive studies on the ontogenetic and infraspecific variability of organ complexes within a single species of the family Cypraeidae are needed for a better evaluation of anatomical differences.

The radula is an organ that was very thoroughly examined by researchers. It might be variable even within a species (TROSCHEL 1863, SCHILDER 1963a, BRADNER & KAY 1996, LORENZ 2000). WILSON & SUMMERS 1966 compared the radulae of *friendii friendii, f. vercoi* and *thersites*, with the result that there are only slight radula differences between the populations, and the authors concluded that these were not sufficient to support a distinction.

The results of comparative genetic analyses will one day provide clues for a new modern systematics of the Cypraeidae; this certainly has to imply also a new "molecular taxonomy". For the time being, the entire systematic arrangement of the family is based on conchological comparison and in a few cases, on anatomical features, and present–day taxonomy gives credit to those factors only.

Personally, I doubt that at this stage anyone will manage to offer an infallible, universally accepted systematics for all the different scenarios of speciation observed in the Cypraeidae, especially when it comes to evaluating lower level taxa. The question whether a taxon is a valid species, or a subspecies of another, is overemphasized in present–day debates, in my opinion.

At times in which the registration of biodiversity can hardly keep pace with the destruction of worldwide biotopes, giving names along with precise descriptions and good illustrations for separable populations and demes is the task of a modern taxonomist. To ensure precise communication among amateurs and professionals in the field of malacology, it is advisable to work with a differential rather than integrating, retrogressive taxonomy. In other words, different shells should have separate names so that we can talk about them.

Table 1: Comparison of the systematic assignments of the taxa of *Zoila* of recent authors

Taxon	BURGESS 1985	WILSON 1993	RAYBAUDI (World Shells)	LORENZ & HUBERT 2000	herein
albanyensis	-	ssp. *marginata*	ssp. *marginata*	ssp. *marginata*	ssp. *marginata*
aurata	-	f. of *f. jeaniana*	ssp. *jeaniana*	ssp. *jeaniana*	ssp. *jeaniana*
bataviensis	-	-	-	-	ssp. *ketyana*
contraria	syn. *friendii*	f. of *f. thersites*	undecided	f. of *f. vercoi*	ssp. *thersites*
consueta	-	ssp. *marginata*	syn. *marginata*	syn. *marginata*	f. of *marginata*
decipiens	valid	valid	valid	valid	valid
eludens	-	valid	valid	ssp. *perlae*	valid
episema	syn. *venusta*	syn. *venusta*	ssp. *venusta*	ssp. *venusta*	ssp. *venusta*
intermedians	-	syn. *marginata*	ssp. *marginata*	f. of *marginata*	syn. *orientalis*
jeaniana	valid	ssp. *friendii*	valid	valid	valid
ketyana	syn. *marginata*	ssp. *marginata*	ssp. *marginata*	ssp. *marginata*	valid
marginata	valid	valid	valid	valid	valid
mariellae	syn. *decipiens*	valid	valid	valid	valid
orientalis	-	syn. *marginata*	syn. *m. rayb.*	syn. *marginata*	valid
perlae	syn. *decipiens*	valid	valid	valid	valid
raybaudii	-	syn. *marginata*	ssp. *marginata*	ssp. *marginata*	syn. *orientalis*
roseopunctata	-	syn. *venusta*	ssp. *venusta*	ssp. *venusta*	ssp. *venusta*
rosselli	valid	valid	valid	valid	valid
thersites	syn.. *friendii*	ssp. *friendii*	valid	valid	valid
venusta	valid	valid	valid	valid	valid
vercoi	syn. *friendii*	ssp. *friendii*	ssp. *friendii*	ssp. *friendii*	ssp. *friendii*

Table 2: Names introduced for *Zoila*. Only those descriptions were taken into account for subspecies and species names which had defined authorship in a recognized publication, an illustration of a type specimen, a discussion in written form, and trinominal usage in those descriptions published after 1984, according to the ICZN. Descriptions meeting those criteria are marked with (!). Synonyms used as forma names have been marked (*), invalid names are indicated with §, wherever one or more of the above criteria were not met by the descriptions. The names *albolutea* and *lobettiana* both have no taxonomic value as the descriptions were based on manipulated shells.

Taxon	Author	Status	Assignment	Reference
albabasis	RAY. 1996	syn.	*friendii vercoi*	World Shells 17: 3–15 (§)
albanyca	RAY. 1995	syn.	*v. roseopunct.*	World Shells 15: 24 (§)
albanyensis	RAY. 1985	**ssp.**	*marginata*	The Conn. of Seash., 1: 8–9 (!)
albicans	RAY. 1996	syn.	*friendii vercoi*	World Shells 17: 3–15 (§)
albolutea	RAY. 1995	syn.	*rosselli*	World Shells 11, backcover (§)
albosignata	RAY. 1985	syn.	*rosselli*	The Conn. of Seash., 1: 8–9 (§)
armeniaca	RAY. 1985	syn.	*v. venusta*	The Conn. of Seashells 2: 7 (§)
atrata	SULLIOTI 1924	syn.	*decipiens*	Contr. Stud. Cypraeidae, 6: 1 (§)
atrata	SULLIOTI 1924	syn.	*t. thersites*	Contr. Stud. Cypraeidae, 6: 1 (§)
aurata	RAY. 1979	**ssp.**	*jeaniana*	La Conchiglia 120/121: 11–14 (!)
bakeri	GATLIFF 1916	syn.	*v. venusta ?*	Victorian Naturalist 32: 147 (!)
bataviensis	LO. & MORRISON	**ssp.**	*ketyana*	herein (!)
brunea	HIDALGO 1906	syn.	*v. episema*	M. Esp. Mem. Real Acad. Cienc., Madr. 25 (!)
caelestis	RAY. 1985	syn.	*f. friendii*	The Conn. of Seashells 1: 6–7 (§)
candida	RAY. 1996	syn.	*f. vercoi**	World Shells 17: 3–15 (§)
catei	SCHILDER 1963	syn.	*v. venusta*	The Veliger 5/4: 125 (!)
consueta	BIRAGHI 1993	syn.	*m. marginata**	La Conchiglia 25 (266): 39–42 (!)
contraria	IREDALE 1935	**ssp.**	*thersites*	Austr. Zoologist, Vol. 8: 107 (!)
decipiens	SMITH 1880	**valid**		Proc. Zool. Soc. Lond.: 482–483 (!)
delicatura	CH. & DUR. 1997	syn.	*eludens**	World Shells 20: 65–67 (!)
dorata	RAY. 1985	syn.	*venusta venusta*	The Conn. of Seashells 2: 7 (§)
eburnea	RAY. 1985	syn.	*t. thersites**	The Conn. of Seashells, No. 2: 6 (§)
edingeri	RAY. 1990	syn.	*rosselli**	La Conchiglia, No. 256: 26–30 (!)
eludens	RAY. 1991	**valid**		La Conchiglia, No. 260: 8–15 (!)
episema	IREDALE 1939	**ssp.**	*venusta*	Austr. Zool., Vol. 9: 300–301 (!)
extrema	RAY. 1992	syn.	*orientalis*	World Shells 1: 95 (§)
friendii	GRAY 1831	**valid**		The Zool. Misc., London 1: 35 (!)
griseovirgata	RAY. 1996	syn.	*friendii vercoi*	World Shells 17: 3–15 (§)

Table 2 cont.

hypermarginata	RAY., ET AL. 1993	syn.	*k. ketyana**	World Shells 7: 3–14 (§)
insulata	RAY. 1985	syn.	*friendii vercoi*	The Conn. of Seash. 1: 6–7 (§)
intermedians	LOBETTI 1986	syn.	*orientalis*	The Conn. of Seash. 12: 20–22 (!)
jeaniana	CATE 1968	**valid**		The Veliger, Vol. 10: 222–224 (!)
ketyana	RAY. 1978	**valid**		La Conchiglia, No. 106: 11–14 (!)
lentiginosa	RAY. 1996	syn.	*f. vercoi**	World Shells 17: 3–15 (§)
lobettiana	RAY. 1995	syn.	*rosselli*	World Shells 13 p. 15-17 (§)
lutea	RAY. 1993	syn.	*k. ketyana**	World Shells 7: 3–14 (§)
marginata	GASKOIN 1849	**valid**		Proc. Zool. Soc. Lond. 1848:91–92 (!)
mariellae	RAY. 1983	**valid**		La Conchiglia, No. 176: 11–14 (!)
meridionalis	RAY. 1993	syn.	*orientalis*	World Shells 6: 8 fig. 19 (§)
nimbosa	RAY. 1994	syn.	*m. albany.**	World Shells 9: 23 (§)
nordica	RAY. 1995	syn.	*v. venusta*	World Shells 15: 24 (§)
orientalis	RAY. 1985	**valid**		The Conn. of Seashells 1: 8–9 (!)
orientalis	RAY. 1990	syn.	*v. roseopunct.*	La Conchylia 257: 40-41 (!)
pallida	RAY. 1996	syn.	*friendii vercoi*	World Shells 17: 3–15 (§)
perlae	LOPEZ & CHI. 1975	**valid**		The Veliger, Vol. 18: 84–85 (!)
plurifasciata	LOBETTI 1993	syn.	*f. vercoi*	World Shells 6: 40–42 (§)
profunda	RAY. 1990	syn.	*v. roseopunct.**	The Conn. of Seashells 23: 26–27 (§)
profundicola	RAY. 1992	syn.	*t. contraria*	World Shells 17: 3–15 (!)
raybaudii	LORENZ 1992	syn.	*orientalis*	Schr. Malakozool., Nr. 5: 13–18 (!)
roseodorata	RAY. 1985	syn.	*venusta venusta*	The Conn. of Seashells, No. 2: 7 (§)
roseoimmaculata	RAY. 1985	syn.	*v. roseopunct.**	The Conn. of Seashells, No. 2: 6 (§)
roseopunctata	MELVILL 1888	syn.	*venusta*	Mem. Manch. Lit. Soc. (4), 1: 239 (n.nd.) (§)
roseopunctata	RAY. 1985	**ssp.**	*venusta*	The Conn. of Seashells, No. 2: 7 (!)
rosselli	COTTON 1948	**valid**		Trans. Roy. Soc. S. Austr., Vol. 72: 30–31 (!)
satiata	LO. & HU. 2000	syn.	*rosselli**	A Guide to Ww. Cowr. 2: 50, pl. 125 (§)
scottii	BRODERIP 1831	syn.	*friendii friendii*	Zoological Journal Vol. 5: 330 (!)
septemtrionalis	RAY. 1985	syn.	*friendii friendii*	The Conn. of Seash., No. 1: 6–7 (§)
sherylae	RAY. 1990	syn.	*j. jeaniana**	La Conchiglia, 253–255: 24–27 (!)
sorrentensis	SCHILDER 1963	syn.	*v. episema**	The Veliger, Vol. 5: 126–127 (!)
sperata	RAY. 1995	syn.	*v. roseopunct.*	World Shells 15: 24 (§)
thatcheri	COX 1869	syn.	*venusta venusta*	Proc. Zool. Soc. London: 358 (!)
thersites	GASKOIN 1849	**valid**		Proc. Zool. Soc. Lond., 1848: 90–91 (!)
venusta	SOWERBY 1847	**valid**		Proc. Linn. Soc. London, Vol. 1: 314 (!)
vercoi	SCHILDER 1930	**ssp.**	*friendii*	Zool. Anzeiger, Vol. 92: 74–75 (!)

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Distribution maps and color plates

The distribution maps were designed according to the information given to me by dealers and divers. Slight inaccuracies are possible. The maps will, however, demonstrate the general phenotyical trend of the populations along the Australian coast.

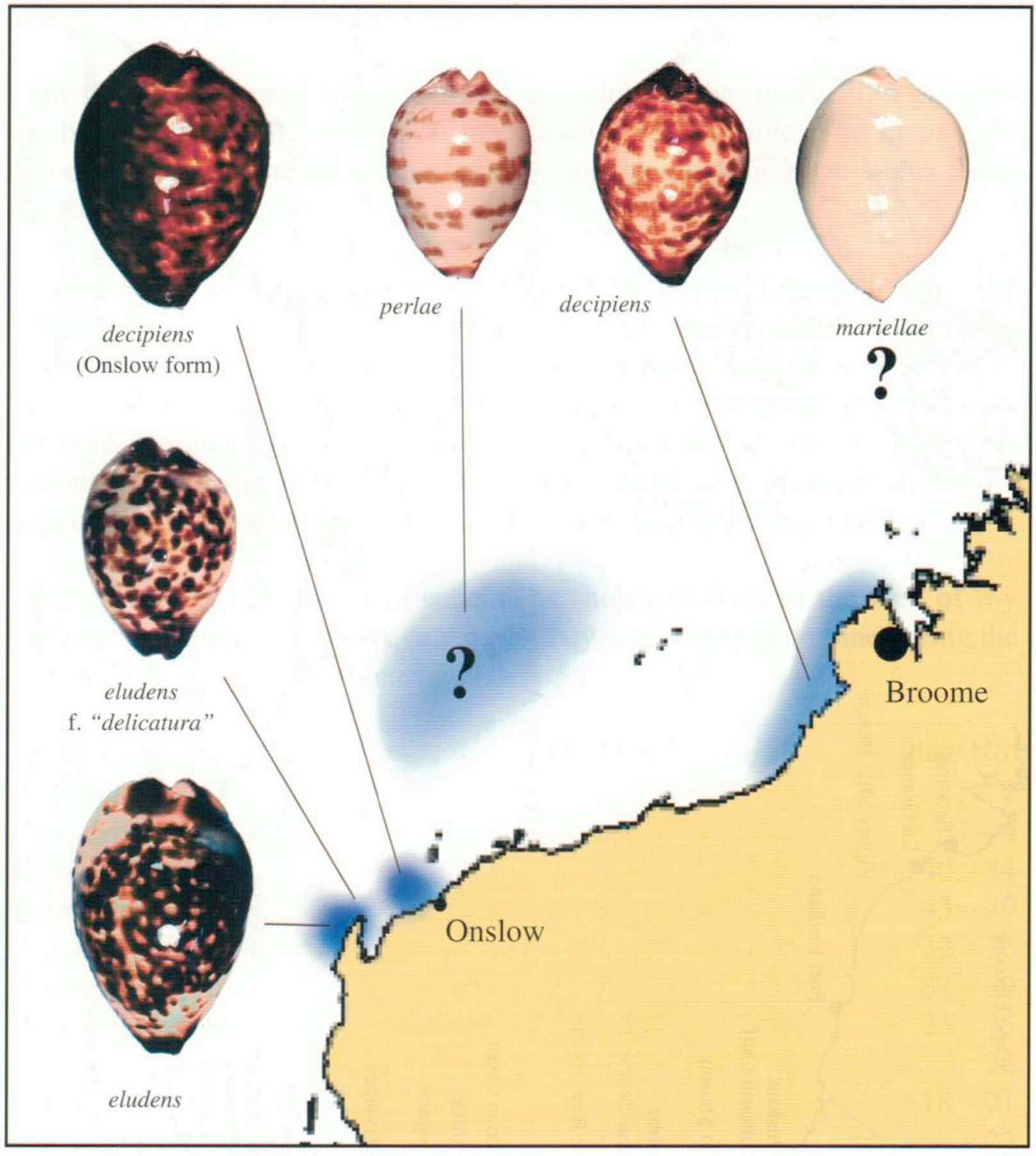
In the color plates, specimens mainly from the author's collection and the collections GABRIELLI, DEMERTZIS and RAYBAUDI are shown. Other illustrations were taken from "World Shells and "The Connoisseur", courtesy L. RAYBAUDI MASSILIA. The sources of the photographs are given, as well as the size, whenever possible. No guarantee can be given that the locality data in the captions is correct, as collecting data is often subject to manipulation. Information that did not come from the original source has therefore been listed in quotes.

The assignment of names to specimens shown is done to the best of my knowledge; different opinions, whenever they were expressed to me during the writing of this book, have been annotated.

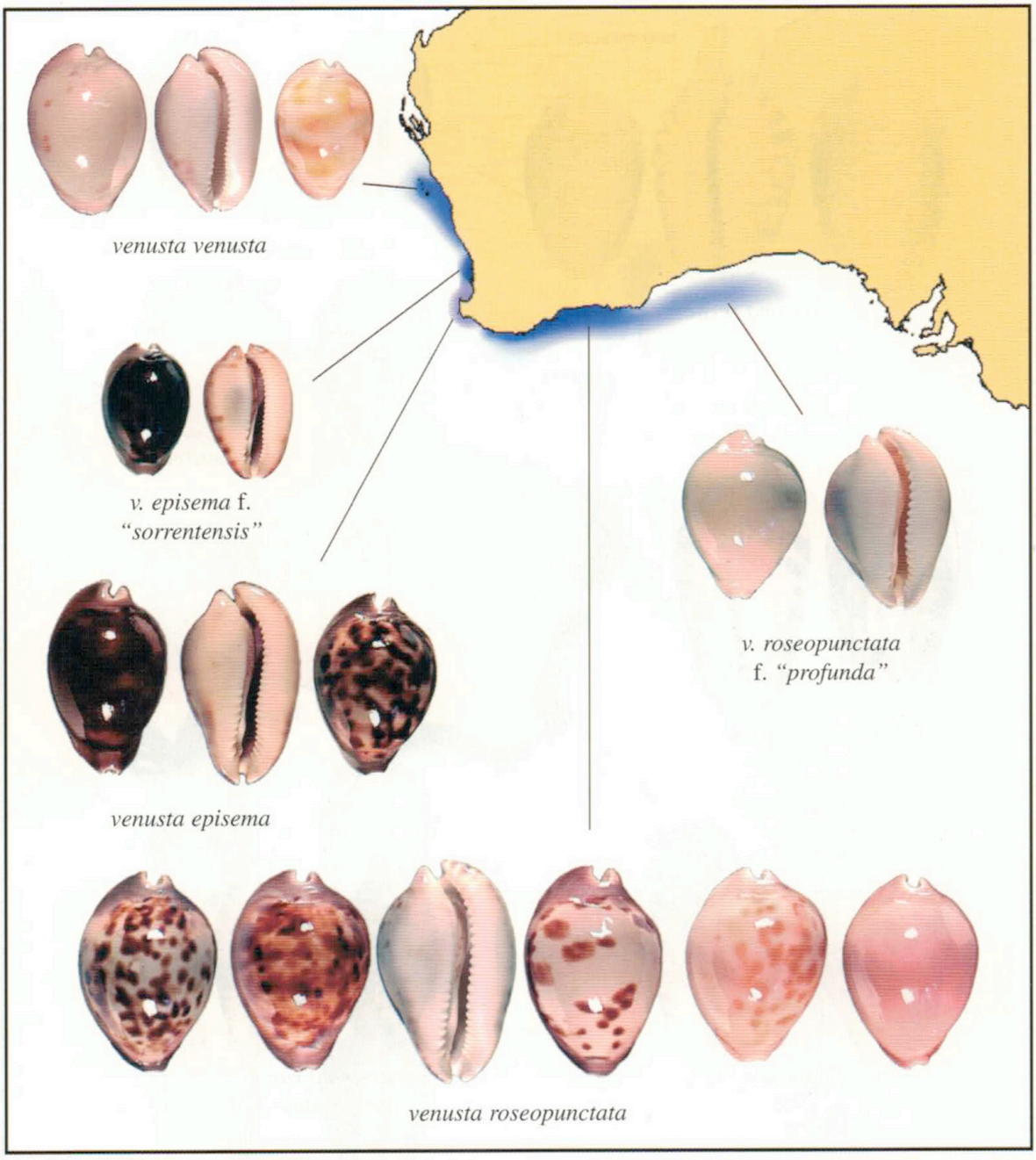
Species, subspecies	Map No.	Plate No.
Z. decipiens	2	1 – 2
Z. eludens	2	3 – 4
Z. friendii friendii	8	40 – 44
Z. friendii vercoi	8	45 – 49
Z. jeaniana jeaniana	7	32 – 36
Z. jeaniana aurata	7	37 – 39
Z. ketyana ketyana	4 – 5	23 – 25
Z. ketyana bataviensis	4 – 5	26
Z. marginata marginata	4 – 5	18 – 21
Z. marginata albanyensis	4	22
Z. mariellae	2	6, 39
Z. orientalis	4	27
Z. perlae	2	5
Z. rosselli	6	28 – 31
Z. thersites thersites	9	53 – 54
Z. thersites contraria	9	50 – 52
Z. venusta venusta	3	7 – 8
Z. venusta episema	3	9 – 11
Z. venusta roseopunctata	3	12 – 17



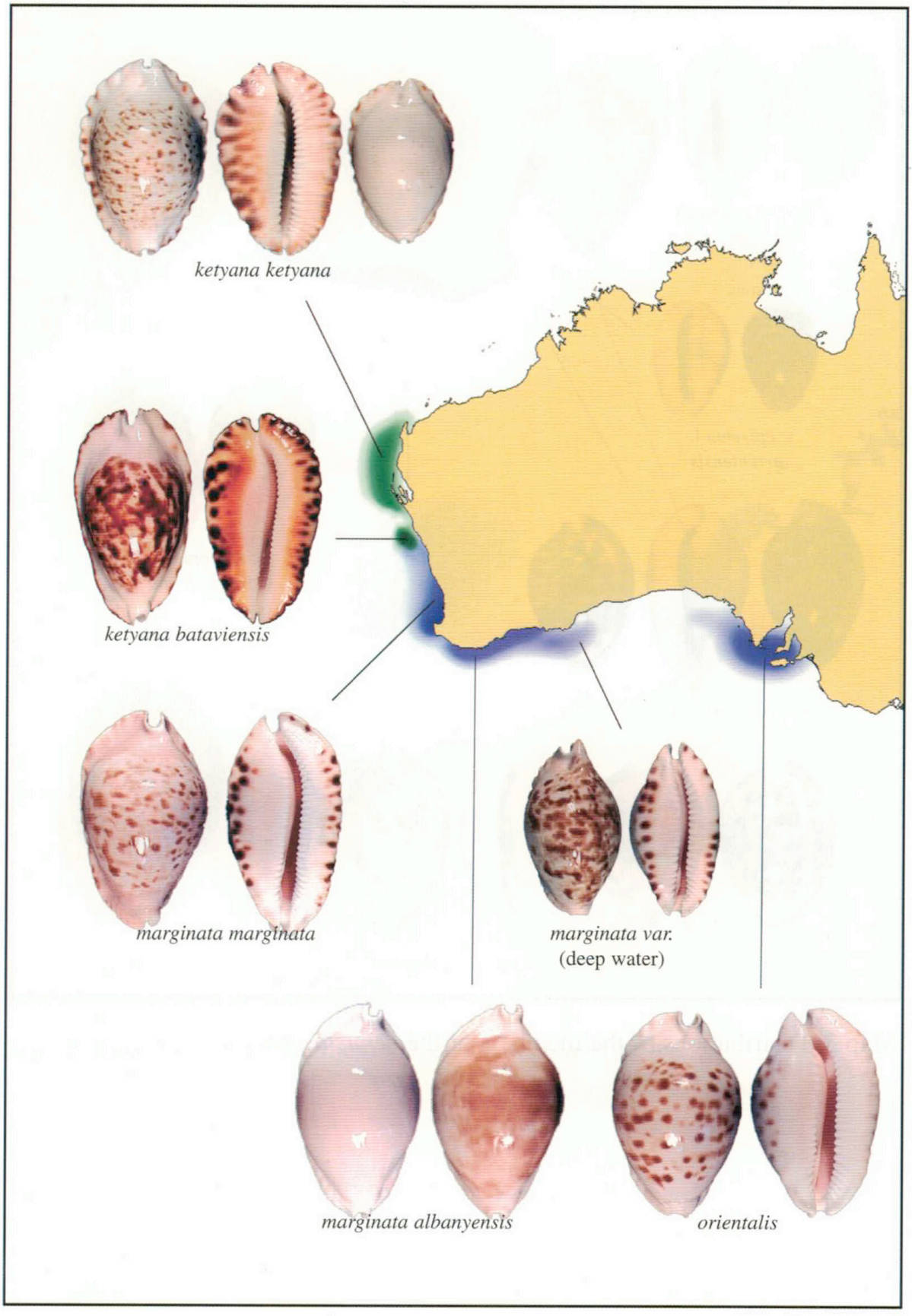
Map 1: Overview map



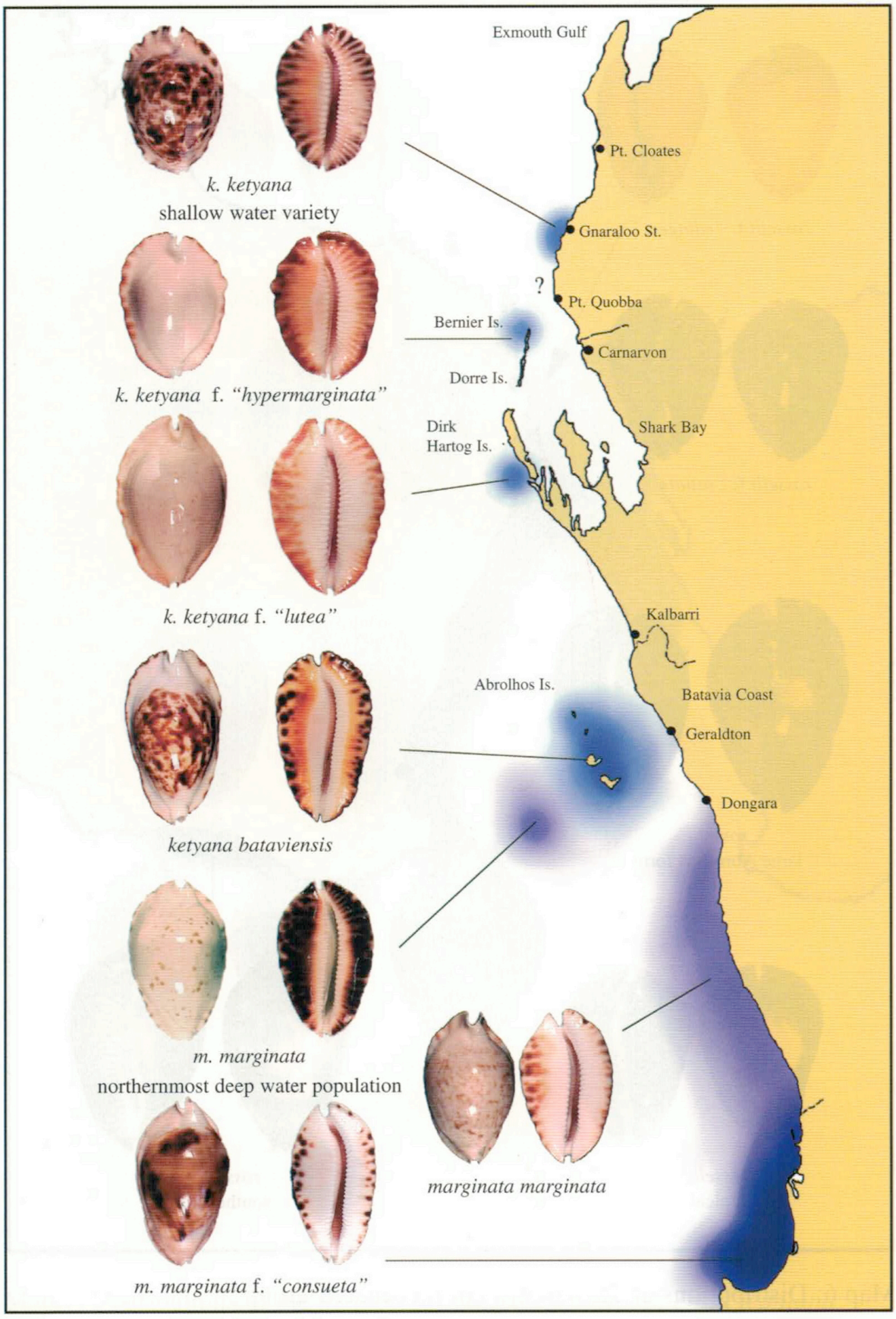
Map 2: Distributions of the members of the *decipiens*-group



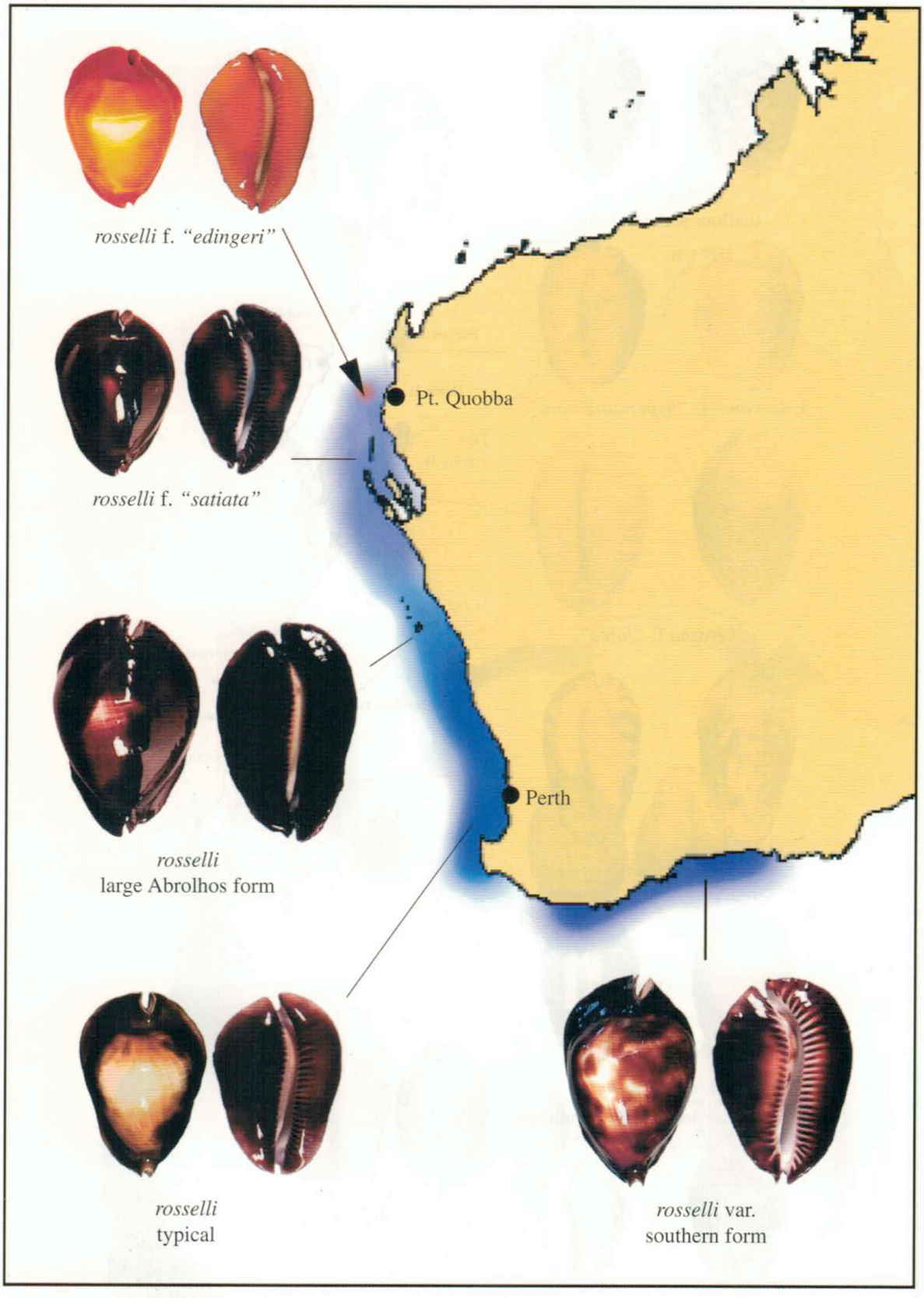
Map 3: Distributions of the members of the *venusta*-group



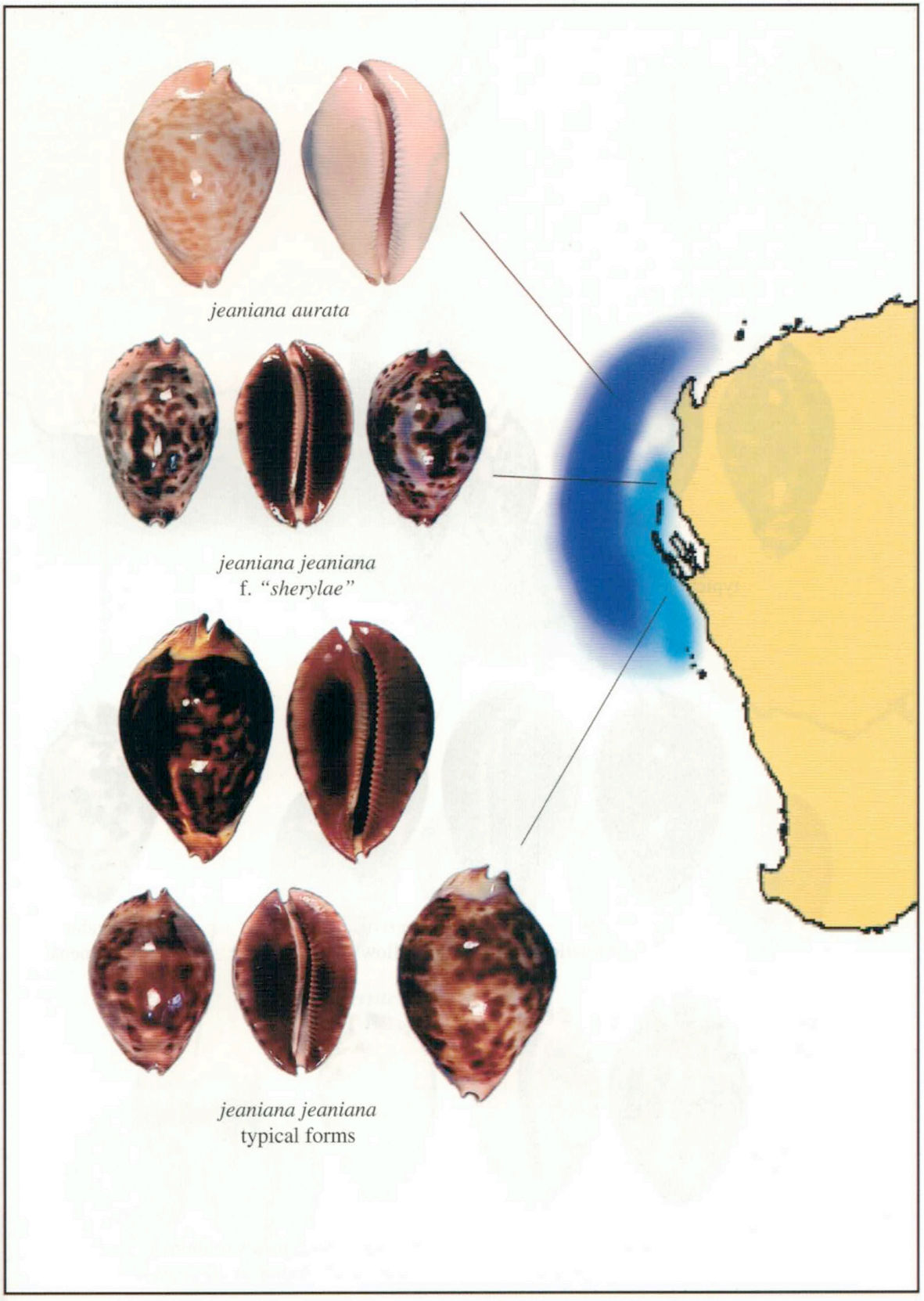
Map 4: Distributions of the members of the *marginata*-group



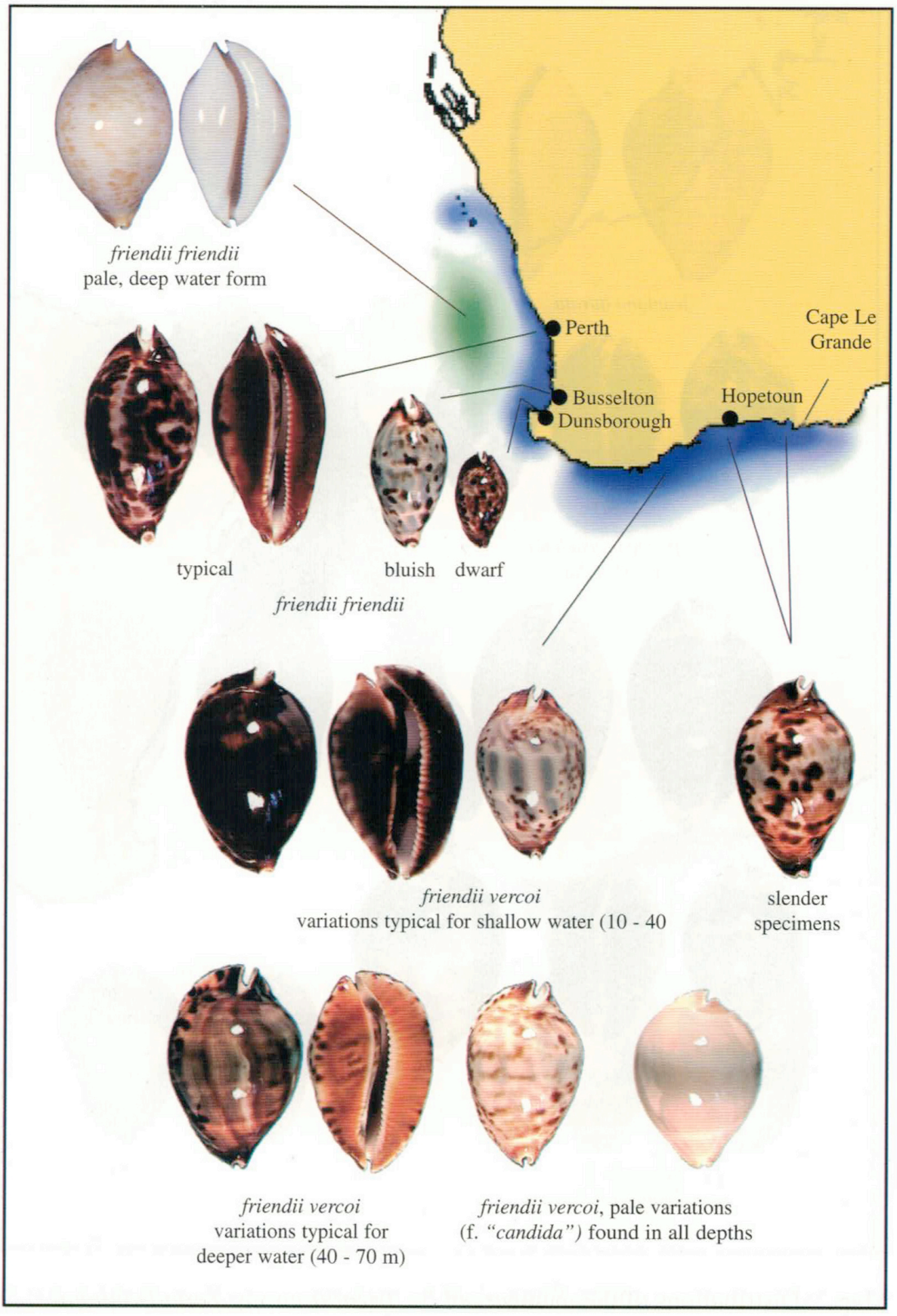
Map 5: Distributions of the members of the *marginata*-group from the Western Coast



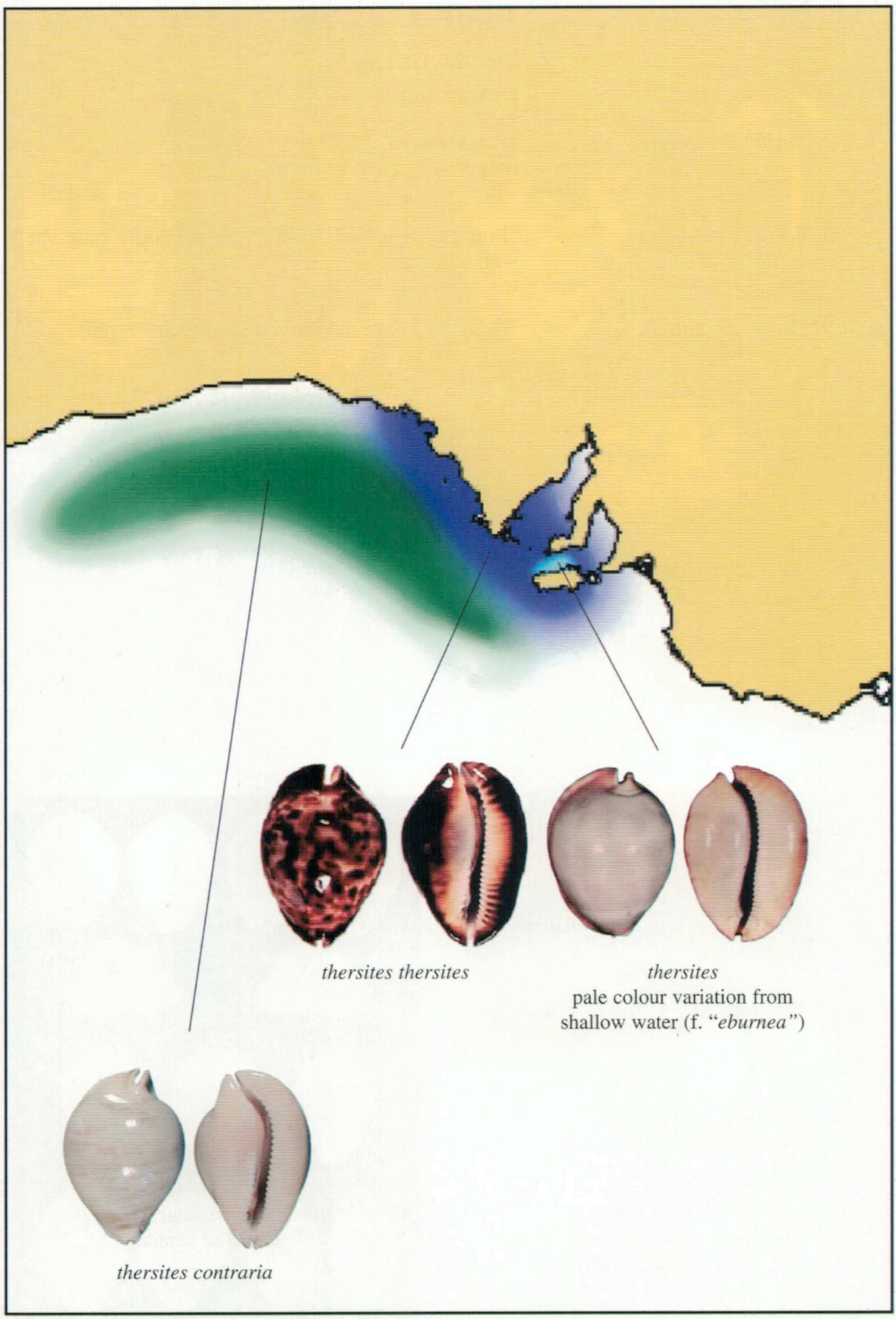
Map 6: Distributions of the members of the *rosselli*-group



Map 7: Distributions of the members of the *friendii*-group: *Zoila jeaniana*



Map 8: Distributions of the members of the *friendii*-group: *Zoila friendii*



Map 9: Distributions of the members of the *friendii*-group: *Zoila thersites*

Plate 1

Zoila decipiens

Typical specimens

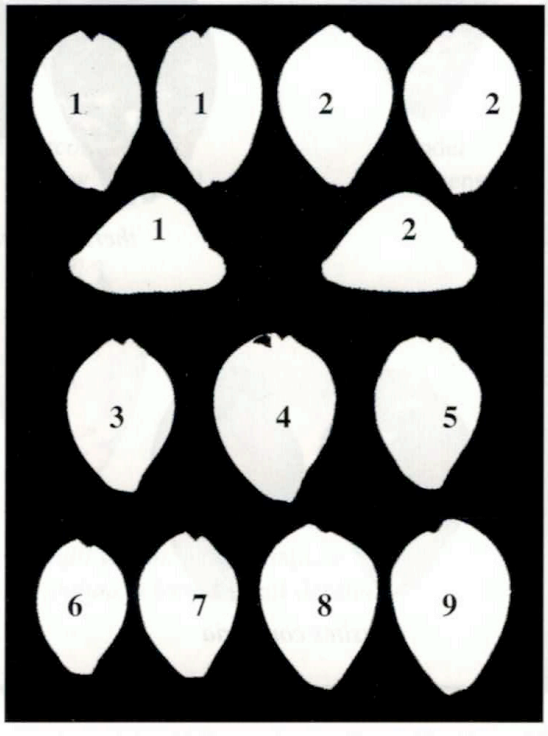
1 – 2 ***Zoila decipiens*** "Broome area, 7 – 20 m" (largest specimen 52 mm).

3 ***Zoila decipiens*** "Port Hedland" (51 mm). Exceptionally pale shell with tall spire.

4 – 9 ***Zoila decipiens*** "Broome, 5 – 25 m" (largest specimen 57 mm).



Zoila decipiens, typical form



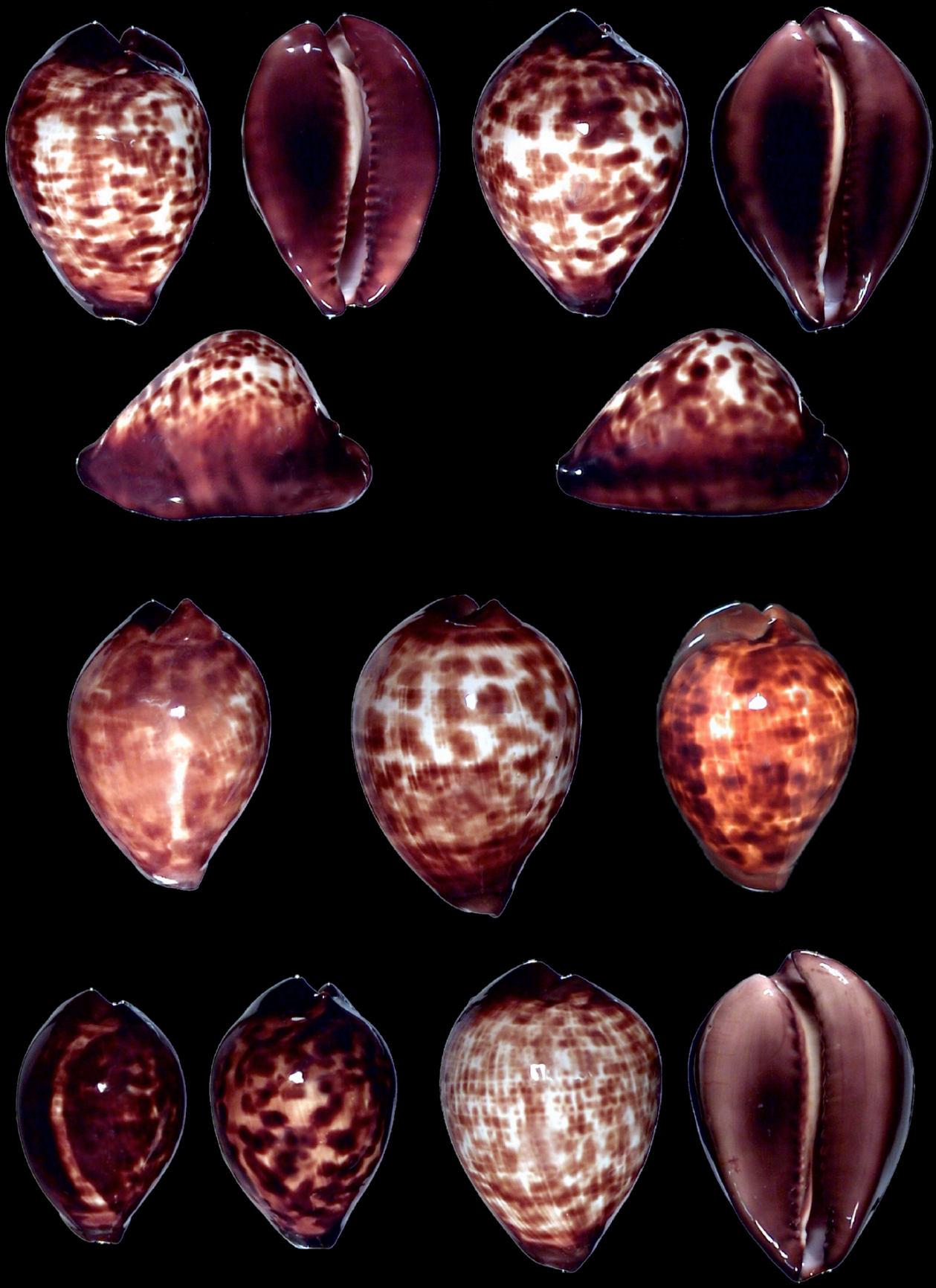


Plate 2

Zoila decipiens

Large Onslow variation and trawled form

1 ***Zoila decipiens*** "Onslow, 35 m" (61 mm).

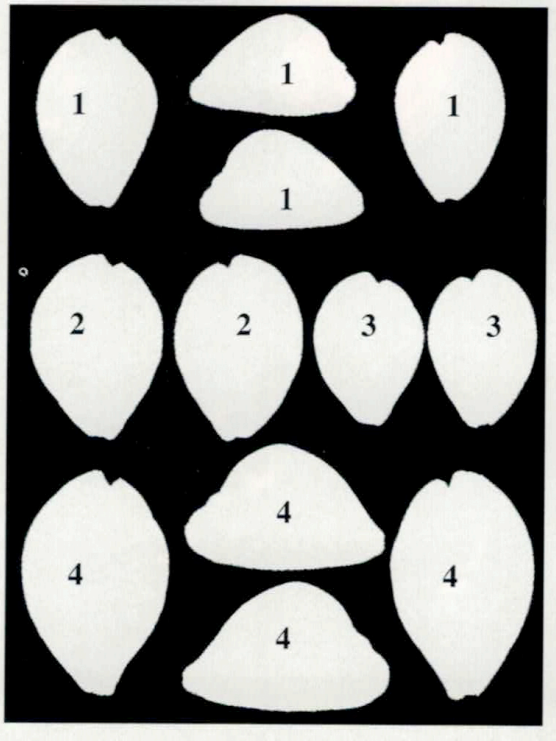
2 – 3 ***Zoila decipiens*** "Near Onslow" (larger specimen 57 mm).

4 ***Zoila decipiens*** "North West Cape, by Taiwanese trawlers, approx. 100 m" (63 mm).

Large, nearly black or heavy individuals are also known from the Broome area and are not exclusively found in the Onslow population.



Zoila decipiens,
Onslow variation



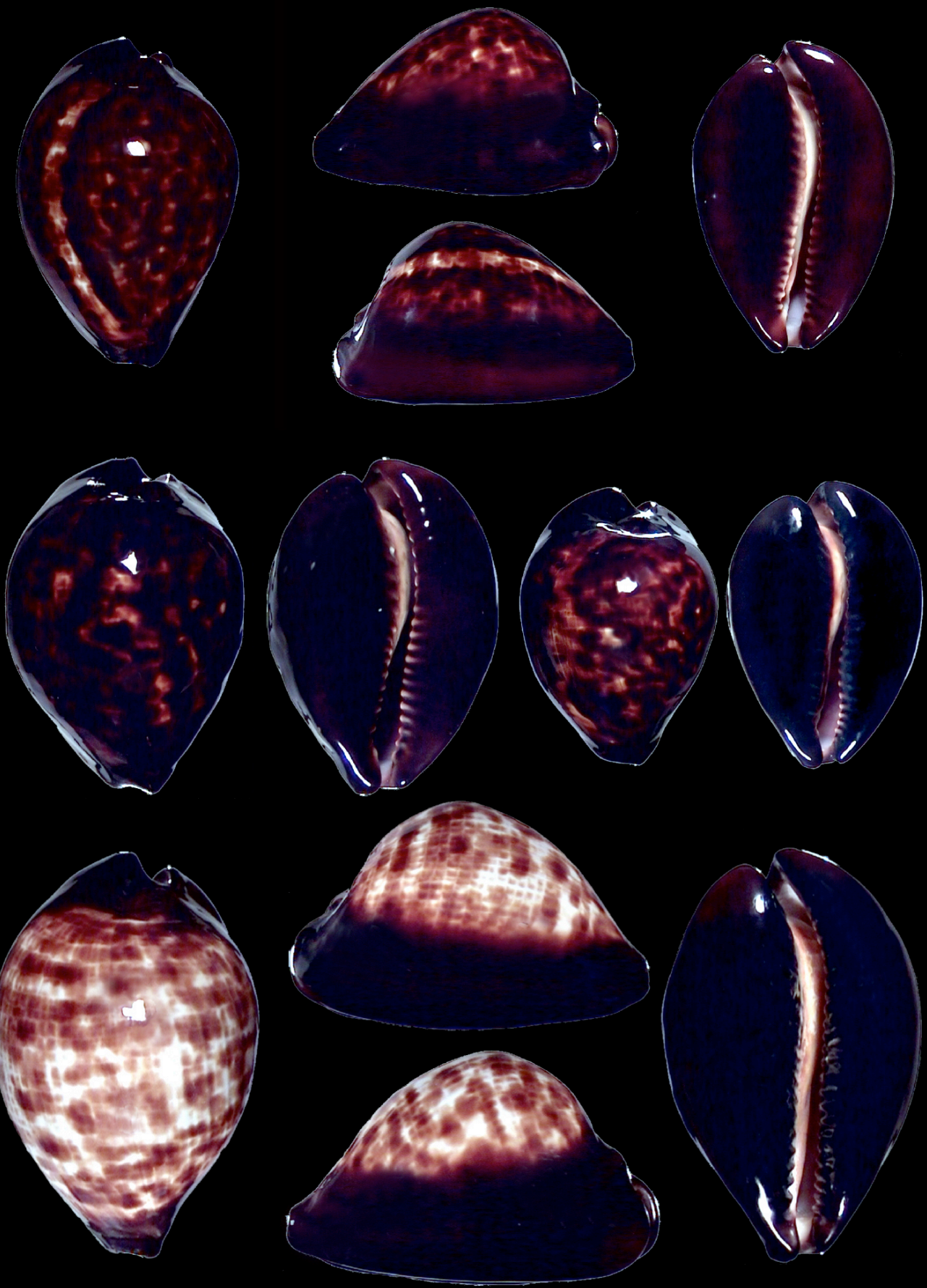


Plate 3

Zoila eludens

Typical and forma *delicatura*

1 – 2 ***Zoila eludens*** — Exmouth, 40 m (larger specimen: 61 mm). Collection and photo GABRIELLI.

3 – 6 ***Zoila eludens*** — Exmouth, 35 – 45 m (largest specimen 68 mm). Lateral view showing variability in marginal spotting.

7 – 8 ***Zoila eludens*** f. ***delicatura*** — "Port Hedland, 35 m" (larger specimen 50 mm). Typical specimens of the smaller form of *eludens*. Collection and photo GABRIELLI

9 ***Zoila eludens*** f. ***delicatura*** — "Montebello Islands, 64 – 90 m" (56 mm). Collection and photo GABRIELLI.

10 ***Zoila eludens*** f. ***delicatura*** — "North of Exmouth, 35 m" (50 mm).



Zoila eludens
and f. *delicatura*

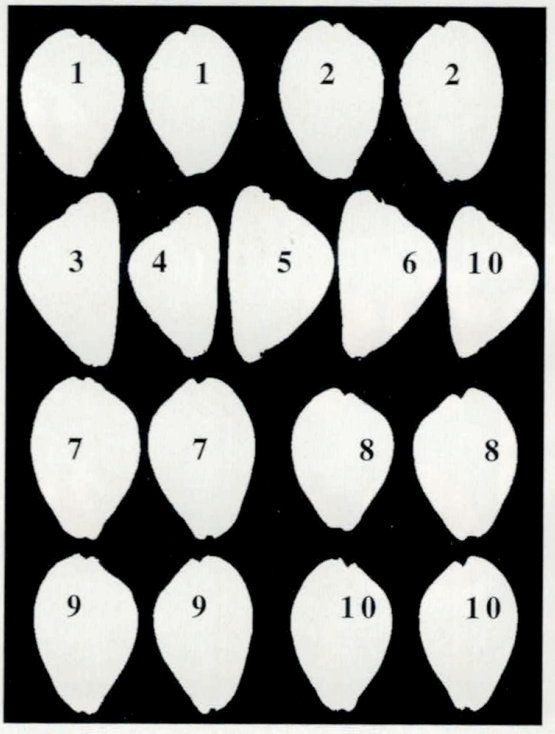




Plate 4

Zoila eludens

Typical specimens

1 – 8 *Zoila eludens* Exmouth, 40 m (largest specimen 68 mm). Typical variations. No. 3 and 4 collection and photo GABRIELLI.



Zoila eludens

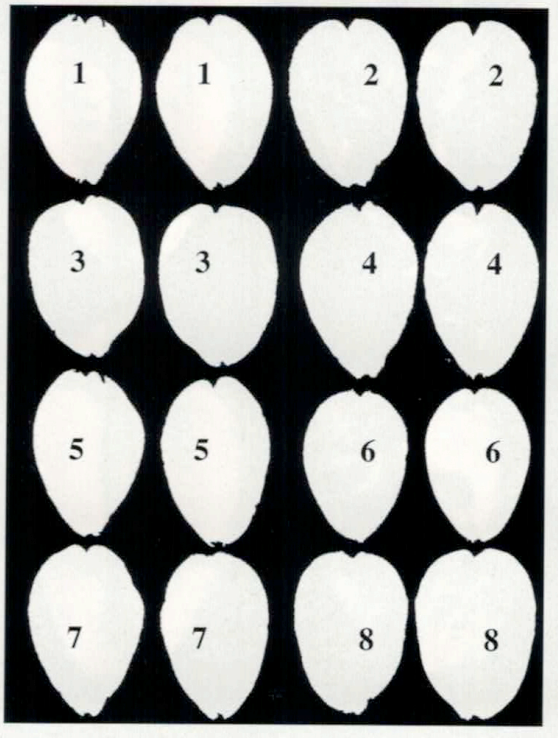




Plate 5

Zoila perlae

1 – 2 ***Zoila perlae*** "Dampier, by Taiwanese trawlers" (both 44 mm). Collection and photo GABRIELLI.

3 ***Zoila perlae*** "North West Australia, deep water" (43 mm).

4 ***Zoila perlae*** "North West Australia, deep water" (40 mm). Lightweight specimen, note the exposed spire.

5 ***Zoila perlae*** variation "Off Dampier" (60 mm). Large, heavy specimen resembling *eludens* in size and pattern. Note the pale convex base typical in *perlae*.



Zoila perlae

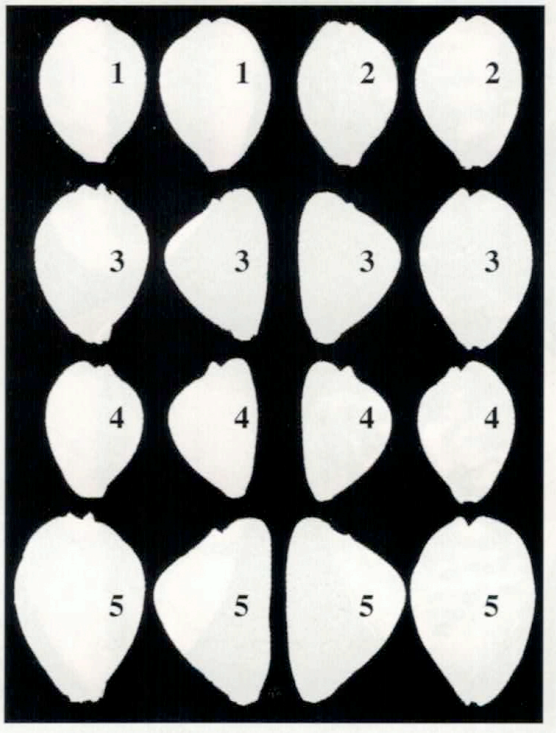




Plate 6

Zoila mariellae

1 ***Zoila mariellae*** — Holotype. Locality unknown, believed to be "off Kimberley" (56 mm).
Collection and photo RAYBAUDI.

2 ***Zoila mariellae*** — Locality unknown (55 mm).

3 ***Zoila mariellae*** — "Dampier Archipelago, trawled" (57 mm). Collection and photo GABRIELLI.

4 ***Zoila mariellae*** — "Northwestern Australia" (64 mm).

See also Plate 39 fig. 3.



Suspected locality of
Zoila mariellae

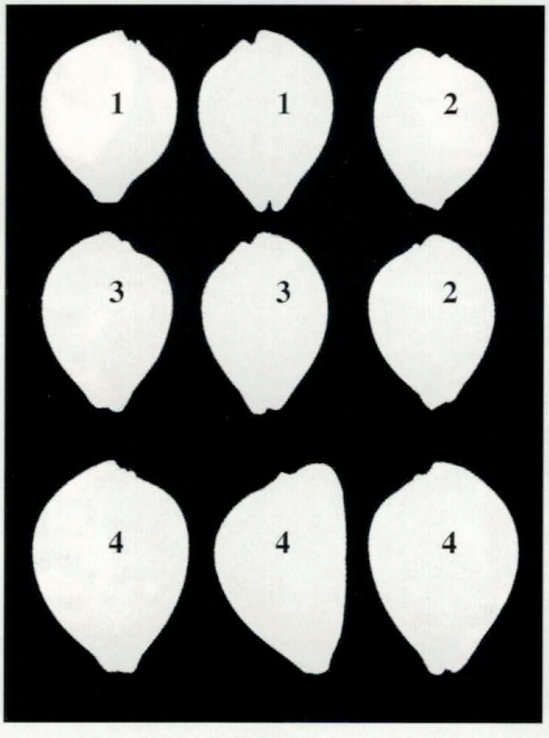




Plate 7

Zoila venusta venusta

Typical western specimens

1 ***Zoila venusta venusta*** Holotype of *thatcheri*. "Western Australia". British Museum of Natural History.
Photo courtesy RAYBAUDI.

2 ***Zoila venusta venusta*** Holotype of *venusta*. "Western Australia". Cambridge University Museum.
Photo courtesy RAYBAUDI.

3 ***Zoila venusta venusta*** "Jurien Bay, 35 m" (74 mm).

4 ***Zoila venusta venusta*** "Geraldton area" (79 mm).
Collection and photo GABRIELLI.

5 ***Zoila venusta venusta*** "Cervantes, 25 m" (59 mm).



Zoila venusta venusta,
typical form

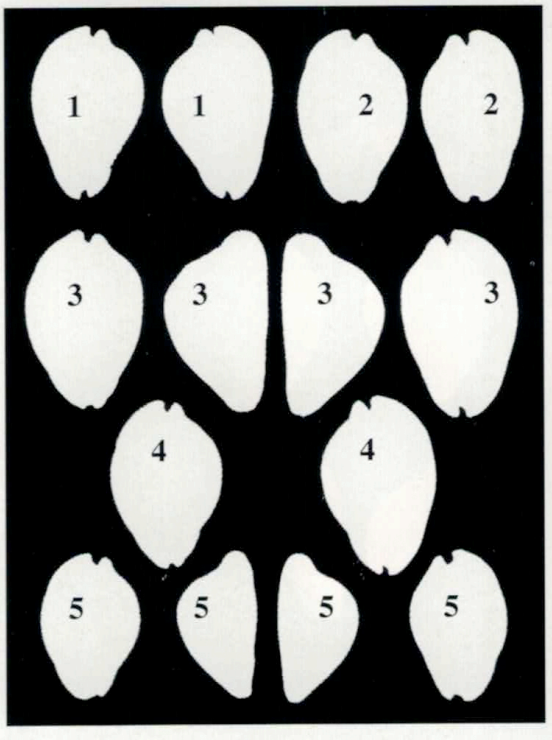




Plate 8

Zoila venusta venusta

Typical western specimens

1 ***Zoila venusta venusta*** Holotype of *catei*. "Abrolhos Is.". Note the distinct dorsal line. Photo from BURGESS 1970.

2 ***Zoila venusta venusta*** "Geraldton, 35 m" (67 mm). Collection and photo GABRIELLI.

3 ***Zoila venusta venusta*** "Dongara, 25 m" (70 mm).

4 ***Zoila venusta venusta*** "Cervantes area, 25 m" (60mm).

5 ***Zoila venusta venusta*** "Abrolhos Is., 40 m" (75 mm).



Zoila venusta venusta, typical form

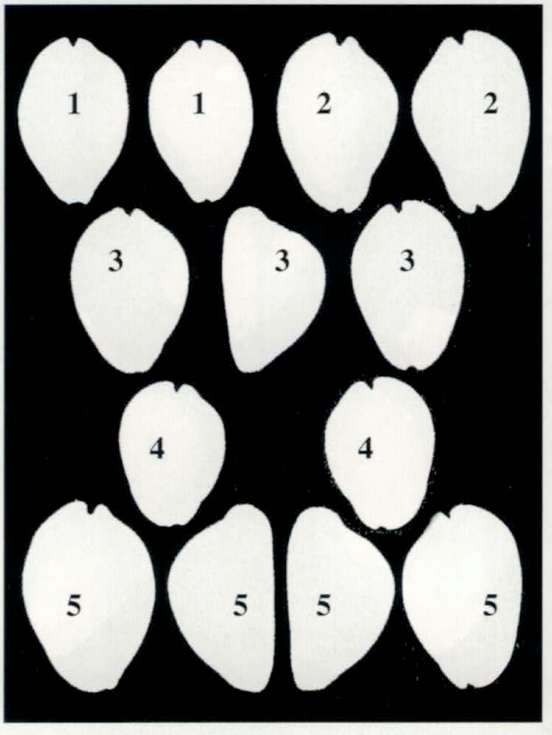




Plate 9

Zoila venusta episema

Typical large specimens

1 – 2 ***Zoila venusta episema*** Canal Rocks, Yallingup, 20 – 25 m (larger specimen 72 mm).

3 – 4 ***Zoila venusta episema*** "Rottnest Is., 15 – 20 m" (larger specimen 80 mm).

5 ***Zoila venusta episema*** "Augusta, 12 m" (68 mm).



Zoila venusta episema

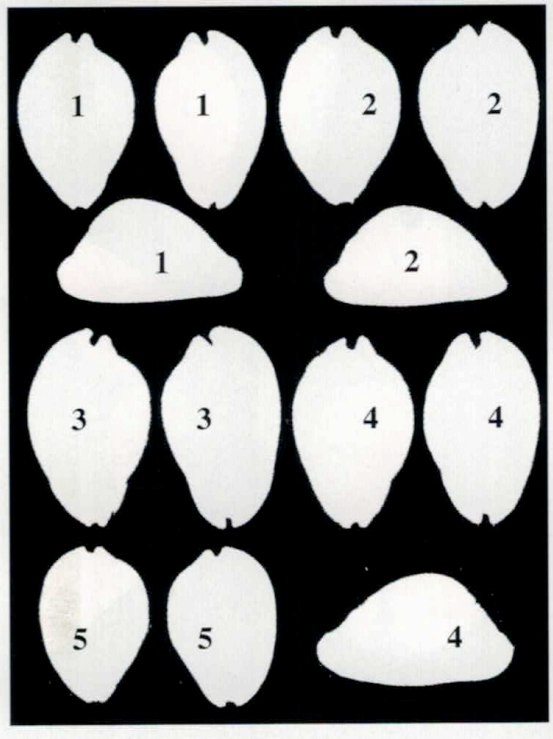




Plate 10

Zoila venusta episema

Typical large specimens

1 ***Zoila venusta episema*** Holoype of *episema*. Photo courtesy RAYBAUDI.

2 – 6 ***Zoila venusta episema*** "Yallingup, 10 – 20 m" (largest specimen 71 mm). Typical variations.



Zoila venusta episema

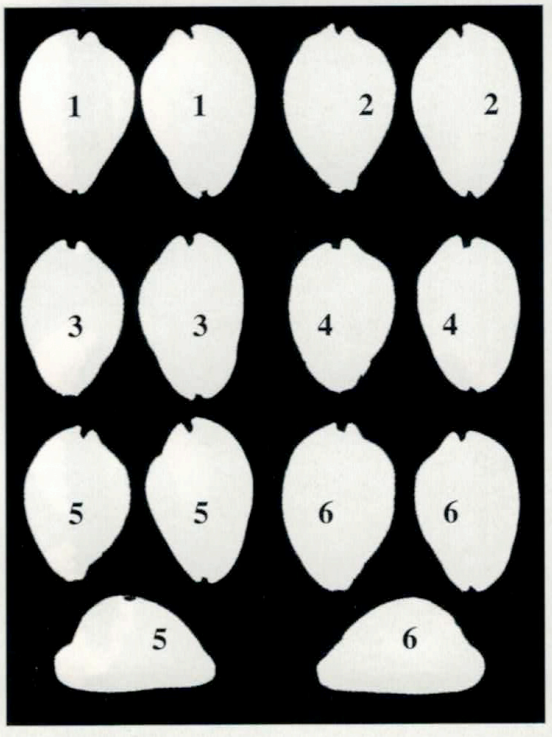




Plate 11

Zoila venusta episema

Variation "*sorrentensis*"

1 – 2 ***Zoila venusta episema*** f. ***sorrentensis*** — Cockburn Sound, Fremantle 8 – 15 m (larger specimen 62 mm).

3 ***Zoila venusta episema*** f. ***sorrentensis*** — "Sorrento Bay" (60 mm). Specimen with distinct dorsal line.

4 – 9 ***Zoila venusta episema*** f. ***sorrentensis*** — "Fremantle, 5 – 15 m" (largest specimen 59 mm). Note brownish teeth in shell No. 6.

10 ***Zoila venusta episema*** f. ***sorrentensis*** — "James Servis Reef, Mandurah" (approx. 55 mm). Collection and photo DEMERTZIS.



Zoila venusta episema and f. *sorrentensis*

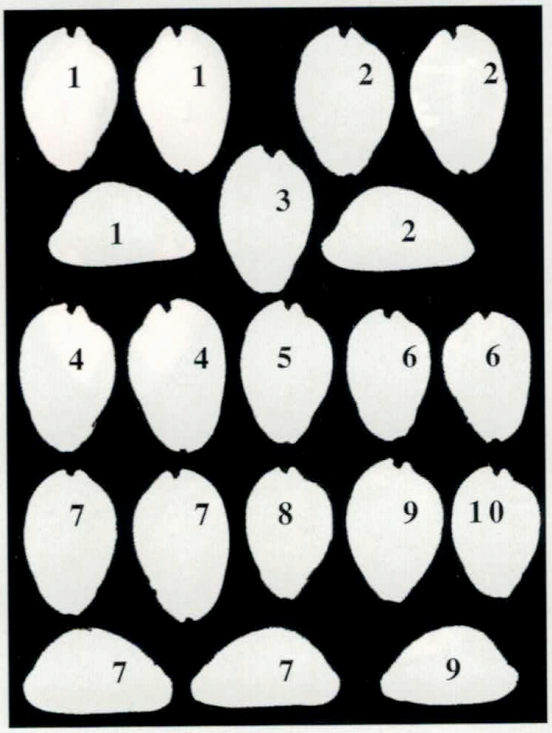




Plate 12

Zoila venusta roseopunctata

Typical dark mottled shells

1 – 2 ***Zoila venusta roseopunctata*** — Albany, 30 m (larger specimen 75 mm). Note distinct dorsal line, compare with Pl. 8, fig. 1. Collection and photo GABRIELLI.

3 ***Zoila venusta roseopunctata*** — "Esperance area, dived from 30 m" (68 mm).

4 – 6 ***Zoila venusta roseopunctata*** — "Esperance, 30 – 40 m" (largest specimen 71 mm). Dark spotted variations.

7 ***Zoila venusta roseopunctata*** — Two People's Bay, Albany, 25 m (72 mm).

8 ***Zoila venusta roseopunctata*** — Locality unknown (71 mm). Melanistic specimen. Collection and photo GABRIELLI.



Zoila venusta roseopunctata

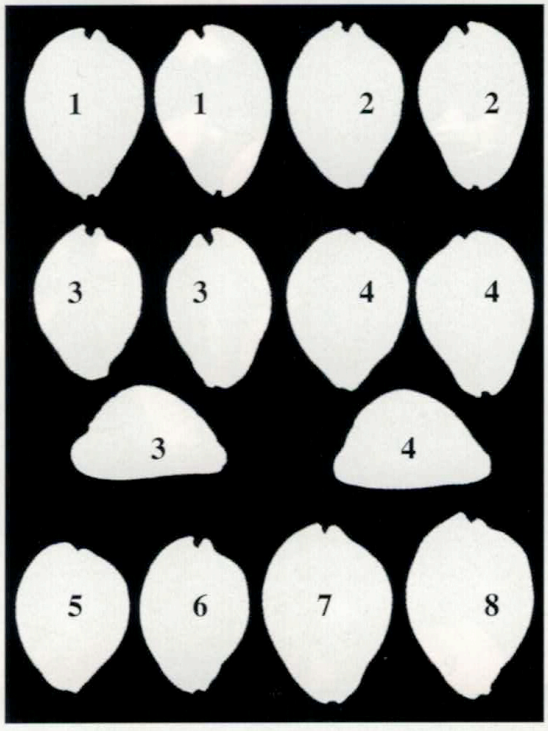




Plate 13

Zoila venusta roseopunctata

Typical sparsely spotted specimens

1 – 5 ***Zoila venusta roseopunctata*** "Albany, 30 – 40 m" (largest specimen 76 mm). Sparsely spotted variations.

6 – 8 ***Zoila venusta roseopunctata*** "Esperance, 25 – 40 m" (largest specimen 75 mm).



Zoila venusta roseopunctata

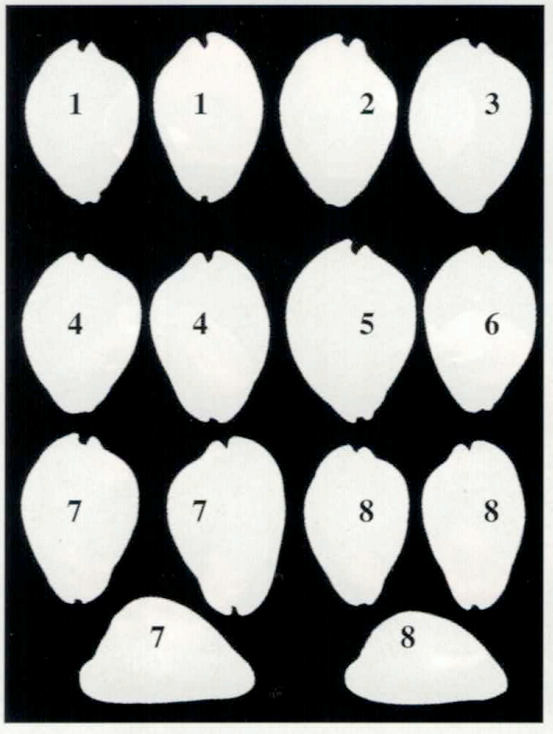




Plate 14

Zoila venusta roseopunctata

Color variations

1 – 8 ***Zoila venusta roseopunctata*** "Albany area" (largest specimen 76 mm). Selection of colorful variations. No. 7 and 8 Collection and photo GABRIELLI.



Zoila venusta roseopunctata

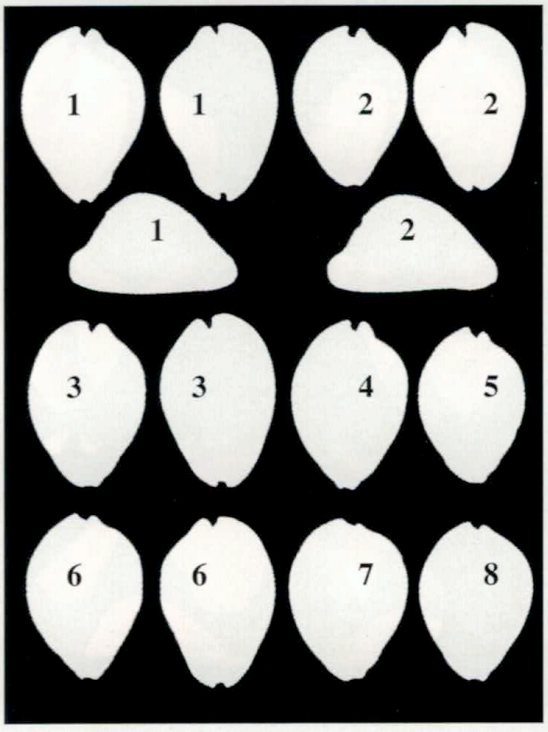




Plate 15

Zoila venusta roseopunctata

Variations

1 – 4 ***Zoila venusta roseopunctata*** "Albany, 25 – 40 m" (largest specimen 77mm). Sparsely spotted shells.

5 ***Zoila venusta*** ? variation Locality unknown. Exceptional specimen with rostrate extremities and blotched dorsum. Collection and photo DEMERTZIS.

6 – 7 ***Zoila venusta roseopunctata*** Munglinup, Starvation Bay, 12 – 15 m (largest specimen 61 mm). Small, lightweight variation.



Zoila venusta roseopunctata

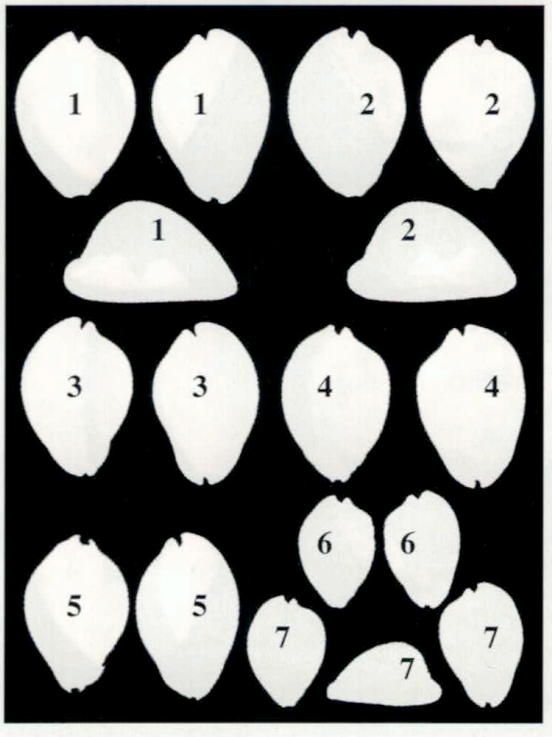




Plate 16

Zoila venusta roseopunctata

Variations with sparse or absent pattern

1 – 2 ***Zoila venusta roseopunctata*** — Albany, 25 – 40 m (largest specimen 74 mm). Collection and photo GABRIELLI.

3 – 7 ***Zoila venusta roseopunctata*** f. ***roseimmaculata*** — "Esperance, 25 – 40 m" (largest specimen 75 mm). Immaculate specimens. No. 4, 6 and 7 collection and photo GABRIELLI.



Zoila venusta roseopunctata

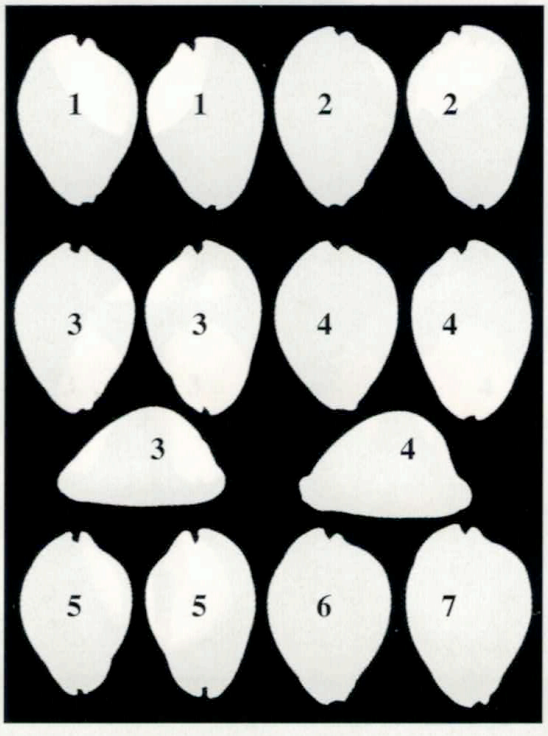




Plate 17

Zoila venusta roseopunctata

Eastern deep water variation "*profunda*"

1 – 4 ***Zoila venusta roseopunctata*** f. ***profunda*** "Great Australian Bight, 110 – 150 m, trawled" (largest specimen 75 mm).
No. 2 collection CHIAPPONI, No. 3 coll. OMI.



Zoila venusta roseopunctata f. *profunda*

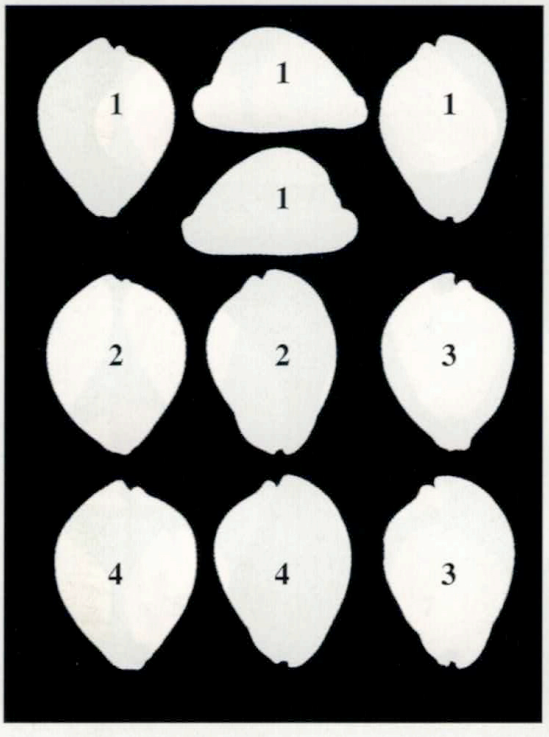




Plate 18

Zoila marginata marginata

Variations of the western populations

1 ***Zoila marginata marginata*** — "North of Geraldton, 25 m" (49 mm).

2 ***Zoila marginata marginata*** — "Dongara, in crayfish trap, 100 m" (52 mm).

3 ***Zoila marginata marginata*** — Dongara, 30 – 40 m (55 mm).

4 ***Zoila marginata marginata*** — Rottnest Island, 25 m (56 mm).

5 – 6 ***Zoila marginata marginata*** — "Southern Abrolhos Is. in fishtrap, approx. 90 m depth, late 60ies" (larger specimen 54 mm). Ex collection GURR.

Compare the specimens 5 and 6 with those of *ketyana bataviensis* on Pl. 26. Although the dark basal color and the distinct dorsal spotting are features they have in common, the shape of the base (convex in *k. bataviensis*, flattened in those *marginata* shown here), and the absence of the white frame encircling the dorsum in the specimens 5 and 6 distinguish them.



Zoila m. marginata, and the Abrolhos variation

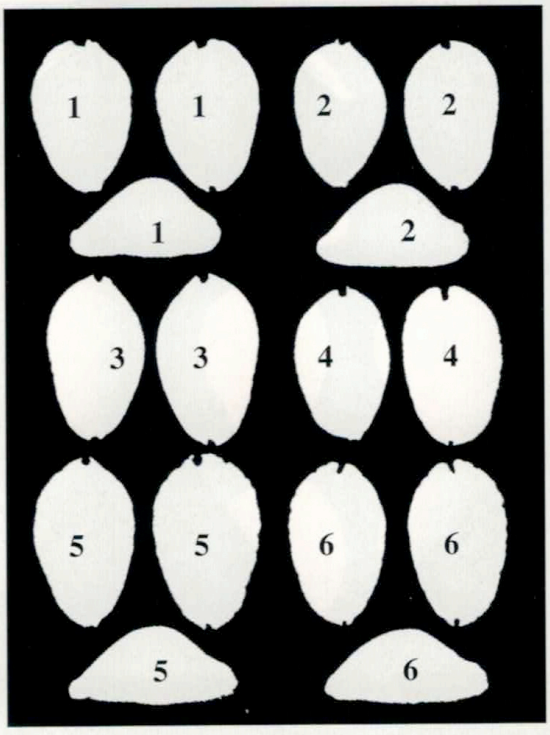




Plate 19

Zoila marginata marginata

Typical western specimens and var. "*consueta*"

1 ***Zoila marginata marginata*** — Holotype of *marginata*. British Museum of Natural History. Photo courtesy RAYBAUDI.

2 ***Zoila marginata marginata*** — Geraldton, 12 m (52 mm).

3 ***Zoila marginata marginata*** — "Dongara, 30 – 40 m" (52 mm).

4 – 6 ***Zoila marginata marginata*** f. ***consueta*** — "Carnac Is., 15 – 20 m" (largest specimen 62 mm).

Note the similarity between the holotype (locality unknown) of *marginata* and the specimen in fig. 2. Compare the holotype of *marginata* also with the specimens of *orientalis* (formerly known as *raybaudii*) on Pl. 27 fig. 3 – 6.



Zoila marginata marginata and f. *consueta*

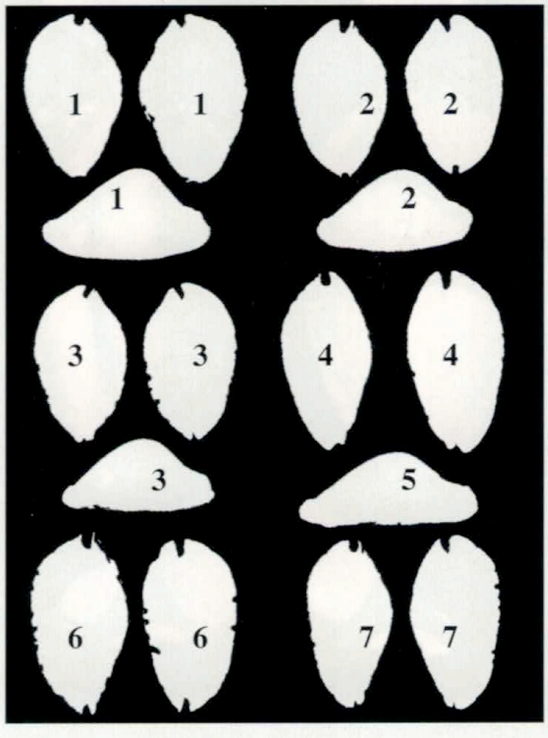




Plate 20

Zoila marginata marginata

Southwestern variation "*consueta*"

1 – 2 ***Zoila marginata marginata*** f. ***consueta*** — "Garden Island, 8 – 15 m" (larger specimen 64 mm).

3 – 8 ***Zoila marginata marginata*** f. ***consueta*** — "Carnac Is., 15 – 20 m" (largest specimen 59 mm).

9 ***Zoila marginata marginata*** f. ***consueta*** — "Lancelin Island, 18 m" (58 mm).

Compare the dark spotted specimens with the sparser spotted ones on Pl. 21; both series are from the same area (Carnac Island). The density of dorsal spotting is a very variable feature in most species of *Zoila*.



Zoila m. marginata f. *consueta*

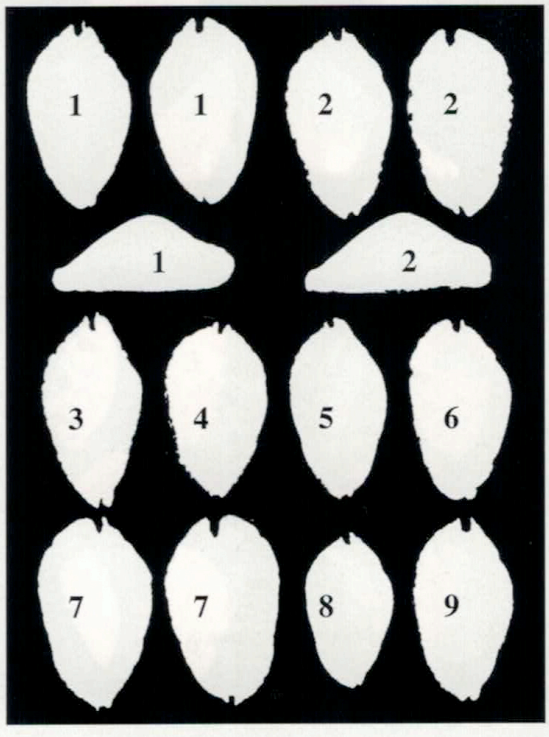




Plate 21

Zoila marginata marginata

Variations

1 – 5 ***Zoila marginata marginata*** f. ***consueta*** — Carnac Is., 8 – 20 m (largest specimen 63 mm).

6 ***Zoila marginata*** variation — "Augusta, trawled from approx. 100 m" (59 mm).

7 ***Zoila marginata albanyensis*** variation — "Breaksea Is., Albany, 120 m, trawled" (67 mm). Unusual specimen with flaring margins.



Zoila m. marginata (blue) and *m. albanyensis* var. (green)

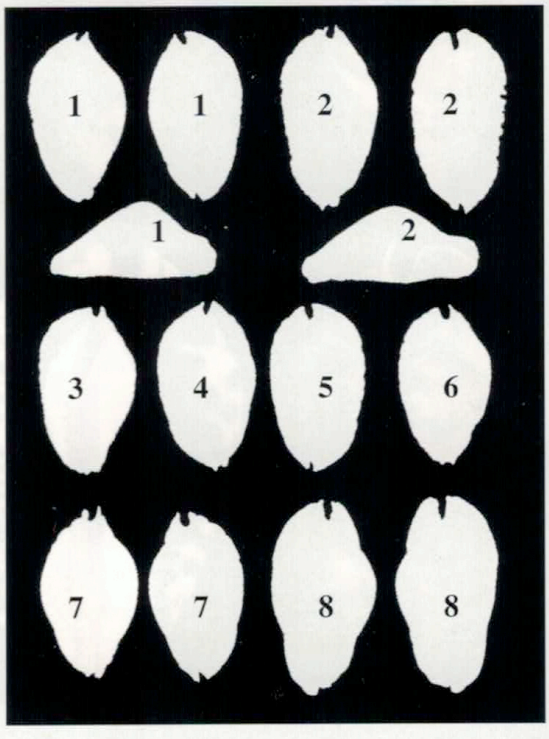




Plate 22

Zoila marginata albanyensis

Typical white and cloudy shells of var. □*nimbosa*□

1 ***Zoila marginata albanyensis*** Albany, 15 — 35 m (largest specimen 64 mm). Typical plain white shells.

2 ***Zoila marginata albanyensis*** Hood Point, 8 m (75 mm). Very large specimen.

3 - 4 ***Zoila marginata albanyensis*** Between Denmark and Albany, 10 — 35 m (largest specimen 64 mm).

5 - 8 ***Zoila marginata albanyensis*** f. ***nimbosa*** Between Denmark and Albany, 10 — 35 m. Series of dorsally mottled shells.

Note that the dark marginal spotting is not well visible form dorsal view in *m. albanyensis*, in comparison to *marginata* f. *consueta* (see Pl. 20), in which it is rather conspicuous.



Zoila marginata albanyensis

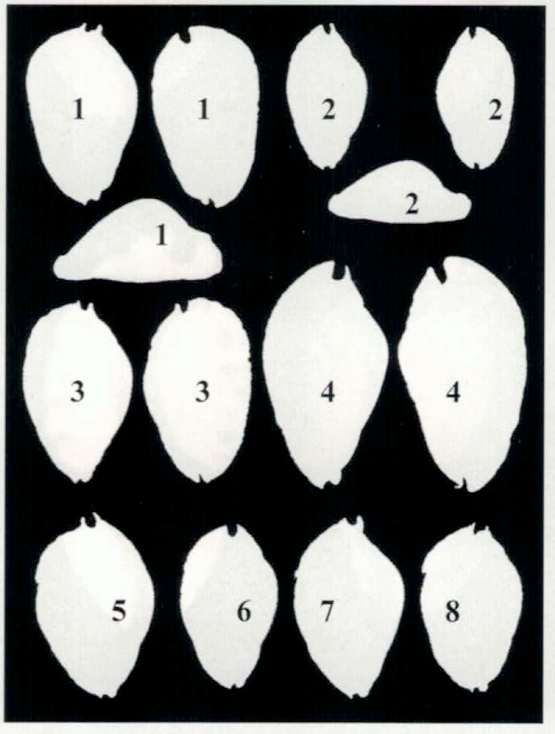




Plate 23

Zoila ketyana ketyana

Deep water specimens

1 – 3 ***Zoila ketyana ketyana*** Northwestern Australia, by Taiwanese trawlers, 100 – 150 m (largest specimen 48 mm).

4 – 6 ***Zoila ketyana ketyana*** Northwestern Australia, by Taiwanese trawlers, 100 – 150 m (largest specimen 44 mm). Sparsely spotted shells, some with a tall spire.



Zoila ketyana ketyana, typical trawled form

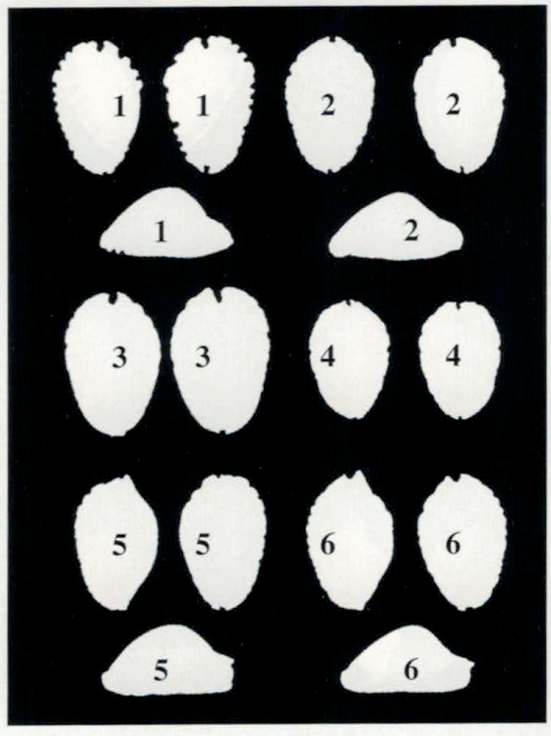




Plate 24

Zoila ketyana ketyana

Spotted shallow water specimens

1 – 4 ***Zoila ketyana ketyana***
shallow water variation

Gnaraloo, 35 – 45 m (largest specimen 53 mm).
No. 4 collection and photo GABRIELLI.

The shallow water form of *ketyana ketyana* is usually much larger, more densely spotted, with wider margins, and a more convex base.



Zoila ketyana ketyana,
larger dived form

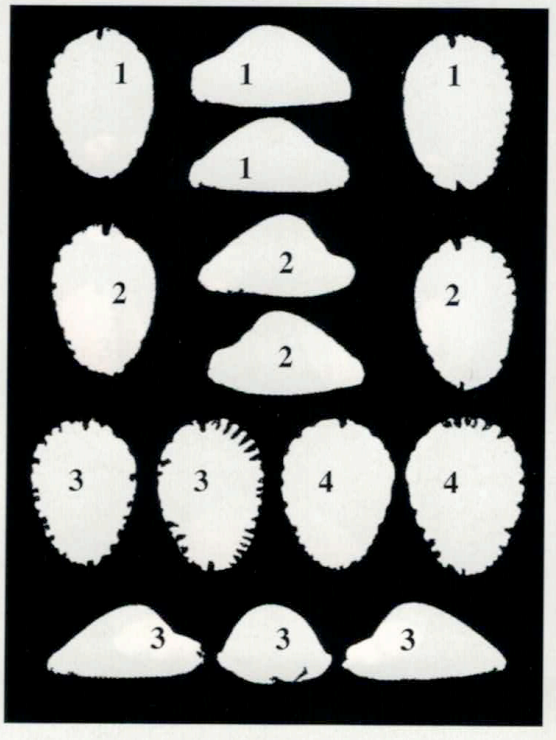




Plate 25

Zoila ketyana ketyana

Variations "*hypermarginata*" and "*lutea*"

1 – 4 ***Zoila ketyana ketyana*** f. ***hypermarginata*** — Bernier Island, 45 m (largest specimen 53 mm). Typical specimens of the plain form.

5 – 6 ***Zoila ketyana ketyana*** f. ***lutea*** — Southern end of Dirk Hartog Island, 35 – 45 m (larger specimen 56,2 mm).

Note the differences in shape and dentition (teeth more numerous in f. *lutea*).



Z. ketyana ketyana f. *hypermarginata* (blue) and f. *lutea* (green)

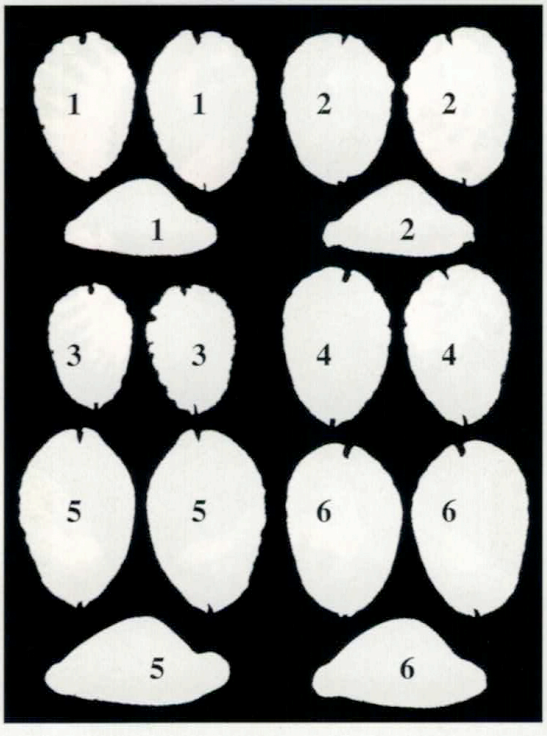




Plate 26

Zoila ketyana bataviensis

Typical specimens of the new southern subspecies

1 ***Zoila ketyana bataviensis*** Holotype. Abrolhos Islands, 35 m (56 mm). Collection South Australian Museum.

2 ***Zoila ketyana bataviensis*** Abrolhos Islands, 35 m (57 mm).

3 ***Zoila ketyana bataviensis*** Paratype 1. Abrolhos Islands, 35 m (56 mm).

4 ***Zoila ketyana bataviensis*** Abrolhos Islands, 35 m. Collection CHIAPPONI.

5 ***Zoila ketyana bataviensis*** Abrolhos Islands, trawled off 80 m (56 mm). Collection and photo GABRIELLI.

6 ***Zoila ketyana bataviensis*** Paratype 2. "Geraldton area, from fishtrap" (55mm).



Zoila ketyana bataviensis

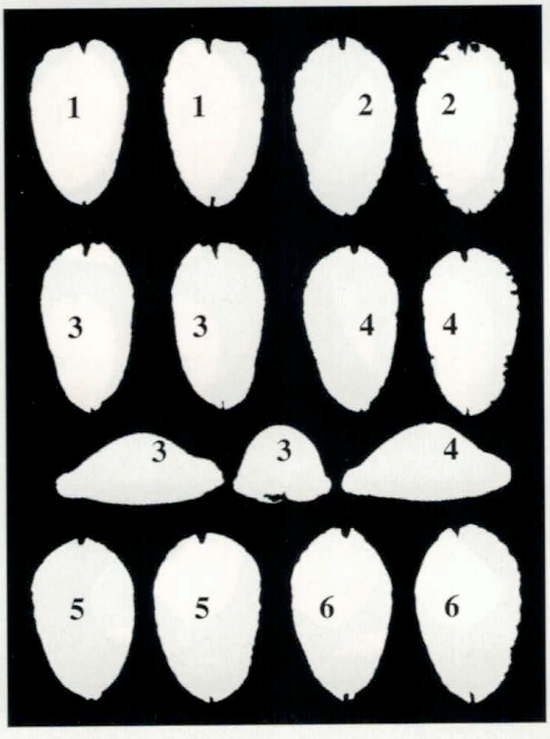




Plate 27

Zoila orientalis

and an unnamed variation of *Zoila marginata*

1 ***Zoila marginata*** variation — "Cape Recherche, trawled off 120 m" (51 mm). Note the tall spire, narrow base and the coarse very numerous teeth.

2 ***Zoila marginata*** variation — "Cape Recherche, trawled off 120 m" (49 mm). See below for more information.

3 ***Zoila orientalis*** — Paratype 1 of *raybaudii*. "Port Lincoln, 40 m" (55 mm).

4 ***Zoila orientalis*** — Kangaroo Island, 12 m (57 mm).

5 ***Zoila orientalis*** — Grindle Island, Port Lincoln, 25 m (66 mm).

6 ***Zoila orientalis*** — Kangaroo Island, 19 m (58 mm).

The peculiar narrow–shelled variation is known to me only by the two specimens illustrated here. They appeared on the European market as a pair, some time in the early 90ies. Specimen No. 2 was also illustrated by WILSON 1993 Pl. 29 fig. 6B.



Zoila orientalis (blue) and *marginata* variation (green)

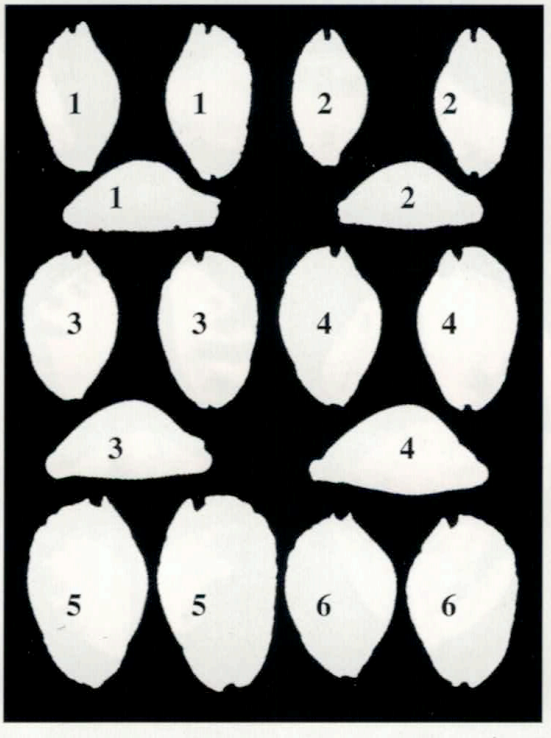




Plate 28

Zoila rosselli

Typical southwestern shells

1 – 4 ***Zoila rosselli*** "Fremantle, 4 – 18 m" (largest specimen 54 mm).

5 – 7 ***Zoila rosselli*** "Rottnest Island, 9 – 24 m" (from 42 – 54 mm).

Note the characteristic short but distinct columellar teeth, the uniformly dark brown to black base, and the bent–up margins (e.g. in No. 2).



Zoila rosselli,
typical form

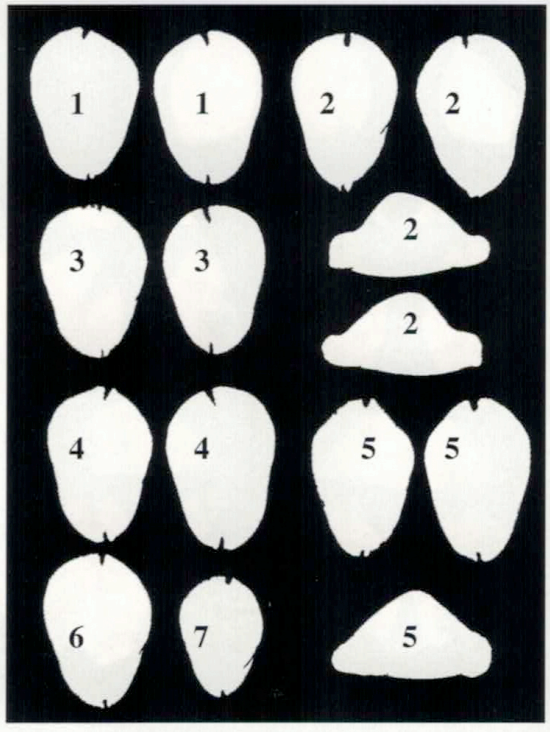




Plate 29

Zoila rosselli

Southeastern variation

1 – 4 ***Zoila rosselli*** "Albany area, 12 – 35 m" (largest specimen 63 mm). Typical specimens of the southern form.

5 ***Zoila rosselli*** Two People's Bay, Albany, 15 m (56 mm). Subadult specimen.

Zoila rosselli found between Albany and Esperance differ from west coast specimens by having a wider aperture, mostly fainter mid-columellar teeth, longer labral teeth, a distinctly spotted base (when viewed under bright light, the spotting becomes apparent), and a mottled dorsum not as distinctly white–blotched as in western shells. The margins are also less bent up, the shells are generally a bit larger. This geographic variation has so far not been given a separate name.



Zoila rosselli, southern form

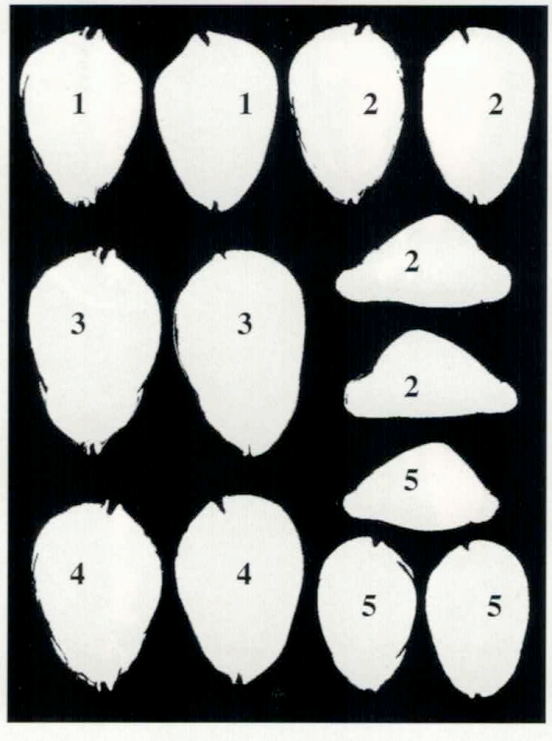




Plate 30

Zoila rosselli

Northwestern variation "*satiata*"

1 – 4 ***Zoila rosselli*** f. ***satiata*** Point Quobba, 35 – 45 m (largest specimen 55 mm).

5 – 6 ***Zoila rosselli*** variation Abrolhos Islands, 40 m (larger specimen 63 mm).

The northwestern population of *rosselli* is famous for its occasional golden variation "*edingeri*" (see Pl. 31). The dark shelled specimens differ from typical southern *rosselli* by the longer, coarser columellar teeth, the paler, often orange tinting of the base, the stunted, hardly rostrate extremities, and the small to absent dorsal window.

The large, spectacular shells from the Abrolhos Islands share the coarse dentition with their northern relatives, whereas the rostrate, flaring extremities resemble southern shells.



Z. rosselli f. *satiata* (blue)
and the Abrolhos variation (green)

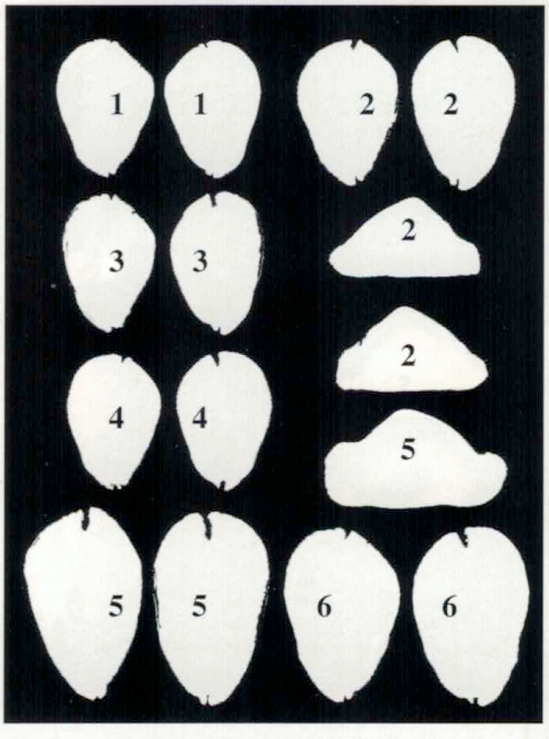




Plate 31

Zoila rosselli

Golden variation "*edingeri*"

1 ***Zoila rosselli*** f. ***edingeri*** Point Quobba, 38 m (50 mm). Collection and photo GABRIELLI.

2 ***Zoila rosselli*** f. ***edingeri*** Holotype. Point Quobba, 35 m, found by ANDREW EDINGER. Collection and photo RAYBAUDI.

3 ***Zoila rosselli*** variation Point Quobba. Unique specimen, anterior third with "*edingeri*" coloration.
Collection and photo FRANZ HUBER.

4 ***Zoila*** sp. ? ***rosselli*** "Live taken on the Southwest Coast". After a b/w photo, colors digitally reconstructed following the description given by BOARD 1979.

5 ***"Zoila obettiana"*** or ***Zoila rosselli*** f. ***"albolutea"*** Artificially coated and air–brushed specimen of a *rosselli*. Collection and photo RAYBAUDI.



Zoila rosselli forma *edingeri*

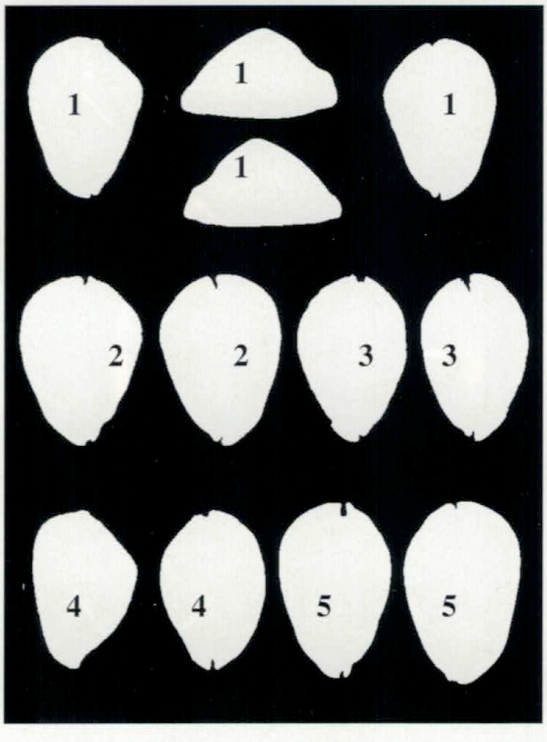




Plate 32

Zoila jeaniana jeaniana

Typical specimens

1 ***Zoila jeaniana jeaniana*** Paratype 3. Dorre Island, Shark Bay, trawled from 120 m, July 1965 (73 mm).
Ex collection GURR.

2 ***Zoila jeaniana jeaniana*** Paratype 4. Dorre Island, Shark Bay, trawled from 120 m, July 1965 (70 mm).
Ex collection GURR.

3 ***Zoila jeaniana jeaniana*** "Montebello Islands, trawled from 100 m" (73 mm).

4 ***Zoila jeaniana jeaniana*** "Northwestern Australia, by Taiwanese trawlers, approx. 100 m" (89 mm).



Zoila jeaniana jeaniana, typical trawled form

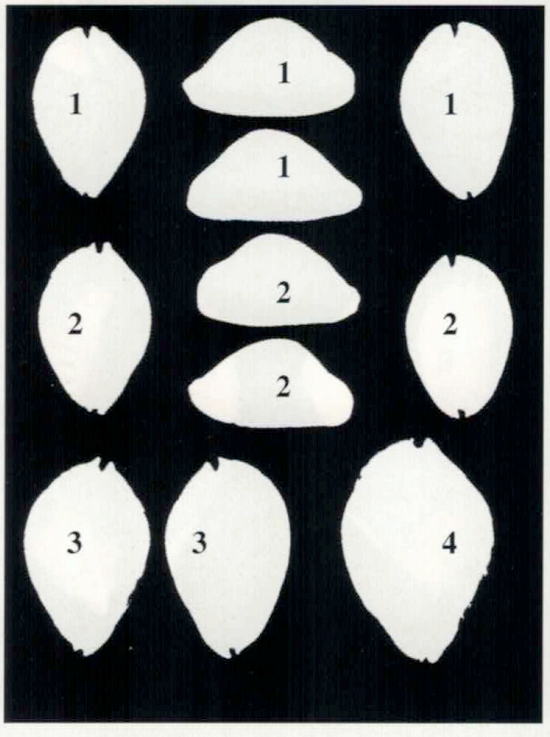




Plate 33

Zoila jeaniana jeaniana

Typical specimens

1 – 4 ***Zoila jeaniana jeaniana*** "Northwestern Australia, by Taiwanese trawlers" (size range 52 – 69 mm).

5 ***Zoila jeaniana jeaniana*** "Northwestern Australia, by Taiwanese trawlers" (62 mm). Collection and photo GABRIELLI.



Zoila jeaniana jeaniana, typical trawled form

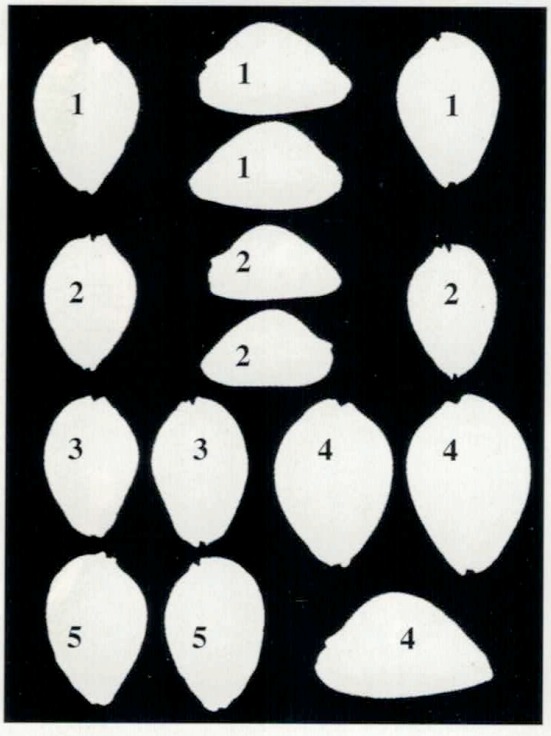




Plate 34

Zoila jeaniana jeaniana

Snowy white margined form

1 ***Zoila jeaniana jeaniana*** "Northwestern Australia, by Taiwanese trawlers, deep water" (77 mm).

2 ***Zoila jeaniana jeaniana*** Bernier Island, 45 m (71 mm).

3 ***Zoila jeaniana jeaniana*** Bernier Island, 42 m (74 mm).

Note the similarity of these exceptionally beautiful specimens to *eludens*.



Zoila jeaniana jeaniana, snowy white form

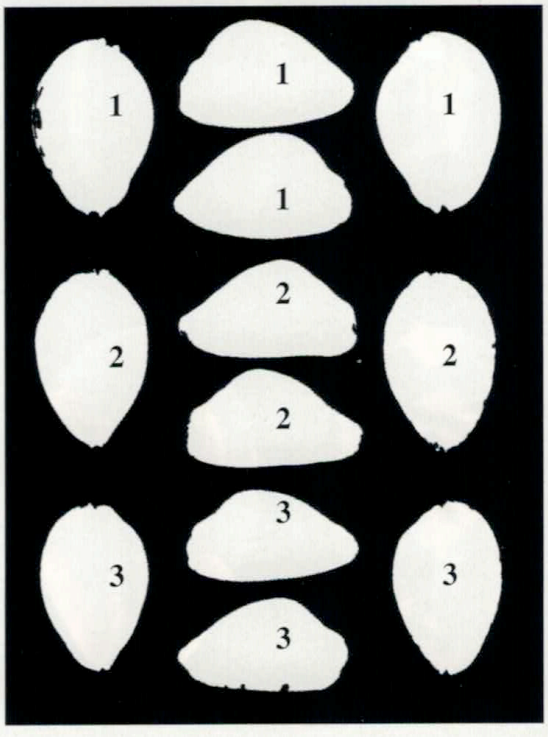




Plate 35

Zoila jeaniana jeaniana

Slender shells and the dark variation "*sherylae*"

1 – 2 ***Zoila jeaniana jeaniana*** "Carnarvon, 35 m" (larger specimen 87 mm). Unusually slender shells resembling *f. friendii* in general shape. Collection and photo GABRIELLI.

3 – 8 ***Zoila jeaniana jeaniana*** f. ***sherylae*** Point Quobba, 30 – 45 m (size range 56 – 74 mm). Typical specimens of the smaller and darker variation.

9 ***Zoila jeaniana jeaniana*** "Northwestern Australia. By Taiwanese trawlers" (33 mm). Extreme dwarf specimen. Collection and photo RAYBAUDI.



Zoila j. jeaniana and f. *sherylae*

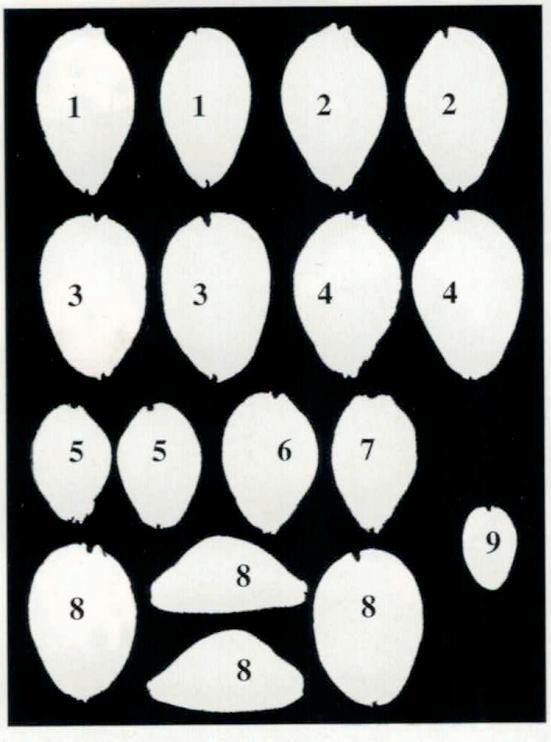




Plate 36

Zoila jeaniana

Conchological intermediates to *jeaniana aurata*

1 ***Zoila jeaniana jeaniana*** / ***aurata*** intermediate form — "Northwestern Australia" (66 mm).

2 ***Zoila jeaniana jeaniana*** / ***aurata*** intermediate form — "Shark Bay, trawled, 90 m" (81 mm).

3 ***Zoila jeaniana jeaniana*** / ***aurata*** intermediate form — "Onslow, trawled from 160 m" (59 mm).

These three shells have transitional features between *j. jeaniana* and *j. aurata*: The base is paler than in typical *jeaniana*, but not whitish as in *aurata*; the marginal and dorsal pattern is reduced, but still darker than in *aurata*. Since such specimens are comparatively common, the systematic status of *aurata* is that of a subspecies herein.



Zoila jeaniana,
intermediate form

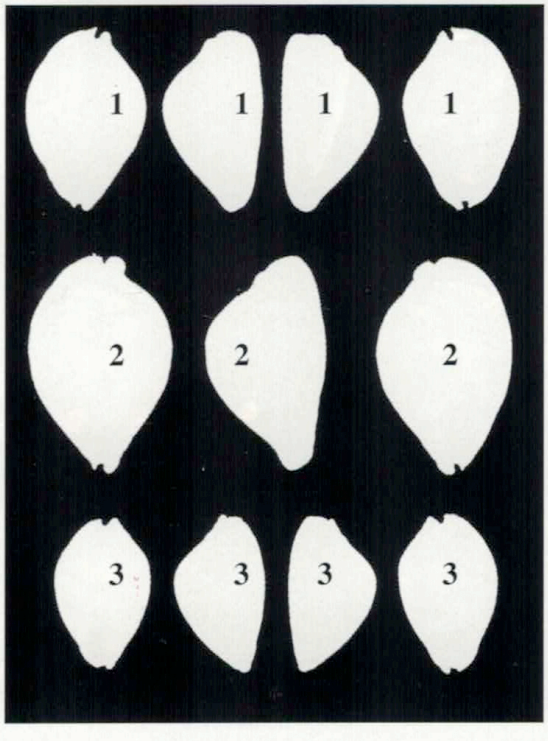




Plate 37

Zoila jeaniana aurata

Typical specimens

1 ***Zoila jeaniana aurata*** "Northwestern Australia, by Taiwanese trawlers, approx. 150 m" (78 mm). Note the uncommon orange tint of the base.

2 – 3 ***Zoila jeaniana aurata*** "Shark Bay area, by Taiwanese trawlers" (84 – 88 mm). Typical specimens of a more rostrate type.



Zoila jeaniana aurata

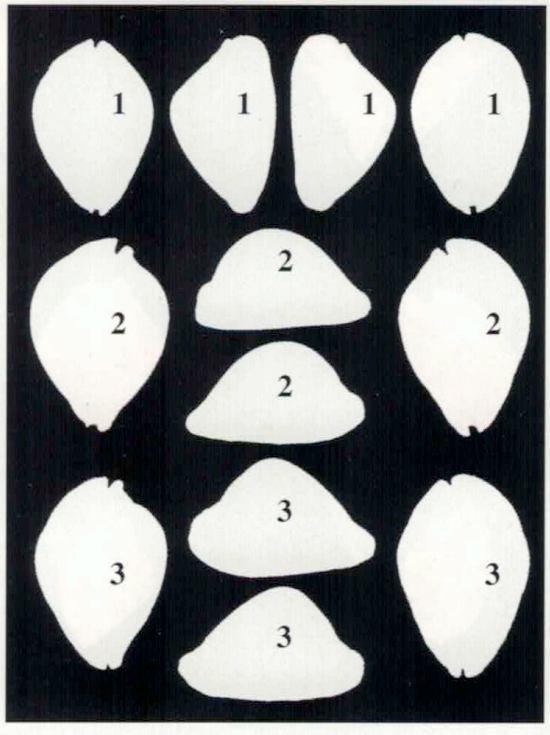




Plate 38

Zoila jeaniana aurata

Typical specimens

1 ***Zoila jeaniana aurata*** "Northwest Cape, by Taiwanese trawlers" (87 mm).

2 ***Zoila jeaniana aurata*** "Northwestern Australia, by Taiwanese trawlers" (33 mm). Extreme dwarf specimen. Collection and photo RAYBAUDI.

3 – 4 ***Zoila jeaniana aurata*** "Northwest Cape, by Taiwanese trawlers" (larger specimen 92 mm).

5 ***Zoila jeaniana aurata*** "Northwest Cape, by Taiwanese trawlers" (54 mm).



Zoila jeaniana aurata

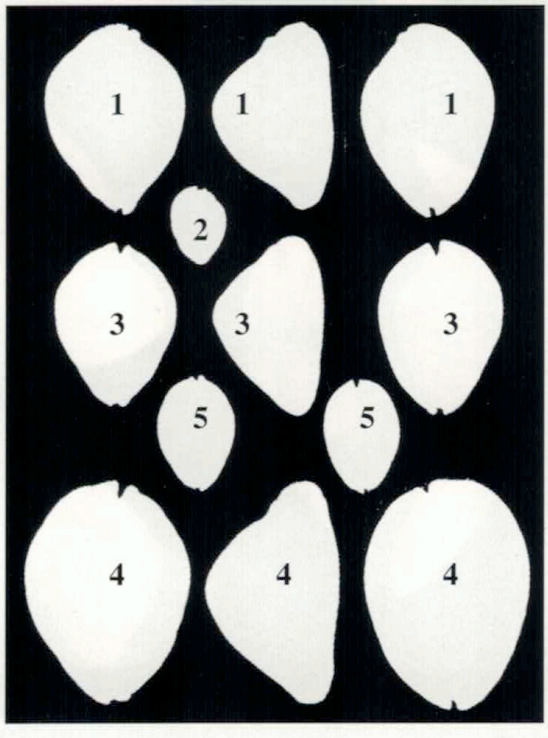




Plate 39

Zoila jeaniana aurata

Immaculate specimens and a query

1 – 2 ***Zoila jeaniana aurata*** immaculate specimens — Northwest Cape, by Taiwanese trawlers (larger specimen 82 mm). No. 1 coll. GABRIELLI.

3 ***Zoila*** sp. cf. ***mariellae*** variation — "Northwestern Australia, 230 m" (55 mm). Unusual shell of uncertain position, probably *mariellae*. Collection and photo GABRIELLI.

Note the tall spire of specimen 3, whose shape resembles *j. aurata*. This unique shell has faintly brown tinted teeth indicating a closer relationship to *mariellae* rather than *jeaniana aurata*, in which the teeth are paler than the surrounding (see plate 36).



Zoila jeaniana aurata
and *Zoila* sp. cf. *mariellae*

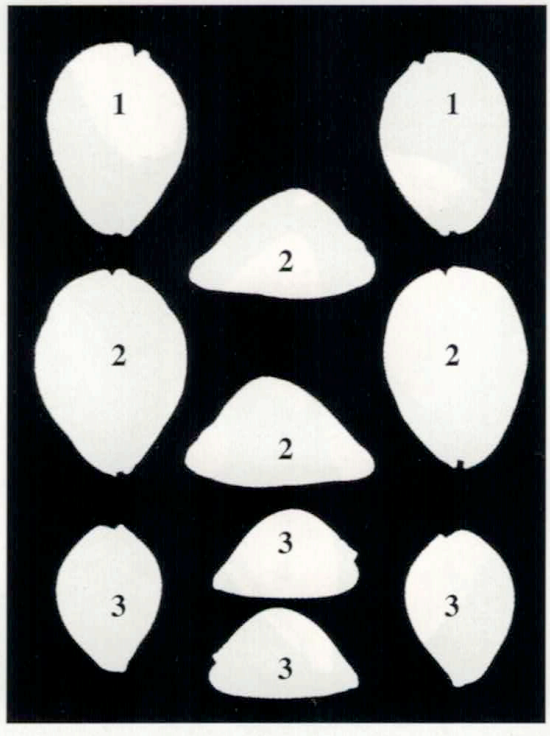




Plate 40

Zoila friendii

The mysterious deep water variation

1 ***Zoila friendii***
deep water variation

Wedge Island, 100 km north of Perth, in crayfish pot, off 90 m (72 mm). This shell was also illustrated by GURR 1981b, fig. 3.

2 ***Zoila friendii***
deep water variation

"Perth area, trawled from 80 m" (approx. 75 mm). Photo courtesy RAYBAUDI.

3 ***Zoila friendii***
deep water variation

Perth, crabbed in crayfish pot, 75 m (74 mm). Ex collection PAUL FISCHER.

The rare deep water form of *friendii* bears intermediate features between *friendii* and *jeaniana*. The teeth on columellar side are distinct and dense as in *jeaniana*, whereas the rostrate sharp extremities, the tall spire, and the rounded base resemble *friendii*. This is one of the rarest variations in the genus, less than ten well preserved specimens are known to me.



Zoila friendii,
deep water variety

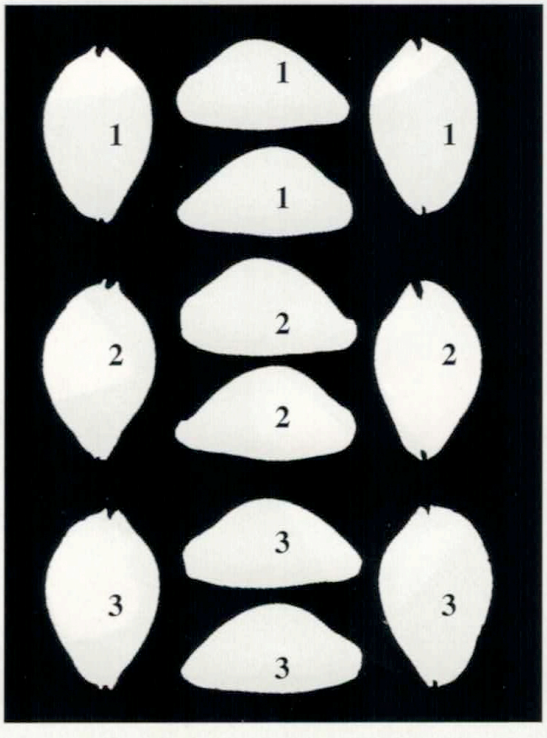




Plate 41

Zoila friendii friendii

Typical specimens

1 – 4 ***Zoila friendii friendii*** "Sorrento Beach, 5 – 15 m" (size range 81 – 95 mm). Moderately broad but otherwise typical specimens.

5 ***Zoila friendii friendii*** Binningup, 12 – 20 m (larger shell 95 mm)

The specimens on this plate were chosen because of their relatively broad shape. Compare them with *f. vercoi* on plate 45. The relatively wider aperture, the pyriform shape, and the more consipcuous white frame along the aperture characterize *f. vercoi* against the specimens of *f. friendii* shown here.



Zoila friendii friendii

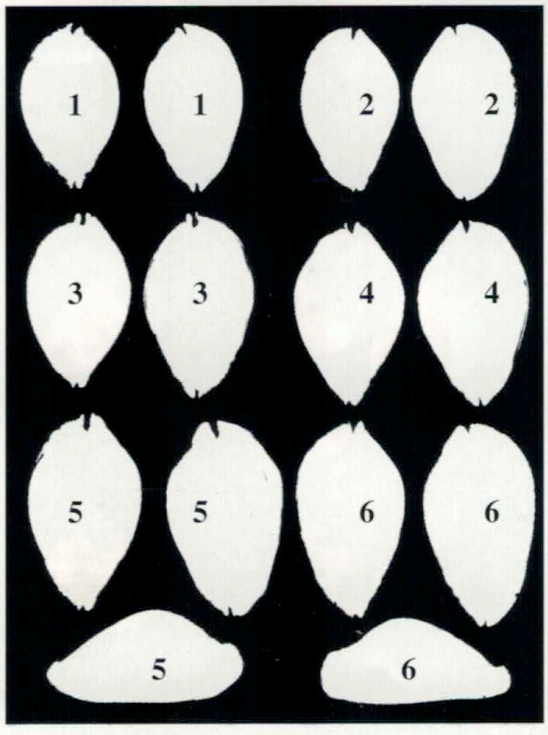




Plate 42

Zoila friendii friendii

Typical specimens

1 ***Zoila friendii friendii*** Rottnest Island, 30 m (101 mm).

2 ***Zoila friendii friendii*** "Sorrento Beach, 10 m" (91 mm). Specimen with distinct dorsal line. Collection and photo GABRIELLI.

3 – 5 ***Zoila friendii friendii*** "Fremantle, 15 – 25 m" (size range 85 – 103 mm). Typical large and slender specimens.

6 ***Zoila friendii friendii*** "Carnac Island, 6 m" (83 mm).



Zoila friendii friendii

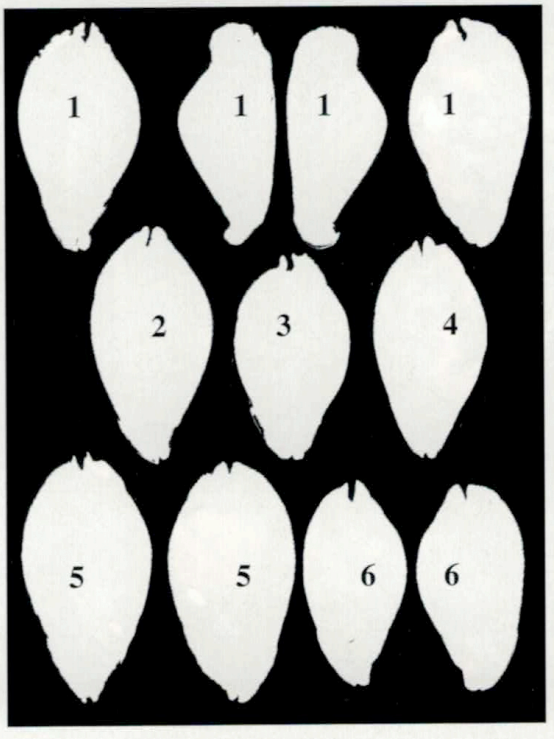




Plate 43

Zoila friendii friendii

Typical smaller specimens

1 – 6 ***Zoila friendii friendii*** Bunbury to Dunsborough, 2 – 6 m (largest specimen 76 mm). Typical smaller form with bluish sparsely spotted dorsum.

7 ***Zoila friendii friendii*** Busselton, 5 m (87 mm). Specimen with large, projecting spire.

8 ***Zoila friendii friendii*** Garden Island, 22 m (77 mm).

The relation of the spire to the posterior extremity is highly variable in *friendii friendii*.



Zoila friendii friendii, smaller bluish form

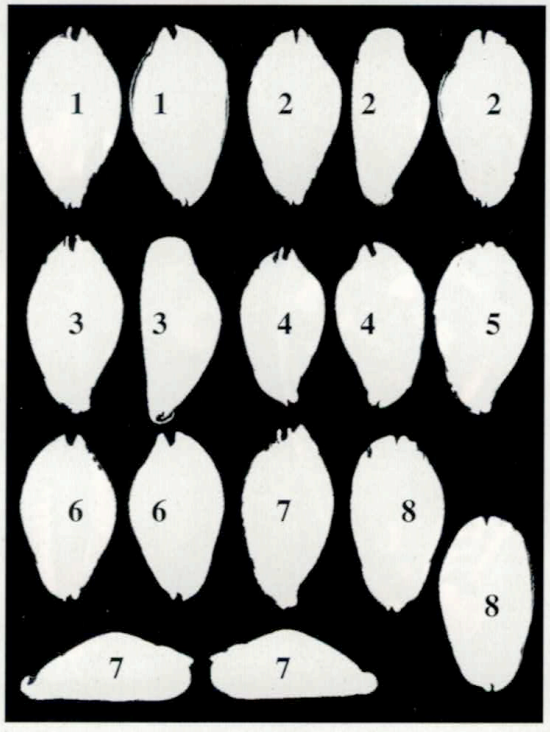




Plate 44

Zoila friendii friendii

Dwarf and golden variations

1 – 5 ***Zoila friendii friendii*** — Dunsborough, 2 – 5 m (size range 49 – 57 mm). Typical specimens of a dwarf local population.

6 ***Zoila friendii friendii*** — "Fremantle" (87 mm). Very pale specimen.

7 ***Zoila friendii friendii*** Golden colored variation — "Peppermint Bay, 8 m" (76 mm). Collection and photo GABRIELLI.

8 ***Zoila friendii friendii*** Golden colored variation — "Busselton, 15 m" (68 mm). Collection CHIAPPONI.



Zoila friendii friendii,
dwarf and pale variations

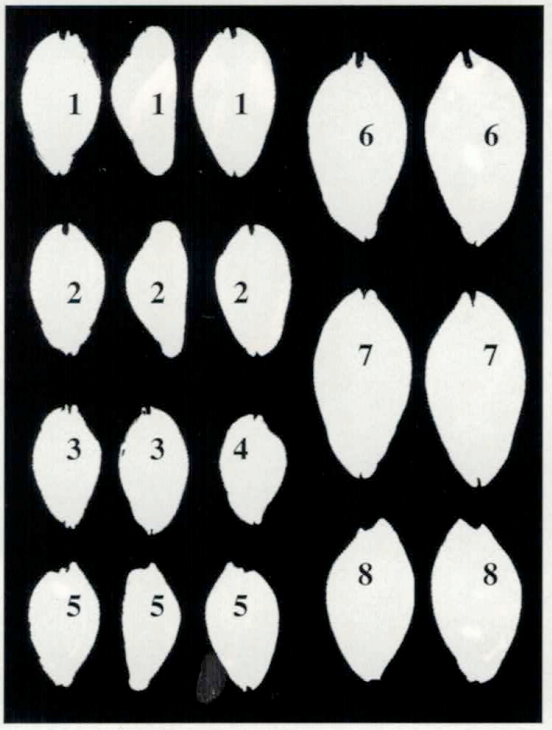




Plate 45

Zoila friendii vercoi

Typical specimens

1 ***Zoila friendii vercoi*** "Hopetoun, 35 m" (96 mm). Specimen resembling *f. friendii*.

2 – 3 ***Zoila friendii vercoi*** "Esperance, 15 – 25 m" (larger specimen 93 mm). Slender but otherwise typical shells.

4 ***Zoila friendii vercoi*** Holotype. Esperance. Collection South Australian Museum. Photo FORREST, courtesy RAYBAUDI.

5 ***Zoila friendii vercoi*** Cape Le Grande, 40 m (94 mm). Specimen resembling *f. friendii*.

6 ***Zoila friendii vercoi*** "Esperance, trawled 125 m" (81 mm). Collection and photo GABRIELLI.

Note that in all variations of *f. vercoi*, the aperture is wider in relation tcompared to *f. friendii*. The whitish frame along the aperture is also broader in *f. vercoi* than in the western subspecies.



Zoila friendii vercoi

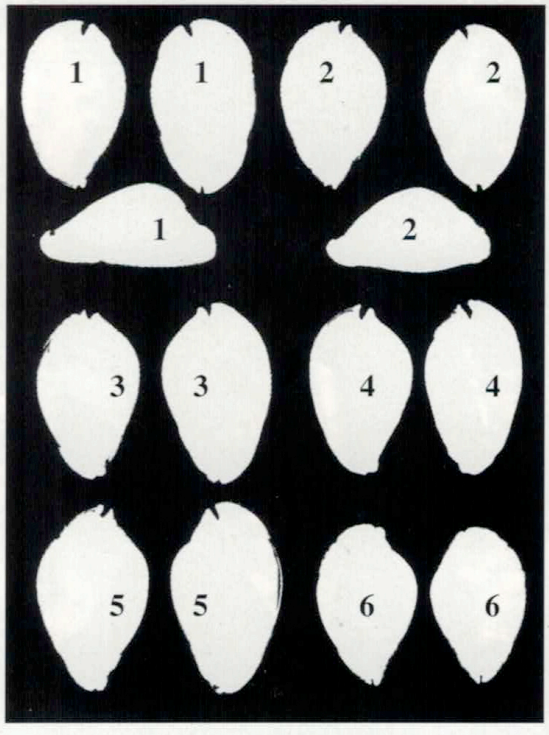




Plate 46

Zoila friendii vercoi

Typical specimens

1 – 6 *Zoila friendii vercoi* "Albany, 5 – 35 m" (size range 69 – 89 mm). Typical inflated, dark spotted shells.



Zoila friendii vercoi

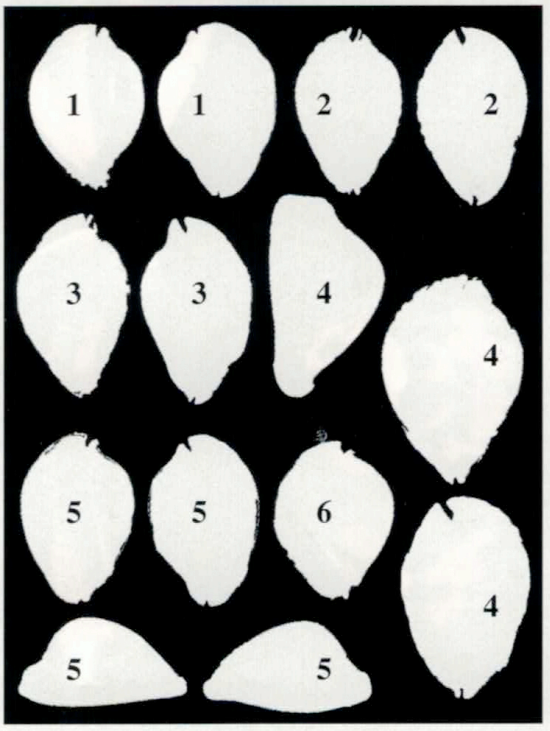




Plate 47

Zoila friendii vercoi

Color variations

1 – 2 ***Zoila friendii vercoi*** "Albany, 15 – 25 m" (larger specimen 87 mm).

3 ***Zoila friendii vercoi*** Two People's Bay, Albany, 20 m (91 mm).

4 ***Zoila friendii vercoi*** "Albany area, 60 m" (77 mm).

5 ***Zoila friendii vercoi*** Esperance, 45 m (81 mm).

6 ***Zoila friendii vercoi*** Albany area. Remarkable specimen with regular patches. Collection and photos DEMERTZIS.

7 ***Zoila friendii vercoi*** "S. W. Australia" (83 mm). Spectacular banded shell. Collection CHIAPPONI.



Zoila friendii vercoi

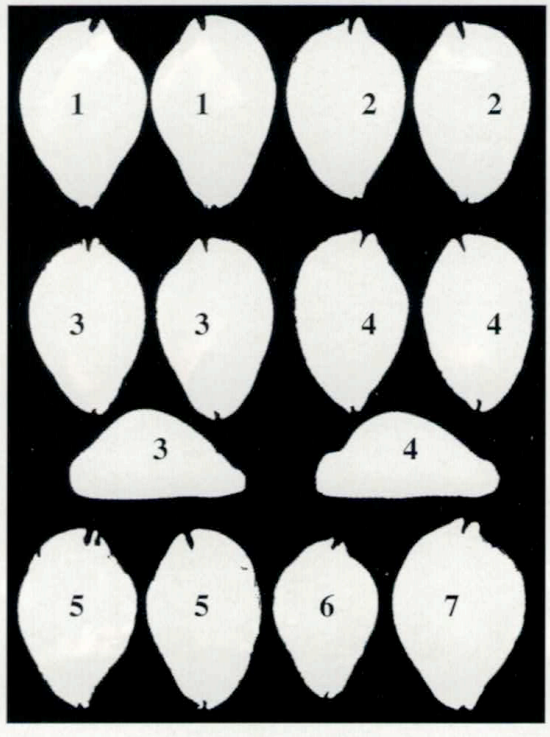




Plate 48

Zoila friendii vercoi

Variations and light colored specimens

1 – 2 ***Zoila friendii vercoi*** variation — "Cape Recherche area, trawled late 60ies" (larger specimen 70 mm). Note the coarser teeth.

3 ***Zoila friendii vercoi*** variation — Locality unknown (approx. 80 mm). Globluar, slightly distorted shell. Collection and photo DEMERTZIS.

4 ***Zoila friendii vercoi* / *thersites*** variation — Great Australian Bight, off 150 m" (71 mm). Resembling *thersites* conchologically.

5 – 8 ***Zoila friendii vercoi*** f. ***lentiginosa*** — "Albany area" (approx. 75 mm). Set of exceptional light colored specimens. Collection and photo DEMERTZIS.

The color variations of *f. vercoi* are most extreme, and stragely, all may be found on the same spot, at any depth. Light colored shells become more abundant in deeper water. Numerous names have been introduced for those, two of which have been adopted here, merely to assist communication between collectors and dealers: forma *lentiginosa*, which retains sparse darker spotting, and forma *candida* which has no spots at all (erroneously called "*vercoi contraria*" in former publications).



Zoila friendii vercoi variations

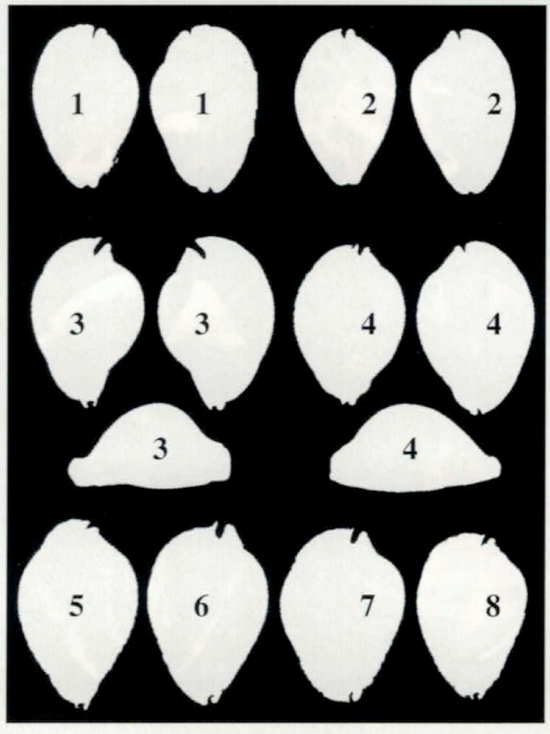




Plate 49

Zoila friendii vercoi

Pale, unspotted specimens (forma "*candida*")

1 ***Zoila friendii vercoi*** f. ***candida***
"Esperance, by diver 60 m" (77 mm).

2 ***Zoila friendii vercoi*** f. ***candida***
"Albany area, trawled off 120 m" (67 mm). Beautiful shell showing distinct embryonic banding.

3 ***Zoila friendii vercoi*** f. ***candida***
Termination Island, Esperance, 55 m (75 mm).

4 ***Zoila friendii vercoi*** f. ***lentiginosa***
"Albany area" (approx. 80 mm). Sparsely spotted form. Collection and photo DEMERTZIS.

5 ***Zoila friendii vercoi*** f. ***lentiginosa***
Flinders Bay, Margaret River (74 mm). Sparsely spotted form. Collection and photo GABRIELLI.

6 ***Zoila friendii vercoi*** f. ***lentiginosa***
Albany, by diver 25 m (82 mm). Sparsely spotted form. Collection and photo GABRIELLI.



Zoila friendii vercoi
variations

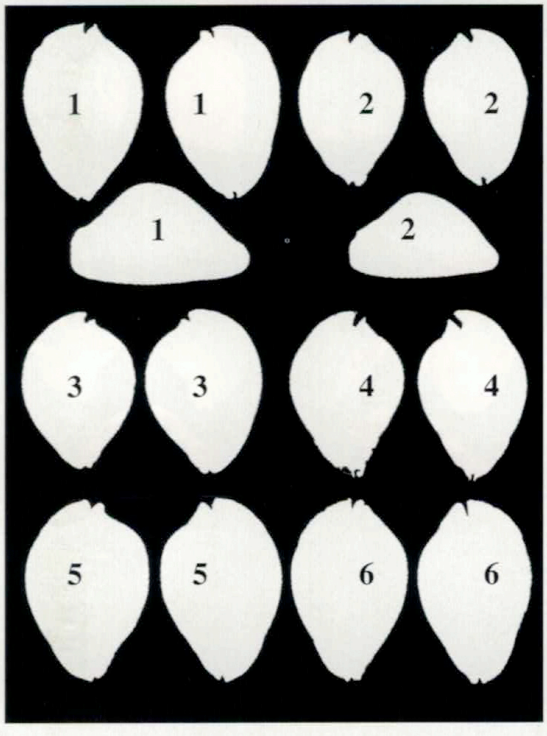




Plate 50

Zoila thersites contraria

Typical pale specimens

1 ***Zoila thersites contraria*** "Eucla, tralwed off 180 m" (64 mm). Rostrate, heavy shelled, plain white specimen. Collection and photo GABRIELLI.

2 ***Zoila thersites contraria*** "Ceduna, trawled off 150 m" (71 mm).

3 ***Zoila thersites contraria*** "Off Port Lincoln, 150 m" (70 mm). Collection and photo DEMERTZIS.

4 ***Zoila thersites contraria*** "Port Lincoln, trawled, 115 m" (71 mm).



Zoila thersites contraria

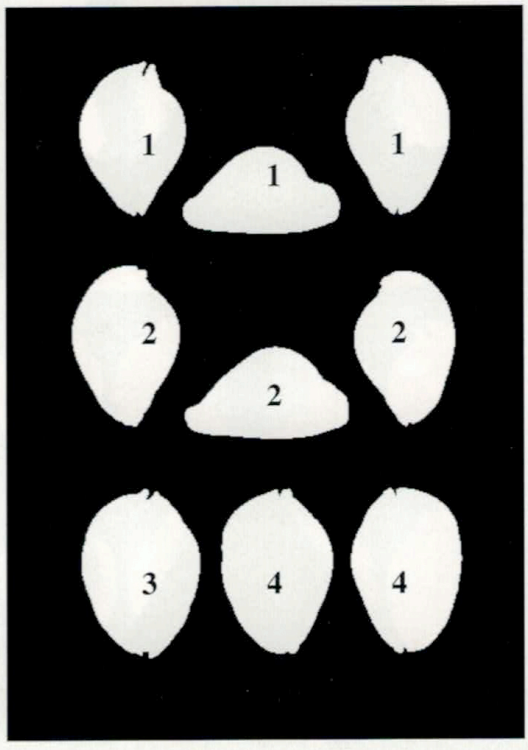




Plate 51

Zoila thersites contraria

and *thersites thersites* var. "*eburnea*"

1 ***Zoila thersites thersites*** f. ***eburnea*** Original figure. Kangaroo Island, by diver 15 m. Rare light variation of *thersites*, resembling *t. contraria* conchologically.

2 ***Zoila thersites contraria*** "Great Australian Bight, trawled" (66 mm). Collection and photo GABRIELLI.

3 ***Zoila thersites contraria*** "Port Lincoln, trawled off 150 m" (82 mm). Collection NORPOTH.

4 ***Zoila thersites contraria*** Ceduna, trawled off 200 m (72 mm).

5 ***Zoila thersites contraria*** Eucla area, trawled off 200 m (69 mm). Collection and photo GABRIELLI.

6 ***Zoila thersites contraria*** "Great Australian Bight, deep water" (72 mm).

The very rare light colored forma *eburnea* from shallow water is very similar to *thersites contraria* from deep water.



Zoila thersites contraria

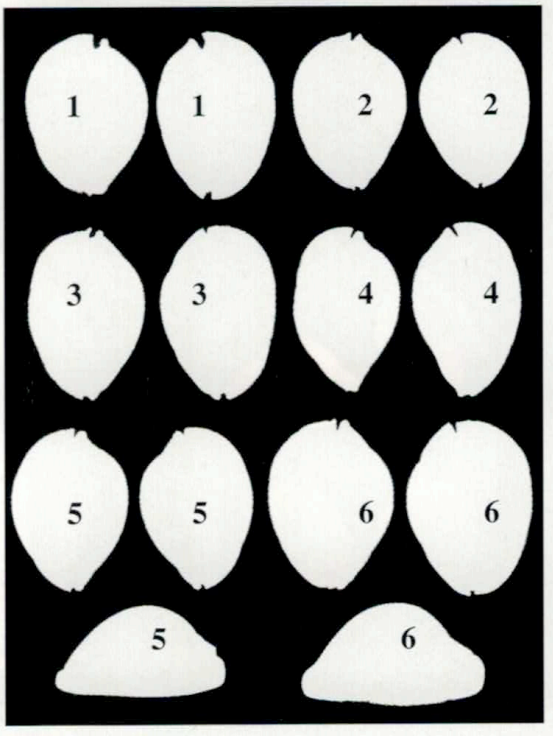




Plate 52

Zoila thersites contraria

Typical pale shells and spotted forms

1 ***Zoila thersites contraria*** Ceduna, trawled from 150 m (approx. 65 mm). Lightweight specimen resembling the lectotype. Collection BRIDGES.

2 ***Zoila thersites contraria*** Lectotype. 80 km west of Eucla. Collection Australian Museum, Sydney. Photo FIELDS, courtesy RAYBAUDI.

3 ***Zoila thersites contraria*** Trawled off Port Lincoln (approx. 70 mm). Collection and photo DEMERTZIS.

5 – 6 ***Zoila thersites contraria*** Ceduna area, off 100 m (larger specimen 70 mm). Vividly spotted shells. No. 6 collection and photo DEMERTZIS.



Zoila thersites contraria

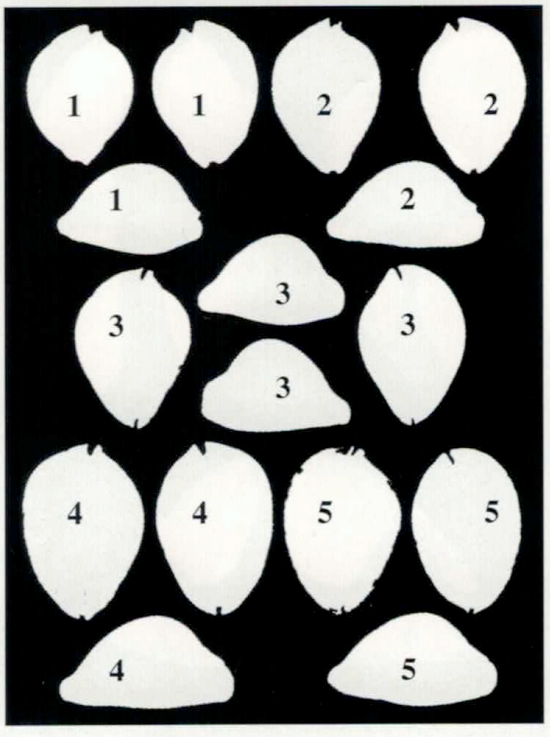


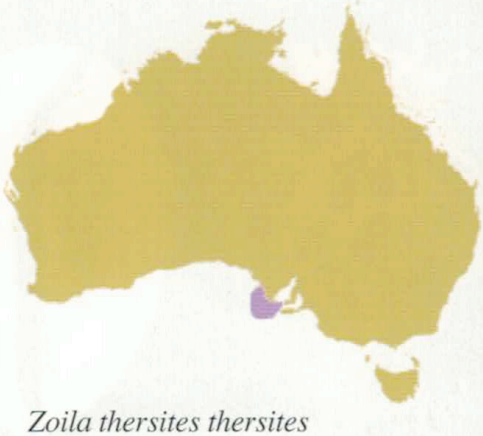


Plate 53

Zoila thersites thersites

Typical specimens

1 – 8 *Zoila thersites thersites* "Port Lincoln, 5 – 25 m" (size range 65 – 77 mm). Typical specimens. Note the variability of the basal color.



Zoila thersites thersites

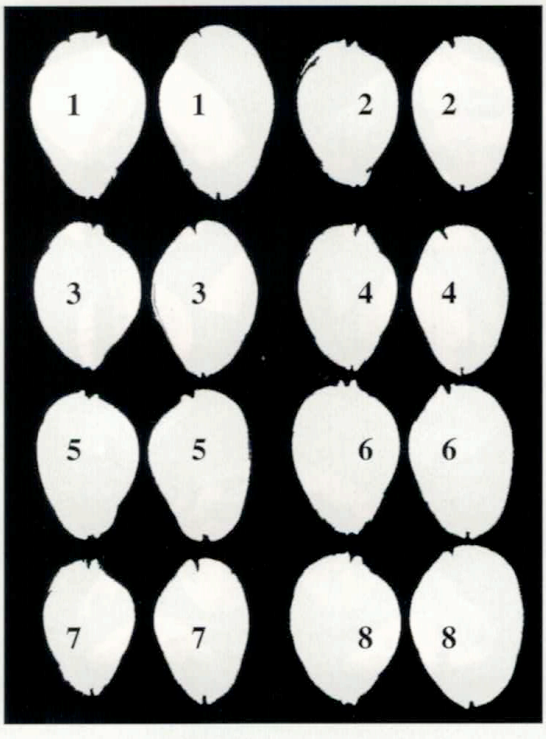




Plate 54

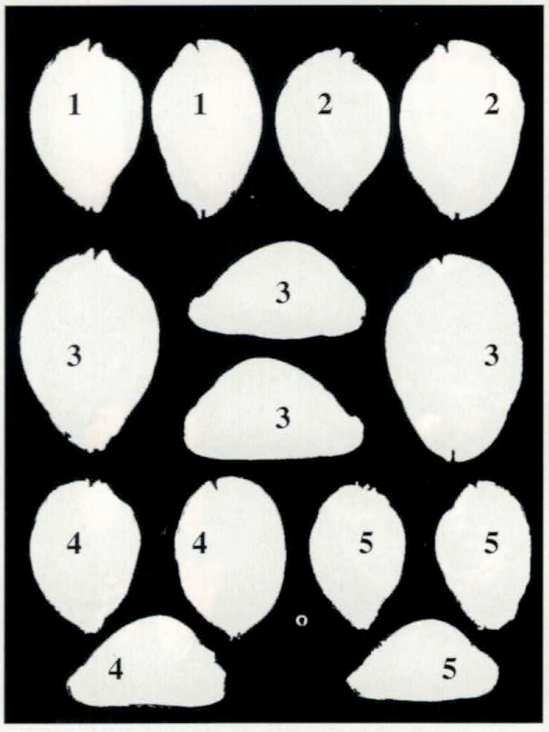
Zoila thersites thersites

Typical specimens

1 – 6 *Zoila thersites thersites* "Port Lincoln, 5 – 25 m" (size range 70 – 97 mm). Typical color variations.



Zoila thersites thersites





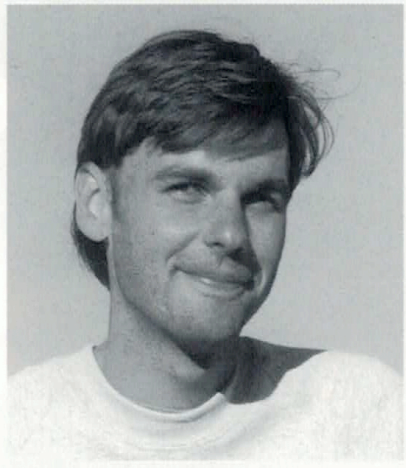
About the Author

Felix Lorenz was born in Lauenburg, Germany in 1967. His interest in seashells started in early childhood and has kept growing ever since. He studied biology, graduated with a thesis on the ring–cowry and presently works as a zoologist at the Justus–Liebig–University of Gießen.

Together with Alex Hubert († 1999) he wrote the "Guide to Worldwide Cowries" and is author of more than seventy papers dealing with cowries and other gastropod families.

As a keen traveller and scuba-diver he has devoted himself to the assemblage and management of several important private and public shell-collections worldwide.

For more information please visit his website: **www.cowries.net**



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