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THE LAND MOLLUSCS OF THE KRAKATAU ISLANDS, INDONESIA

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[Plates 1 and 2]

CONTENTS

The land molluscs collected on the 1984–85 Zoological Expeditions to the Krakatau Islands are reported on, and a synopsis provided of all previous land mollusc records since the 1883 eruption. The current fauna of the islands is 19 species, 16 from Rakata, 12 from Sertung, 7 from Panjang and 1 from Anak Krakatau, the latter being the first record of a land snail from that island. Six species are recorded for the first time from the Krakatau Islands. These are *Filicaulis bleekerii*, *Pupisoma orcula*, *Elasmias sundanum*, *Lamellidea* (*Lamellidea*) *subcylindrica*, *Microcystina gratilla* and *Landouria rotatoria*. Radulae of several of the species are figured. The expeditions produced 19 new records for individual islands.

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1. Introduction

This is a report on land molluscs collected from the Krakatau group of islands (figure 1) in the Sunda Strait, Indonesia, during 1984 and 1985, together with a history of the recolonization of the islands by land molluscs since 1883. The collections were made on two expeditions organized by La Trobe University, Victoria, a general introduction to which is provided by Thornton & Rosengren (1988). Preliminary reports of the expeditions contain further details of the collections made (Thornton 1985, 1986).

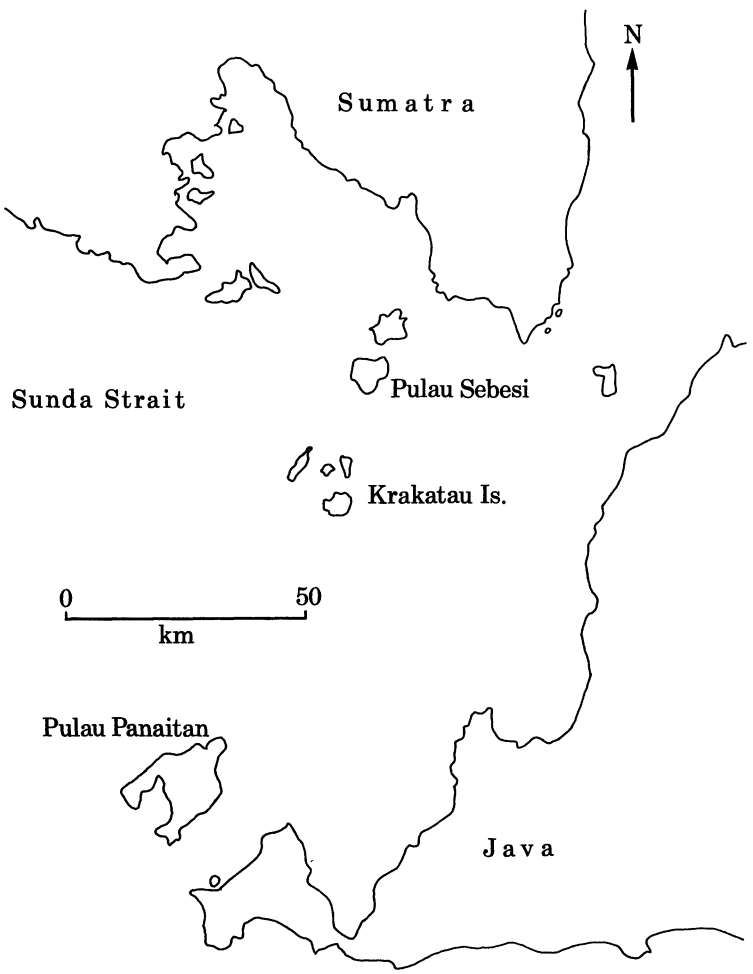

Figure 1. Sunda Strait and the Krakatau Islands, showing places mentioned in text.

Before the 1883 eruption the only published records of land molluscs from Krakatau were by Martens (1867). The five species mentioned were all large animals, the most obvious shells in what was undoubtedly a much more diverse fauna. In the 102 years since the eruption a series of expeditions and scientific visits has been made to the islands to sample and document the progression of recolonization of the flora and fauna to the islands. The first land molluscs recorded after the eruption were two species collected in 1908 by Jacobson (1909). Further collections were made in 1919, 1920, 1921 and 1922 by Dammerman, Docters van Leeuwen, Sunier and Boschma. Some of these were mentioned in general texts by Docters van Leeuwen

(1921) and Dammerman (1922). The first special report on the molluscs of the islands after the eruption was by Benthem Jutting (1925). All islands (three at that time) were visited on these collecting trips but no specialist malacologists ever visited the islands.

Further faunistic survey work by Dammerman from 1929 to 1934 was the basis of a major report on the recolonization of the islands during the first 50 years after the eruption (Dammerman 1948).

In 1929–30 the new island of Anak Krakatau (figure 2) appeared as an active volcano near the northern lip of the old caldera. This early activity resulted in severe damage, particularly on Sertung. Anak Krakatau has continued as an active volcano up to the present with frequent eruptions of ash and lava. Since it first emerged as a permanent island in 1930, it has risen to a height of 195 m above sea level with an emerging terrestrial plant and animal community on the lower slopes of the ash cone. The present community, however, dates from 1952 when major eruptions evidently destroyed the previously established biota (Thornton 1986; Thornton & Rosengren 1988).

Although the islands were visited frequently, and each of the three older islands have been temporarily inhabited during the past fifty years, the next report of land molluscs on the islands resulted from the 1982 expedition of Kagoshima University, Japan. Eight species of land molluscs were collected and reported upon by Yamane & Tomiyama (1986). The collections of land molluscs from the islands since the eruption, including those obtained in the present study, are summarized in table 1 and §3.

In a classic series of papers, Benthem Jutting (1925, 1941, 1948, 1950, 1952, 1959) has documented the land mollusc fauna of both Java and Sumatra and of their satellite islands. In these works she compiled detailed taxonomic treatises of the Indonesian fauna and provided records of species from the Krakatau group. More recently Butot (1955) described the land mollusc fauna of a large island at the southern end of the Sunda Strait, Pulau Panaitan (figure 1), the biota of which was fairly seriously damaged, but not totally destroyed, by the Krakatau eruption of 1883.

2. Methods

Collections of land molluscs were made mainly by the authors on the 1984 expedition, but valuable additional records were obtained in both 1984 and 1985 by the incidental collecting of other members of the expeditions. Many visits were made to various parts of the islands, details of which are listed in Thornton (1985, 1986) and Thornton & Rosengren (1988). Hand searches were made in all likely habitats, including under rocks, in litter, under vegetation, on trees and other vegetation and in supralittoral drift debris. Other collecting techniques that yielded land molluscs included the beating and sweep-netting of vegetation, litter extraction, and pit-fall and water trapping. Several small species were only collected by beating vegetation for small insects.

Although collecting on the archipelago was extensive, several sites received particular attention. On Rakata, Zwarte Hoek (figure 2) provided a vine forest with fairly dense understorey, deep litter and plenty of large and small rocks immediately behind the beach and only a few metres above sea level. Owl and South Bays provided similar habitats on the other side of the island. Several routes to the summit (777 m) were taken from various parts of the island. These ascended through a developing secondary monsoon forest with a large number of tree, shrub and ground cover species, with fairly moist litter on a largely ash and soil base.

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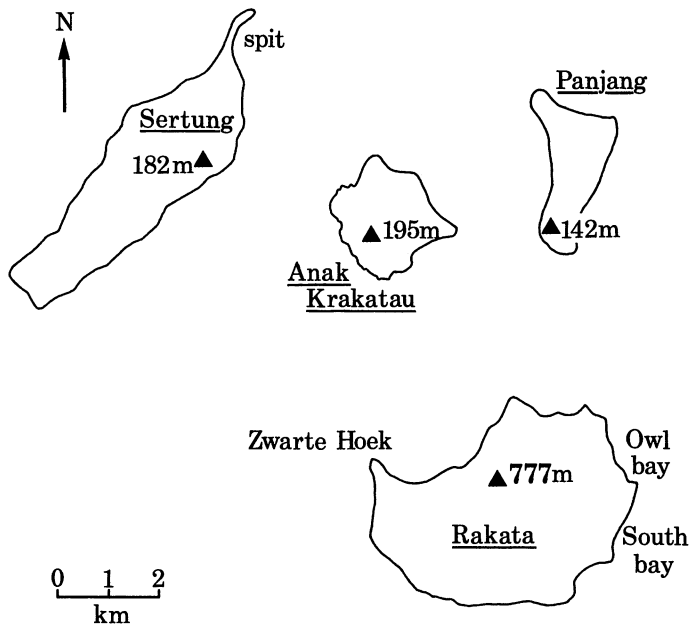

FIGURE 2. The Krakatau archipelago, 1985, showing localities mentioned in text.

At about 600 m this gave way to moss forest, with fewer plant species and more available moisture. Details of the vegetation types of these habitats are given by Whittaker *et al.* (1984).

Sertung (figure 2) is the second largest island, rising to about 180 m above sea level. Much of the island is covered with developing secondary monsoon forest with a diversity of plant species. By contrast, there is a fairly mobile spit on the northern end, with a simpler vegetation dominated by *Casuarina equisetifolia* with a much less complex understorey and little ground cover. Collections were made from the spit, from the vine forest immediately to the south of it, and from approximately half way along the island near the highest point.

Panjang is a much smaller island, again covered in forest, with dense understorey in many places. Collections were made close to the beach at the northern end in 1984 and from several other parts of the island in 1985.

Anak Krakatau emerged as a new island only in 1930 and suffered a sterilizing eruption in 1952 and a very destructive one in 1972. A vegetative fringe has developed on the eastern and northern forelands where the succession is at an early stage, the vegetation being dominated by *Casuarina equisetifolia* with a varied ground cover and deep litter in places.

The general environment of all islands is treated by Thornton & Rosengren (1988).

Voucher specimens of all species from each of the islands are lodged in the Museum Zoologicum Bogoriense, Bogor, Indonesia, and, where present, duplicate voucher specimens are lodged in the Museum of Victoria, Melbourne, Victoria, Australia.

3. THE MOLLUSCAN FAUNA OF THE ISLANDS

The results of sampling on the 1984 and 1985 expeditions are given in tables 1 and 2. Table 1 is a summary of all records of land molluscs from the islands both before the 1883 eruption and on surveys since that time. There is only one record of land molluscs on the island of

TABLE 1. LAND MOLLUSC SPECIES FOUND ON THE KRAKATAU ISLANDS BEFORE THE 1883 ERUPTION AND ON SURVEYS SINCE THEN

(R, Rakata; S, Sertung; P, Panjang; A, Anak Krakatau; K, Krakatau pre-1883.)

	pre-1883	1908	1919–1921	1933–1934	1982	1984–1985
Cyclophoridae						
Cyclophorus perdix	K	.	.	.	.	.
Ellobiidae						
Melampus flavus	.	.	.	P	.	R
Pythia chrysostoma	.	.	RS	RS	.	RSP
Pythia pantherina	.	.	S	S	.	.
Pythia plicata	.	.	p	p	.	RSP
Pythia scarabaeus	.	.	RS	.	S	.
Veronicellidae						
Filicaulis bleekerii	.	.	.	.	.	S
Vertiginidae						
Gastrocopta pediculus ovatula = *Nesopupa mica* = *Pupina*?	.	R	R	RS	.	RS
Succineidae						
Succinea minuta	.	.	.	R	S	RS
Subulinidae						
Lamellaxis gracilis	.	.	RS	RS	RS	RSP
Subulina octona	.	.	.	R	R	RSP
Valloniidae						
Pupisoma orcula	.	.	.	.	.	R
Achatinellidae						
Elasmias sundanum	.	.	.	.	.	RS
Lamellidea (*Lamellidea*) *subcylindrica*	.	.	.	.	.	RS
Helicarionidae						
Elaphroconcha bataviana	K	.	.	.	.	.
Elaphroconcha javacensis	K	.	.	.	.	.
Coneuplecta sitaliformis = *Liardetia convexoconica*	.	.	.	R	RS	R
Liardetia doliolum	.	.	.	R	S	RSPA
Liardetia indifferens	.	.	RS	RS	.	RSP
Microcystina gratilla	.	.	.	.	.	RP
Camaenidae						
Amphidromus (*A.*) *inversus*	K	.	.	.	.	.
Amphidromus (*A.*) *banksi*	.	.	.	.	S	S
Amphidromus (*S.*) *porcellanus*	.	R	R	R	.	R
Chloritis helicinoides	K	.	.	.	.	.
Landouria rotatoria	.	.	.	.	.	R
Pseudopartula arborascens	.	.	.	.	S	.
total	5	2	8	12	8	18

Krakatau before 1883. Martens (1867) reported five species, all of which are large and obvious, likely to be collected by a casual, non-specialist search. More information on who collected these specimens and where and when they were collected is given by Steenis-Kruseman & Steenis (1950). Although these species occur today on the adjacent land masses of Java and Sumatra, none has so far recolonized the Krakataus.

Since the eruption of 1883, 19 species have successfully established populations on one or more of the Krakatau Islands. The collecting effort over the 102 years has been too superficial

Table 2. Distribution of land mollusc species found on the Krakatau Islands in 1984–85

(On Rakata: ZH, Zwarte Hoek; SS, south side; MR, main ridge (300–400 m); S, summit (777 m). X, collection of a species previously recorded from the island; XX, collection of a species not previously recorded from the island; *, species recorded in 1982 but not seen in 1984–85.)

	Rakata						Anak
	ZH	SS	MR	S	Sertung	Panjang	Krakatau
Ellobiidae							
Melampus flavus	XX	XX	.	.	.	.	.
Pythia chrysostoma	X	X	.	.	X	XX	.
Pythia plicata	XX	.	.	.	XX	X	.
Veronicellidae							
Filicaulis bleekerii	.	.	.	.	XX	.	.
Vertiginidae							
Gastrocopta pediculus ovatula = *Nesopupa mica* = *Pupina*?	X	.	.	.	X	.	.
Succineidae							
Succinea minuta	X	.	X	.	X	.	.
Subulinidae							
Lamellaxis gracilis	X	X	X	X	X	XX	.
Subulina octona	X	X	X	X	XX	XX	.
Valloniidae							
Pupisoma orcula	.	.	XX	XX	.	.	.
Achatinellidae							
Elasmias sundanum	XX	.	XX	XX	XX	.	.
Lamellidea (*Lamellidea*) *subyclindrica*	.	XX	.	.	XX	.	.
Helicarionidae							
Coneuplecta sitaliformis = *Liardetia convexoconica*	.	X	X	X	.	.	.
Liardetia doliolum	X	X	X	.	X	XX	XX
Liardetia indifferens	X	X	X	X	X	XX	.
Microcystina gratilla	.	.	XX	XX	.	XX	.
Camaenidae							
Amphidromus (*A.*) *banksi*	.	.	.	.	X	.	.
Amphidromus (*S.*) *porcellanus*	X	X	X	X	.	.	.
Landouria rotatoria	XX	.	XX	XX	.	.	.
Pseudopartula arborascens	.	.	.	.	X*	.	.
total (new records in parentheses)		16(7)			12(5)	7(6)	1(1)

and unbalanced to allow a good assessment of the sequence of colonizations of the islands by the land molluscs. Table 1 shows a steady increase in numbers of species on the island group since the first two species were collected in 1908. The report of Yamane & Tomiyama (1986) should be treated as partial coverage only; some of the common and long-standing species, such as *Amphidromus* (*Syndromus*) *porcellanus* on Rakata, were unaccountably not recorded. Only one species was recorded from Panjang before 1984 when six new records for that island were obtained. No species appears to have become established on the islands in the early period of recolonization and then become extinct. Once established, species appear to have consolidated and spread. Exceptions to this generalization may be accounted for by amended identifications rather than by loss of species.

Table 2 shows the species that have established themselves on the islands up to 1985. Rakata, being the largest island, with the variation in habitat conferred by its height, has the greatest number, 16 with 7 new records from the 1984–85 expeditions. Several species are only found on the upper parts of the island. Some of these are small to minute and live on the foliage of trees and shrubs. One way in which these species could have colonized is by transportation on wind-borne leaves. The 'big triangle' of Rakata's 777 m high profile, as well as its greater plan area, makes a good target for this form of transport.

One of the main features of the fauna, particularly of the two larger islands Rakata and Sertung, is the number of species unique to one island. Of Rakata's 16 species, five are not found on any other island of the group. These include the large and very common *Amphidromus* (*Syndromus*) *porcellanus* that has been on Rakata since 1908. Three of the others are new records for the islands. On Sertung, 3 of the 12 species are unique to that island in the archipelago. One of these is the veronicellid slug, *Filicaulis bleekerii*, which is found in very large numbers in the vine forest litter at the north end of the island. The other two, *Amphidromus* (*Amphidromus*) *banksi* and *Pseudopartula arborascens*, are large arboreal species that may have rafted to the island, although they could have been wind-borne as juveniles.

Only 6 of the 19 species found in the island group occur on all three older islands. One of these was also found on Anak Krakatau, and is the first land snail to be recorded on this island. All six are ground-dwelling litter species which probably came to the islands in surface drift. They are probably fairly readily transported between islands, hence the present distribution.

The 19 new records for individual islands is a measure of the relative lack of adequate sampling over the previous 50 years. Many of these new records are of widespread and well-established populations that have obviously been on the islands for many years. Conversely, some of the distributional gaps presented here are probably themselves collection artefacts due to the small size and patchy distribution of many species.

4. Notes on the species

Brief notes are given below on each species that is currently found on the Krakatau Islands or has been recorded from them in the past. The taxonomic status of each species is given, together with notes on its ecology, habitat preference and distribution within Java and Sumatra and beyond. In several cases, hitherto unrecorded information on radula and anatomical structure is provided to support the taxonomic placement. The original reference to each species is given, together with the more important references to its earlier records on the Krakataus and, where possible, a reference to a good figure or description or both of the species.

(*a*) *Cyclophoridae*

Cyclophorus perdix Broderip & Sowerby, 1829

1829. Broderip & Sowerby, p. 50 (*Cyclophorus perdix*).
1867. Martens, p. 136.
1948. Dammerman, p. 520.
1955. Butot, p. 88, fig. 10.

This species was recorded from the island of Krakatau before the 1883 eruption (Martens 1867), although from a different part of the work from the other four species, as Benthem Jutting does not mention this species in listing the pre-1883 records. Several subspecies are

recognized and there is no direct evidence as to which of these the record should be referred. The nominate subspecies is known from Java, including Pulau Panaitan at the southern end of Sunda Strait (Butot 1955). *C. perdix tuba* is the subspecies found on Sumatra.

This species has not been found on the Krakatau Islands since the 1883 eruption.

(*b*) *Ellobiidae*

Melampus flavus (Gmelin, 1791)

1791. Gmelin, p. 3436 (*Voluta flava*).
1931. Oostingh, p. 222 (as *Melampus fasciatus* and *Melampus luteus*).
1972. Cernohorsky, p. 213, pl. 61, fig. 1–1c.

This marginal marine species was found in the supralittoral zone under rocks and logs at two sites on Rakata. It is common throughout the tropical Pacific region and was recorded from Panjang by Oostingh (1931) as *M. fasciatus* and *M. luteus*, now considered to be colour morphs and synonyms of this species (Cernohorsky 1972). It is the most marine-dependent of all the ellobiids recorded from the islands and probably needs a habitat covered by seawater several times a year.

The specimens found on Rakata show the wide variety of colour patterning typical of the shells of this species. Some are the typical *flavus* form, being a uniformly greyish-brown; others are the orange-brown form, having a light orange shell with several dark chocolate horizontal bands.

Notes on *Pythia* records: At various times four species of *Pythia* have been recorded from the Krakatau Islands. These are *P. scarabaeus* (Linnaeus, 1758); *P. plicata* (Ferussac, 1821); *P. pantherina* (Adams, 1850) and *P. chrysostoma* Tapparone-Canefri, 1883. We consider that only two species of *Pythia* should be listed for the island group. The allocation of the previous records to these should be as follows.

1. *Pythia chrysostoma*: listed in error as *P. scarabaeus* (Benthem Jutting 1925); with *P. pantherina* as a synonym of *P. scarabaeus* (Cernohorsky 1972).

2. *Pythia plicata*: as itself.

In contrast to *M. flavus* (above), the *Pythia* species have largely broken the dependence on marine contact and can be found in true non-marine environments.

Pythia chrysostoma Tapparone-Canefri, 1883

1883. Tapparone-Canefri, p. 237, pl. 1, fig. 25 (*Pythia chrysostoma*).
1925. Benthem Jutting, p. 144 (as *Pythia scarabaeus*).
1931. Oostingh, p. 221 (as *P. scarabaeus*).
1948. Dammerman, pp. 517 and 518 (as *P. scarabaeus* and *P. pantherina*).

This is the larger of the two *Pythia* species with a fairly short spire and obtuse outline, conspicuously flattened with two semi-keeled lateral edges. The shell is brown with pale to white irregular bands and blotches and a flesh-coloured to white peristome. The umbilicus is an almost closed round canal.

The species is widespread on Rakata, Sertung and Panjang where it occurs in litter and under vegetation on the ground in the coastal forest. It is often found some distance from the sea, living a fully terrestrial existence. The species is found through much of the tropical Indo-Pacific, including both Java and Sumatra.

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Pythia plicata (Ferussac, 1821)

1821. Ferussac, p. 105 (*Scarabus plicata*).
1931. Oostingh, p. 226.
1948. Dammerman, p. 518.

This is a smaller species than *P. chrysostoma* with an oblique, narrow aperture leaving the umbilicus as a transverse slit rather than the more round canal of *P. chrysostoma*. It is less common than *P. chrysostoma* but is found in similar habitats on the three older islands. It was first recorded on the Krakataus from Panjang by Oostingh (1931), and has a distribution from India to Java, being widespread on both sides of Sunda Strait.

(*c*) *Veronicellidae*

Filicaulis bleekerii (Kefestein, 1865)

1865. Kefestein, p. 118 (*Veronicella* (*Vaginulus*) *bleekerii*).
1952. Benthem Jutting, p. 331, figs 9–14.

This species is here newly recorded from the Krakataus although it is common on Java, Sumatra and Sebesi (figure 1) as well as Borneo and the Moluccas. It was found to be common under logs and litter in the vine forest at the northern end of Sertung, but was found on no other island of the group.

F. bleekerii is a small, dark brown slug with some individuals of the Sertung population measuring 20 mm in length but most being much smaller. Figure 3, plate 1, shows that the radula consists of solid, almost triangular, single-cusped teeth which are raised on a wide supporting buttress from a square base plate. Each tooth is similar in size and shape except the rachidian which is about a quarter of the size of the adjacent teeth and is very slender. The radula formula is 29–1–29.

(*d*) *Vertiginidae*

Gastrocopta pediculus ovatula (Moellendorff, 1890)

1890. Moellendorff, p. 253 (*Leucochilus pediculus ovatula*).
1909. Jacobson (as *Pupina* or *Porocallia* sp.).
1925. Benthem Jutting, p. 140, fig. 1 (as *Nesopupa micra*).
1948. Dammerman, p. 517.
1952. Benthem Jutting, p. 355, fig. 35.

Because all earlier collections are unavailable for examination, we follow Dammerman (1948) in assuming that two early records of *Pupa*-like shells are referrable to this species. One of the first two species of land molluscs recorded from the islands after the eruption was a small shell identified as *Pupina* sp. or *Porocallia* sp. (Jacobson 1909). Dammerman (1948) states that the specimen was sent to the Basle museum for further study, and Benthem Jutting received later advice from Basle that the specimen was an indeterminable *Pupa* which, being badly preserved, was thrown away. Benthem Jutting (1925) recorded a small vertiginid, collected from Rakata in 1920, as *Nesopupa* cf. *N. micra*. From her figure it could be a juvenile of this species.

Large populations of the species occur in the litter and under rocks and moss in the vine forest of the Zwarte Hoek area of Rakata and on the northern end of Sertung. They are found

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associated with *Liardetia* spp., *Succinea minuta* and the subulinids. The shells are very small (about 2 mm long), of 4 or 5 whorls, with a round, oblique aperture and several prominent apertural teeth.

The species occurs in both Java and Sumatra and throughout western Indonesia and the Philippines.

(*e*) *Succineidae*

Succinea minuta Martens, 1867

1867. Martens, p. 388 (*Succinea minuta*).
1948. Dammerman, p. 517 (as *Succinea javanicus*).
1952. Benthem Jutting, p. 342, fig. 23.

This small succineid occurs in fairly large numbers in the litter of the vine forest of the Zwarte Hoek and west ridge regions of Rakata and the northern end of Sertung. The shell is very thin and fragile and the animal light coloured with dark spots and streaks on the foot and mantle. Benthem Jutting (1952) showed this species to be the senior synonym of the more widely quoted *Succinea javanicus*. The species was first collected from Rakata in 1931 and from Sertung in 1982.

It is also known from Java, Bali, Lombok and Sumba but not from Sumatra.

(*f*) *Subulinidae*

Lamellaxis gracilis (Hutton, 1834)

1834. Hutton, p. 84 (*Bulimus gracilis*).
1948. Dammerman, p. 516.
1952. Benthem Jutting, p. 378, figs 55 and 56 (as *Opeas gracile*).

This is a tropicopolitan species that appears to be extremely vagile. It is found even on fairly small islands and seems to be able to cross ocean barriers with ease. It was first recorded from Rakata in 1920 and is now found all over the island including the summit. It was first recorded from Sertung in 1921, but this report is the first record from Panjang. Surprisingly, the species was not found on Anak Krakatau but we expect that it will colonize soon.

L. gracilis is usually found with the larger subulinid, *Subulina octona*, in large numbers in litter and under rocks. It differs from *S. octona* by its much smaller size and more slender and delicate shell and by the columellar margin not being truncated at the base. It is widespread and abundant in both Java and Sumatra.

Subulina octona (Bruguieres, 1789)

1789. Bruguieres, p. 325 (*Bulimus octonus*).
1948. Dammerman, p. 517.
1952. Benthem Jutting, p. 376, figs 52 and 53.

This species is also tropicopolitan and is usually found in great numbers where it occurs. It was first recorded from Rakata in 1928 and is now found all over the island. The present record is the first from Sertung and Panjang although the species was widespread and abundant on both islands in 1984. It lives in litter and on the surface of the soil and is easily recognized by its long, slender shape (up to 20 mm in height) with 9 or 10 whorls and the white to yellow

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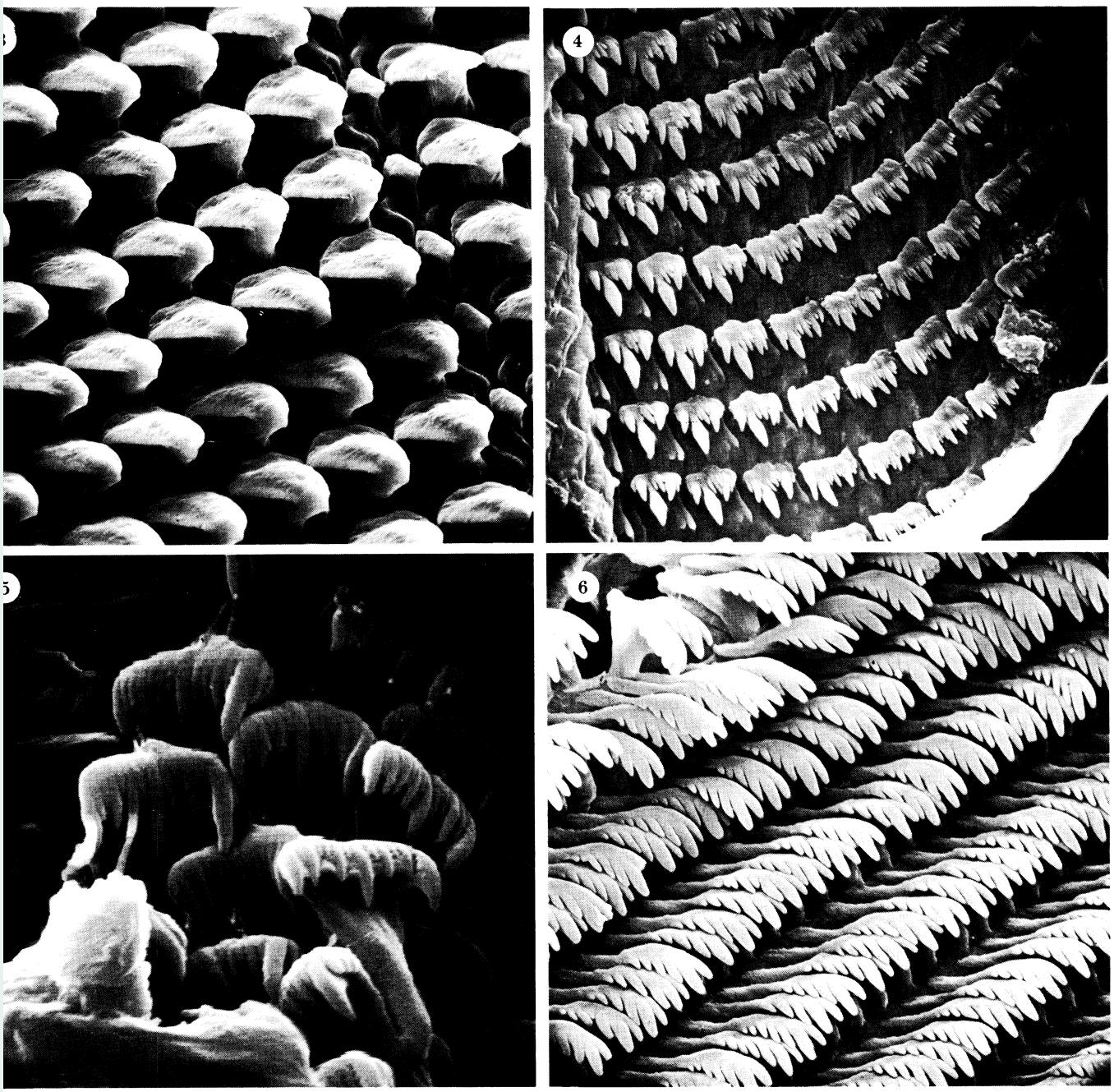

FIGURE 3. Radula of *Filicaulis bleekerii* from Sertung (magn. × 760).

FIGURE 4. Radula of *Pupisoma orcula* from the summit of Rakata (magn. × 1700).

FIGURE 5. Radula of *Elasmias sundanum* from the summit of Rakata (magn. × 6000).

FIGURE 6. Radula of *Coneuplecta sitaliformis* from the summit of Rakata (magn. × 2100).

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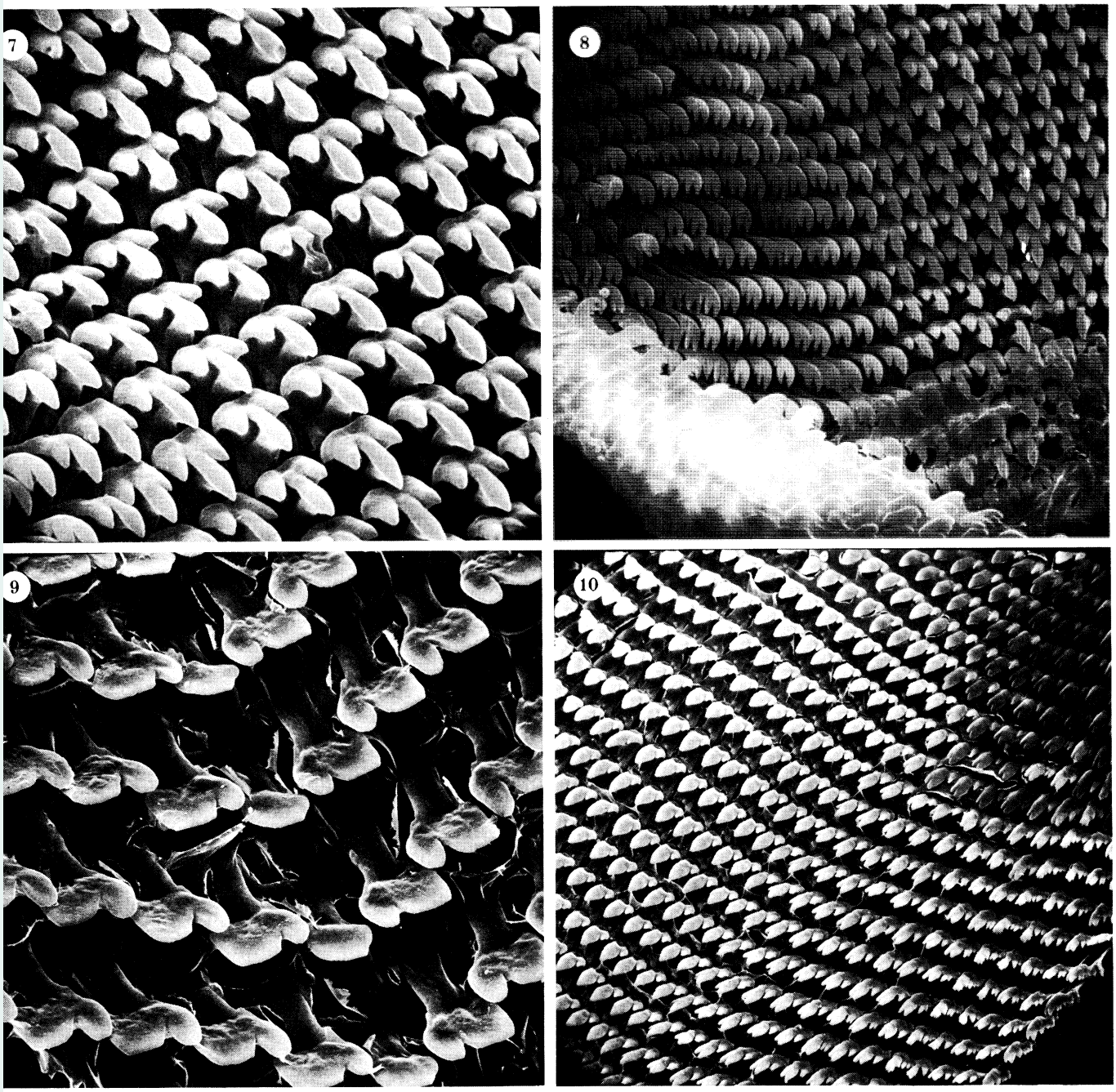

FIGURE 7. Radula of *Liardetia doliolum* from Sertung showing the central teeth (magn. × 1760).
FIGURE 8. Radula of *Liardetia uoliolum* from Sertung showing the central and lateral teeth (magn. × 880).
FIGURE 9. Radula of *Amphidromus* (*Syndromus*) *porcellanus* from Zwarte Hoek, Rakata (magn. × 560).
FIGURE 10. Radula of *Landouria rotatoria* from Zwarte Hoek, Rakata (magn. × 300).

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animal showing through the almost transparent shell. The columellar is truncated at its lower extremity. The species is widespread and common in both Java and Sumatra and like the previous species can be confidently expected to colonize Anak Krakatau fairly soon.

(*g*) *Valloniidae*

Pupisoma orcula (Benson, 1850)

1850. Benson, p. 251 (*Helix orcula*).
1952. Benthem Jutting, p. 363, fig. 40.

A few specimens of a small, conico-globose, fragile almost transparent shell were found by beating vegetation on the upper parts of Rakata. They had a sculpture of fine riblets crossed by finer spiral lines, a narrow to almost closed umbilicus and a round, oblique aperture devoid of teeth. They are tentatively referred to this species and constitute a new record for the islands. The species is widespread throughout tropical regions and is thought to be readily transported and introduced into new areas through commerce (Benthem Jutting 1952). It is recorded from both Java and Sumatra.

Referral to the genus *Pupisoma* is confirmed by examination of the radula (figure 4, plate 1). The tricuspid laterals and 4- or 5-cuspid marginals with extra minor cusps are characteristic of *Pupisoma*.

(*h*) *Achatinellidae*

Elasmias sundanum (Moellendorff, 1897)

1897. Moellendorff, p. 90 (*Tornatellina sundana*).
1952. Benthem Jutting, p. 348, fig. 28.
1960. Cooke and Kondo, p. 232.

This is a new record for the Krakatau Islands of a species that occurs in both Java and Sumatra (Benthem Jutting 1952, 1959). Several specimens were found on vegetation at all levels on Rakata from Zwarte Hoek to the summit, and three specimens were swept from vegetation in the vine forest on the northeast of Sertung. The shells are about 2–3 mm high, squat, globose, of about 3 or 4 whorls with an inflated last whorl and parietal and columellar lamellae. A radula preparation (figure 5, plate 1) reveals a few wide multicuspid teeth typical of the family.

Lamellidea (*Lamellidea*) *subcylindrica* (Quadras & Moellendorff, 1894)

1894. Quadras & Moellendorff, p. 16 (*Tornatellina* (*Lamellina*) *subcylindrica*).
1952. Benthem Jutting, p. 349, fig. 26 (as *Tornatellina subcylindrica*).
1960. Cooke & Kondo, p. 183.

This is also a new record for the Krakataus, and is based on specimens collected by beating foliage in the vine forest about 30 m above sea level on Sertung, and one specimen obtained by beating vegetation for 1 h at 400 m on the southern slopes of Rakata. They are therefore presumably living on the foliage.

The species is very small, shell length about 1.5 mm, and is characterized by the columellar and parietal lamellae and the ovate shape with pointed spire and oblique, oval aperture. Cooke & Kondo (1960) report the distribution of the species as the Mariana Islands including Guam,

whereas Benthem Jutting (1952) reports that it occurs on islands off the north coast of west Java but has not yet been found on Java or Sumatra.

(*i*) *Helicarionidae*

Elaphroconcha bataviana (Von dem Busch, 1842)

1842. Von dem Busch, p. 10 (*Helix bataviana*).
1867. Martens, p. 219 (as *Nanina arguta*).
1941. Benthem Jutting, p. 305 (*Hemiplecta bataviana*).
1948. Dammerman, p. 515 (as *Hemiplecta bataviana*).
1950. Benthem Jutting, p. 427, figs 3, 42 and 43.

This is one of the species that was recorded from the island of Krakatau before the 1883 eruption (Martens 1867) and has not been recorded from the group since. It has a large shell (up to 44 mm in diameter) and is common in both Java and Sumatra. It was one of the commonest species recorded on Pulau Panaitan at the southern end of Sunda Strait (Butot 1955).

Elaphroconcha javacensis (Ferussac, 1821)

1821. Ferussac, p. 46 (*Helix javacensis*).
1867. Martens, p. 214 (as *Nanina umbilicaria*).
1941. Benthem Jutting, p. 305 (*Hemiplecta javacensis*).
1948. Dammerman, p. 515.
1950. Benthem Jutting, p. 430, figs 44 and 45.

This species is another of the large, easily seen land molluscs recorded by Martens (1867) from Krakatau before the 1883 eruption that have not been seen since on any of the islands. It also occurs fairly commonly on Java and Sumatra but evidently does not cross ocean barriers easily.

Coneuplecta sitaliformis (Moellendorff, 1897)

1897. Moellendorff, p. 59 (*Kaliella sitaliformis*).
1948. Dammerman, p. 516 (as *Durgellina convexoconica*).
1950. Benthem Jutting, p. 391, figs 7 and 8 (*Coneuplecta sitaliformis*); p. 396, figs 12 and 13 (*Liardetia convexoconica*).
1986. Yamane & Tomiyama, p. 63 (as *Liardetia convexoconica*).

Several small, fragile, conical specimens were found on vegetation in the higher parts of Rakata. Previous workers have referred these to *Liardetia convexoconica* (Dammerman 1948; Benthem Jutting 1950). On examining the radula we found the species closer to the genus *Coneuplecta* than to *Liardetia*. The rachidian appeared more slender than that of *Liardetia* but the preparation was not good enough to illustrate this point well; the laterals and marginals were uniform with 5 or 6 cusps on the long, almost leaf-like teeth (figure 6, plate 1). This structure, and the high-spired shell with slightly inflated, rounded last whorl, appear most closely to resemble *Coneuplecta sitaliformis* as described by Benthem Jutting (1950). The species occurs in Java and Celebes but is not recorded from Sumatra.

As *Durgellina convexoconica*, the species was first recorded from Rakata in 1933. Yamane & Tomiyama (1986) recorded *L. convexoconica* from both Rakata and Sertung in 1982. The Sertung record was the first for that island. We have not included it in table 2 because without

further details of the Sertung specimens we believe the record must be in doubt. Some specimens of *Liardetia indifferens* have a high spire and fine sculpture and could possibly be confused with this species. Further studies of the fauna are needed to confirm this species record and ascertain whether both this species and *Liardetia convexoconica* occur on any of the islands.

Liardetia doliolum (Pfeiffer, 1846)

1846. Pfeiffer, p. 41 (*Helix doliolum*).
1948. Dammerman, p. 516 (as *Kaliella doliolum*).
1950. Benthem Jutting, p. 410, fig. 28.

Two species of *Liardetia* occur commonly in the litter of the three older islands. They are easily separated by shell shape and sculpture. *Liardetia doliolum* has a small (2–3 mm high) squat, conical shell with strong coarse riblets. *Liardetia indifferens* has a conical shell that is higher than *L. doliolum* and has a sculpture of fine, delicate spiral lines.

Liardetia doliolum is by far the commoner of the two species and occurs in large numbers in the litter of all four islands. It is the first land snail to be recorded from Anak Krakatau, where it occurs in the coarse deep litter under the *Casuarina* trees. It is also found climbing the trunks and foliage of trees and shrubs in the forests of the other islands on wet days. The species is found all over Rakata except the summit and is the most widespread and common species on the Krakataus.

First recorded from Rakata in 1933, it was recorded from Sertung in 1982 (Yamane & Tomiyama 1986) and from Panjang and Anak Krakatau by us in 1984. It is a widespread species on many Indo-Pacific islands including Java and Sumatra.

Placement of the species in the genus *Liardetia* is confirmed by examination of the radula. The central teeth are tricuspid, typical of the family, with a long slender mesocone and two shorter lateral cusps (figure 7, plate 2). The laterals and marginals are tricupsid, hook-shaped teeth (figure 8, plate 2). The teeth of both *Liardetia* species are very similar.

Liardetia indifferens (Boettger, 1891)

1891. Boettger, p. 256 (*Kaliella indifferens*).
1948. Dammerman, p. 515 (as *Kaliella indifferens*).
1950. Benthem Jutting, p. 408, fig. 25.

This species is far less common than *L. doliolum* but is found with it in the deep litter on the three older islands. It is slightly larger than *L. doliolum*, having a moderately conical shell with a sculpture of fine spiral lines and no strong riblets. The shell is yellowish brown in colour, whereas that of *L. doliolum* is usually redder.

On Rakata, *L. indifferens* appears to be more widespread than *L. doliolum*; the former species was found at the summit as well as at other elevations. This apparent difference in habitat range is probably a collection artefact. *L. indifferens* was first recorded from Rakata in 1919 and from Sertung in 1921. The species was first found on Panjang in 1984. It is widespread throughout Indonesia and is recorded from both Java and Sumatra.

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Microcystina gratilla Benthem Jutting, 1950

1950. Benthem Jutting, p. 448, fig. 68 (*Microcystina gratilla*).

This is the first record from the Krakataus. The species was collected from both Rakata and Panjang in 1984–85. It occurs in litter but is so small that it may easily have been missed on the other islands. The shell is small (1–2 mm diameter), flat and highly polished with an almost closed umbilicus. Only a few specimens were taken and no estimate can be made of abundance or distribution. The species occurs in both Java and Sumatra.

(*j*) *Camaenidae*

Amphidromus (*Amphidromus*) *inversus* (Muller, 1774)

1774. Muller, p. 93 (*Helix inversus*).
1848. Reeve, pl. 37, sp. 220.
1867. Martens, p. 337 (as *Bulimus inversus*).
1948. Dammerman, p. 514.

This is another of the large species recorded from Krakatau before its 1883 eruption (Martens 1867) that have not been recorded on the islands since then. There are several accepted subspecies (Laidlow & Solem 1961) with the nominate form having a distribution closest to the Krakatau group, being recorded from Sumatra and islands of the Java Sea, but not from Java. This species is closely related and fairly similar in general appearance to *A.* (*A.*) *javanicus*, common in west Java, and *A.* (*A.*) *banksi*, described from Pulau Panaitan. The species may have been confused in 1867 and *A. banksi* may have been the large *Amphidromus* occurring on Krakatau Island before the eruption. If this is so then this would be the first species recorded before the eruption that has recolonized the islands (see below).

Amphidromus (*Amphidromus*) *banksi* Butot, 1955

1955. Butot, p. 127, fig. 29 (*Amphidromus banksi*).
1986. Yamane & Tomiyama, p. 63.

This is the largest species to colonize the islands since the eruption. It has a large, brightly coloured and patterned shell (up to 50–60 mm in height) and is found on the leaves of a variety of trees in the monsoon forest of north and central Sertung. Several specimens were collected in fig trees, some at a considerable height above the ground. The species was originally described from Pulau Panaitan (Butot 1955), and was first recorded on Sertung in 1982 (Yamane & Tomiyama 1986) but has not been found on any other island of the group.

A. banksi is closely similar to a common Javanese species, *A. javanicus*, but differs from it in having a slightly open umbilicus, a thin, transparent pallial callus rather than a heavy one, and a relative lack of sculpture. Most specimens have a yellow to white shell colour in life, with spiral banding of brown. The yellow colour is largely lost in alcohol, most dead specimens having a white shell with spiral brown bands.

Amphidromus (*Syndromus*) *porcellanus* (Mousson, 1848)

1848. Mousson, p. 266.
1925. Benthem Jutting, p. 143.

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1948. Dammerman, p. 514.
1950. Benthem Jutting, p. 492, fig. 99.

This fairly small, slender, attractively patterned *Amphidromus* was one of the first land-snail species to be recorded from the islands after the eruption. Jacobson (1909) reported it as abundant in the ravines of Rakata up to an elevation of about 370 m in 1908. Dammerman (1948) found it to be less numerous in 1919 and 1922 and reported it to be rather scarce in 1933. Yamane & Tomiyama (1986) did not find the species in 1982 but it was found all over Rakata in 1984, from the coastal forest on both sides of the island to the summit, and in some areas, such as Zwarte Hoek, it was fairly common. It was not seen on any other island. The species is arboreal, being found on the leaves of a variety of trees and was seen high in the forest canopy. It occurs on Java and on Sebesi, but Sumatra records are doubted by Benthem Jutting (1959).

We exploited the large size and relative abundance of the species to obtain well relaxed and preserved specimens for anatomical study. The radula (figure 9, plate 2) consists of essentially similar, spade-shaped, bicuspid teeth with the smallest cusp being about a third of the tooth width and towards the centre of the radula. The rachidian is unicuspid and the radula formula is about 45–1–45.

The general form of the reproductive system is shown in figure 11 and agrees in general with the description given in Bishop (1977). The system is simple, the penis and vagina opening separately into the genital atrium. The spermathecal duct is as long as the spermoviduct,

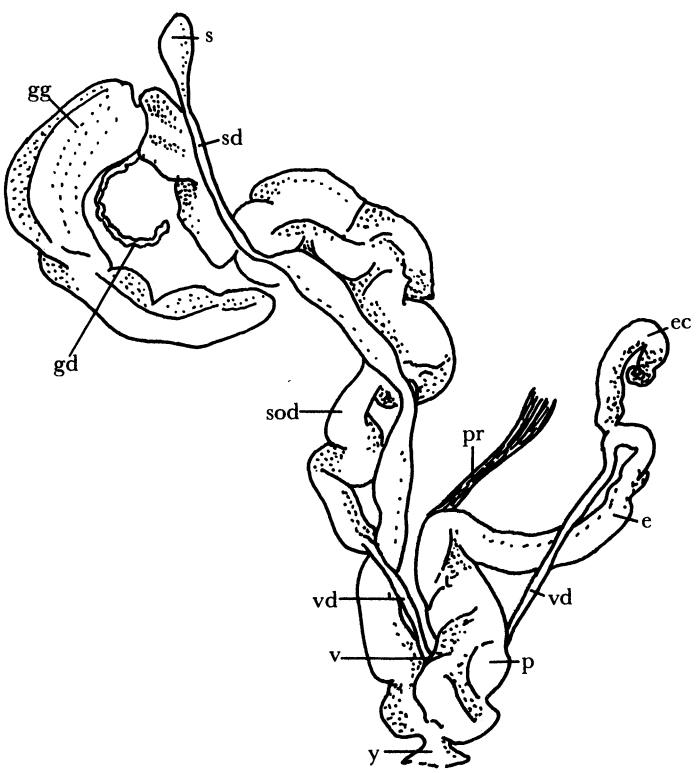

FIGURE 11. Drawing of the reproductive system of *Amphidromus* (*Syndromus*) *porcellanus* from Zwarte Hoek, Rakata. (e, epiphallus; ec, epiphallic caecum; gd, hermaphrodite duct; gg, albumen gland; p, penis; pr, penial retractor muscle; s, spermatheca; sd, spermathecal duct, sod, spermoviduct; v, vagina; vd, vas deferens; y, atrium.)

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opening from the top of the vagina at about the same point that the vas deferens leaves the spermoviduct. The vas deferens is a free tube leading to an epiphallus about equal in length to the penis. A short epiphallic caecum arises from the end of the epiphallus.

Chloritis helicinoides (Mousson, 1848)

1848. Mousson, p. 266 (*Helix helicinoides*).
1867. Martens, p. 270 (as *Helix helicinoides*).
1948. Dammerman, p. 515.
1950. Benthem Jutting, p. 475, fig. 90.

This is yet another large species that was recorded from Krakatau Island before the eruption (Martens 1867) and has not been reported from the islands since. It is very common on Pulau Panaitan (Butot 1955), and has been recorded from west Java (Benthem Jutting 1950) but does not appear to be known from Sumatra.

Landouria rotatoria (Von dem Busch, 1842)

1842. Von dem Busch, p. 2 (*Helix rotatoria*).
1950. Benthem Jutting, p. 461, fig. 79.

This is the first record of the species for the island group. The species is of moderate size (shell up to 20 mm diameter) and is fairly common on Rakata from Zwarte Hoek to the summit. It was found on no other island. The greyish-brown to reddish-brown shell is almost planispiral with a very low spire and peripheral keel. The periostracum bears short fine hairs which wear off in older specimens to leave a series of irregular scales. The umbilicus is wide and the aperture ovoid–lunate with a lateral angle.

Benthem Jutting (1950) refers to the species as ground dwelling, living in leaves and under rocks. Some specimens were found in this habitat on Rakata, but most were beaten from the lower branches of trees and shrubs in the monsoon forest. The species is widespread in Java and Sumatra and through most of the Indonesian islands and the Philippines.

The radula is shown in figure 10, plate 2. The rachidian has a wide spade-shaped central cusp and the merest suggestion of two lateral cusps. Progressing outwards from the rachidian, the central cusp becomes narrower and the outer lateral cusp becomes progressively larger and separates from it. About 11 teeth from the centre, the main cusp becomes notched, then bicuspid and then tricuspid. The lateral cusp also becomes bi- and multi-cuspid and the outer marginals are 5 or 6-cuspid and almost comb-like. The radula formula is 24–1–24.

Pseudopartula arborascens Butot, 1955

1955. Butot, p. 129, fig. 30.
1986. Yamane & Tomiyama, p. 63.

Originally described from Pulau Panaitan (Butot 1955), this species was known only from that locality until found on Sertung in 1982 (Yamane & Tomiyama 1986). It was taken from only one locality on the island and the record may be based on a single specimen. As the name suggests, the species is arboreal, living on the leaves of trees or shrubs. It is a fairly large snail, up to 14 mm in shell height. We did not find the species in 1984 or 1985 and the record is based on the single 1982 collection.

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5. Discussion

The most notable feature of the land mollusc fauna of the Krakatau islands is that, 102 years after the sterilizing eruption of islands about 44 km from the main land-masses of Java and Sumatra, 19 species of land mollusc have become established. There is no way of knowing how any one of these species dispersed to the islands, but informed guesses can be made of the most likely mode of dispersal, bearing in mind the life-style and habitat preferences of each species. Few modes of over-sea dispersal are possible for land molluscs: rafting on floating objects; wind-borne transportation, either by themselves or on leaves, etc.; being carried accidentally by other animals, the most likely being birds or man; or (the least likely) deliberate introduction by man. All these may have been involved in the recolonization of the Krakataus, rafting and wind-borne dispersal being the most likely.

The fauna of the islands can be divided into two groups with respect to habitat preference. One group of species is arboreal, living mainly on the leaves and trunks of the trees and shrubs. The other is almost exclusively litter dwelling, living under decaying leaves, logs and rocks on the forest floor. Table 3 lists the habitat preferences of the 19 species currently found on the islands, and the number of islands on which each of these species is found.

Table 3. Habitat preference of land mollusc species of the Krakatau Islands and number of islands on which each is found

(A, arboreal; L, litter-dweller.)

	habitat	number of islands
Ellobiidae		
Melampus flavus	L	1
Pythia chrysostoma	L	3
Pythia plicata	L	3
Veronicellidae		
Filicaulis bleekerii	L	1
Vertiginidae		
Gastrocopta pediculus ovatula	L	2
Succineidae		
Succinea minuta	L	2
Subulinidae		
Lamellaxis gracilis	L	3
Subulina octona	L	3
Valloniidae		
Pupisoma orcula	A	1
Achatinellidae		
Elasmias sundanum	A	2
Lamellidea (*Lamellidea*) *subcylindrica*	A	2
Helicarionidae		
Coneuplecta sitaliformis	A	1
Liardetia doliolum	L	4
Liardetia indifferens	L	3
Microcystina gratilla	L	2
Camaenidae		
Amphidromus (*A.*) *banksi*	A	1
Amphidromus (*S.*) *porcellanus*	A	1
Landouria rotatoria	A	1
Pseudopartula arborascens	A	1

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It can be seen that there is a marked correlation between habitat preference and multiple colonization success. Five of the seven arboreal species occur on only one island, whereas most of the litter-dwelling species are found on more than one island. Of the two litter-dwellers that are now found on but one island, *Melampus flavus* has been recorded from a second island since the eruption, and *Filicaulis bleekerii* may be a very recent introduction to the islands. Of the arboreal forms, only the two achatinellid species are so far known from more than one island. From these observations it may be postulated that species found on only one island have been established from a single successful colonizing event, and species found on more than one island owe their establishment either to more than one independent successful colonization from the mainland pool of species or to one such mainland colonization followed by one or more inter-island movements. It may also be postulated that the more likely mode of dispersal of arboreal species is wind-borne transport on leaves, whereas that for litter-dwellers is rafting on floating objects. Following on from these postulates it may be suggested that rafting on floating objects is a more common or more successful (or both) mode of dispersal for the colonization of islands by land molluscs than is wind-borne dispersal.

The composition and derivation of land-snail faunas of islands in the Indo-Pacific region has been described and discussed by several workers in recent years (Peake 1969, 1971, 1978; Solem 1973). These and others have shown that a relation exists between the number of species found on an island and the size of the island. Despite the fact that these findings were for established faunas in equilibrium with their environment, rather than a still-expanding fauna in the recolonization phase, such a relation can be demonstrated for the various islands of the Krakatau group.

TABLE 4. COMPARISON OF THE NUMBER OF SPECIES OF LAND MOLLUSCS ON EACH OF THE KRAKATAU ISLANDS WITH THE AREA OF EACH ISLAND

(These figures are contrasted with those of an adjacent island, Pulau Panaitan (Butot 1955).)

island	area/km^2	height/m	number of species
Rakata	11.52	777	16
Sertung	7.84	182	12
Panjang	2.72	142	7
Anak Krakatau	2.35	195	1
Pulau Panaitan	120.00	320	29

Table 4 shows the area, height and number of species found on each of the four islands. It is well to keep in mind that the maximum age of the fauna found on the three older islands is only 102 years. Anak Krakatau is a special case as only about one twentieth or less of the island carries any vegetation and the maximum age of the vegetation on the island is 20–30 years. The table contrasts these figures with data for Pulau Panaitan (Butot 1955), a large island at the southern end of the Sunda Strait which is 10 km from Java, 85 km from Sumatra and 60 km from the Krakatau group. The island was severely damaged by the 1883 eruption but not totally sterilized. Thus some part of the fauna may be derived from the pre-eruption populations of the island. Direct comparison between figures given in the present report and those given by Butot (1955) for Pulau Panaitan are also difficult as he does not include ellobiids in his species list of land molluscs for the island. This same problem arises when trying to

compare the present data with those for the various islands (including Krakatau) put forward by Peake (1969) as he does not give a species list on which he based his figures.

From the figures in table 4 it can be seen that the larger islands have a larger fauna than the smaller ones, with Rakata having perhaps a more diverse fauna, considering its size and distance from the main islands of Java and Sumatra, than even Pulau Panaitan. This may be because of Rakata's much greater height allowing more diversity of habitat.

Peake (1978) also considers size of the adult animal, mode of reproduction of the species and the known range of the species outside the area of immediate interest as being other significant factors in understanding the dispersal of land molluscs to a particular island group. These factors are listed for each species found on the Krakatau group in table 5.

The table shows that all the species are found in either Java or Sumatra or on the adjacent Indonesian islands. Almost one third of the species have a much wider distribution, being found over most of the tropical Indo-Pacific region. About half the species have an average adult size of 5 mm shell length or less, and about half the species have ovoviviparity rather than oviparity as their mode of reproduction. However, there appears to be no correlation between small

TABLE 5. DETAILS OF THE AVERAGE SIZE, METHOD OF REPRODUCTION AND WORLD DISTRIBUTION OF EACH SPECIES OF LAND MOLLUSC RECORDED FROM THE KRAKATAU ISLANDS

(Reproduction, O, oviparous; Ov, ovoviviparous. Species distribution: 1, Java; 2, Sumatra; 3, other Indonesian islands; 4, southeast Asia; 5, west Pacific; 6, Indo-Pacific; 7, circum-tropical.)

species	average size mm	reproduction	distribution
Ellobiidae			
Melampus flavus	10	O	123 5
Pythia chrysostoma	25	O	123456
Pythia plicata	20	O	12 4
Veronicellidae			
Filicaulis bleekerii	20	O	123
Vertiginidae			
Gastrocopta pediculus ovatula	2	Ov	123 5
Succineidae			
Succinea minuta	5	O	1 3
Subulinidae			
Lamellaxis gracilis	15	Ov	1234567
Subulina octona	20	Ov	1234567
Valloniidae			
Pupisoma orcula	3	Ov	1234567
Achatinellidae			
Elasmias sundanum	3	Ov	12
Lamellidea (*Lamellidea*) *subcylindrica*	1.5	Ov	3 5
Helicarionidae			
Coneuplecta sitaliformis	3.5	Ov	1 3
Liardetia doliolum	2.5	Ov	123456
Liardetia indifferens	3	Ov	123
Camaenidae			
Amphidromus (*A.*) *banksi*	60	O	1
Amphidromus (*S.*) *porcellanus*	35	O	1 3
Landouria rotatoria	20	O	123 5
Pseudopartula arborascens	14	O	1

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adult size and presence or absence of ovoviviparity with habitat preference or the number of islands on which a particular species is found. If dispersal by wind, either as free individuals or on leaves, is indicated by arboreal habit, then adult size should not matter as species can be distributed in this manner as small juveniles.

Ovoviviparity does not appear to confer any particular advantage to a species for successful dispersal to the Krakatau group. However, this cannot be properly inferred from these findings as the incidence of ovoviviparity in the entire potential source faunas of Java and Sumatra compared with its incidence on the Krakataus is not known. This is seen to be outside the scope of the present study but the basic data are presented here to assist future, more comprehensive studies.

As the flora of Anak Krakatau develops, more species of mollusc may be expected to become established. From the present observations it can be confidently predicted that the next few species to become established on Anak Krakatau will be from the litter community present on the other islands.

It is surprising that some of the long-established species, still only found on one island, have not made the comparatively short journey to the other islands. This is particularly so for *Amphidromus* (*Syndromus*) *porcellanus*, which has been widespread on Rakata since at least 1908, yet has never been recorded on the other islands. Perhaps equally surprising is the host of other species, common on the mainland areas of Java and Sumatra, that have not yet succeeded in colonizing the Krakataus. One species that we feared would occur, but does not, is the widespread pest *Achatina fulica*. There is a high probability that this species may invade the islands over the next few years as a direct result of the human activities.

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Thanks are due to all the members of the expeditions who collected land molluscs as an incidental to their primary tasks.

In particular, we thank Dr Helen Malcolm who assisted us in the field, and Mr Pat Vaughan who collected many of the smaller foliage-dwellers while beating for insects. Mr Vaughan also sorted and preserved the smaller specimens. Thanks are also due to Mr Phil Hollis, Department of Anatomy, University of Melbourne, Australia, for assistance with the scanning electron microscopy, and Mr Rodney Start, Museum of Victoria, for printing the photographs. We also thank Professor Thornton for comments on an early draft of this paper.

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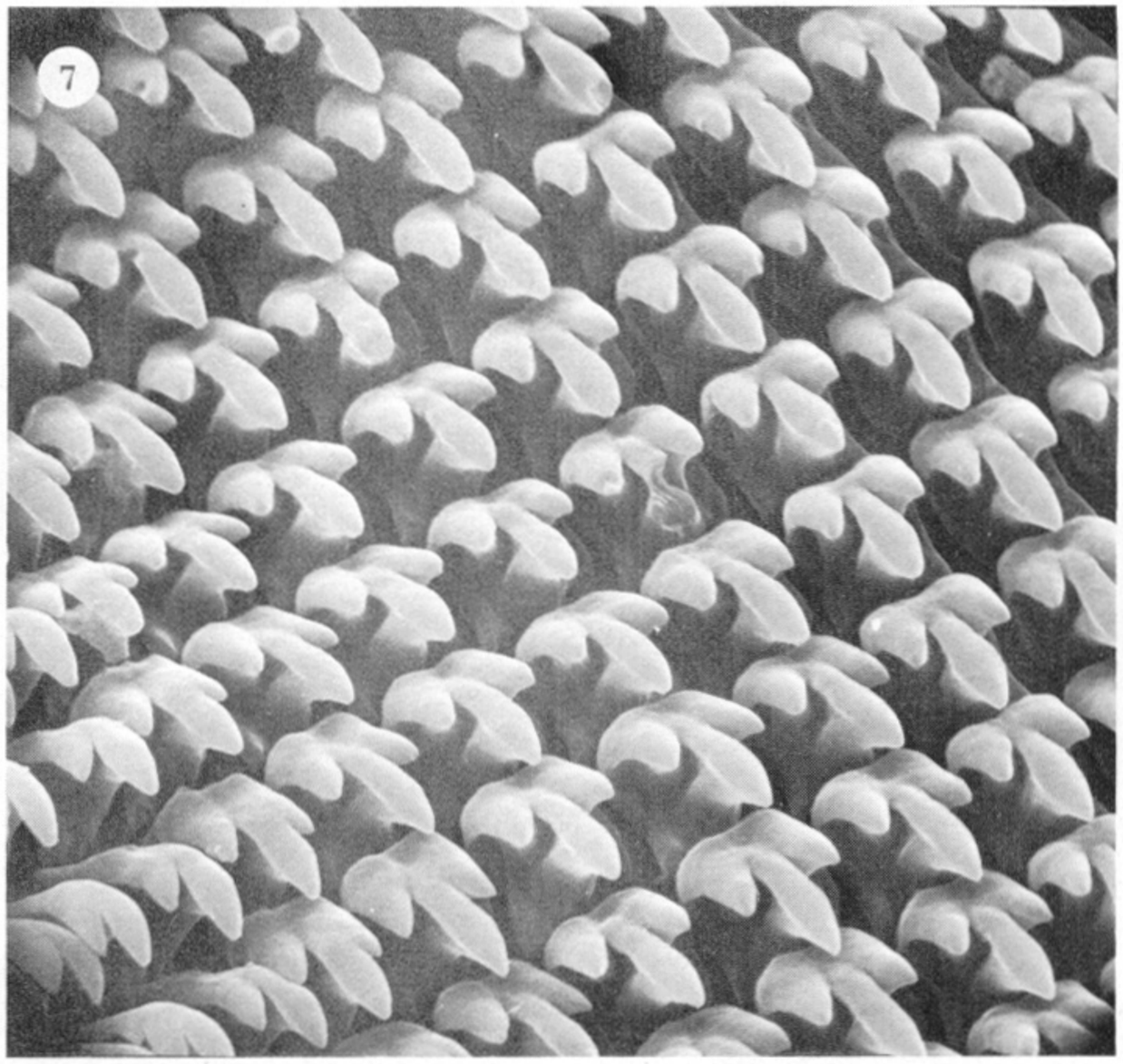
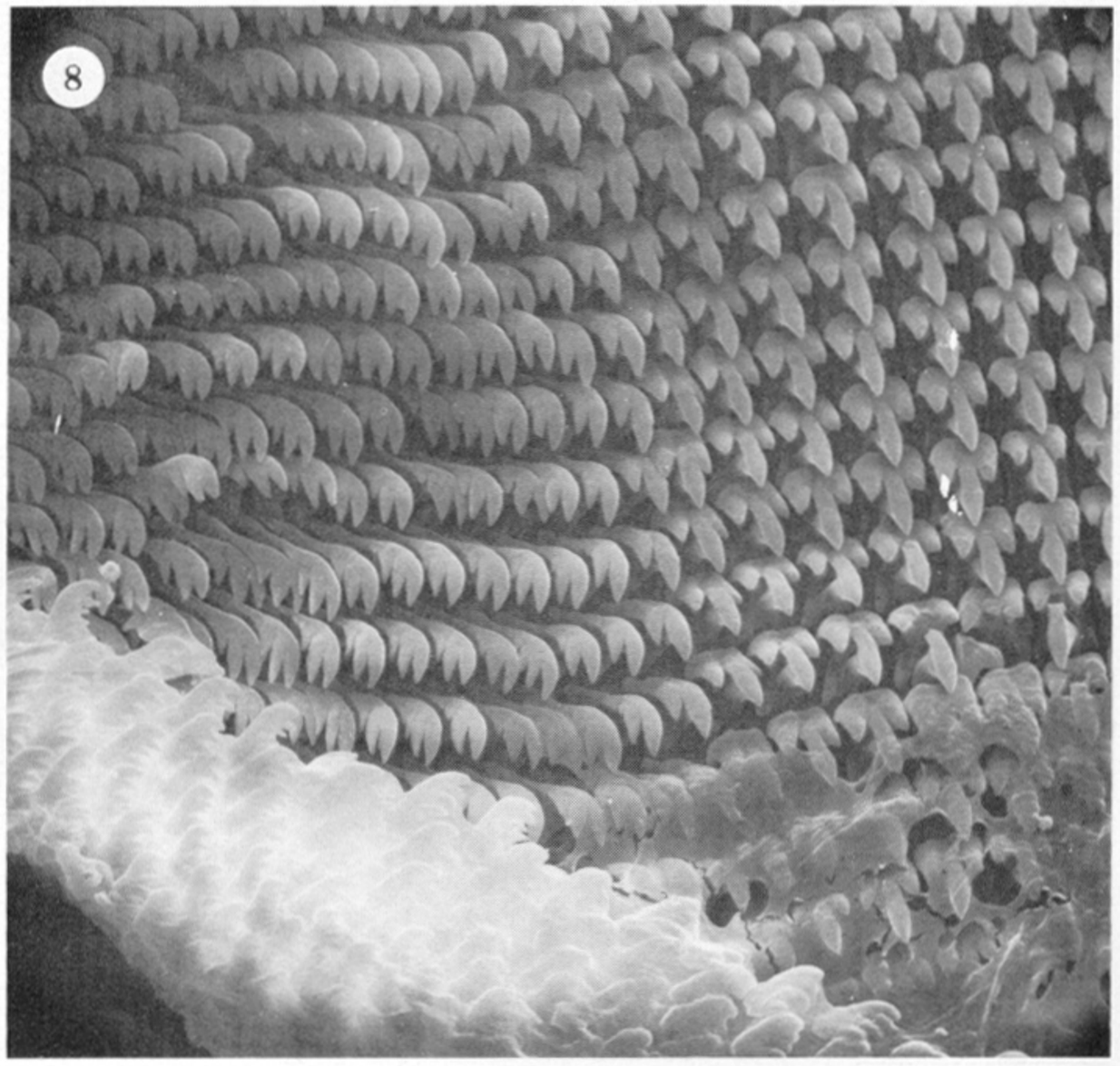
FIGURE 3. Radula of *Filicaulis bleekerii* from Sertung (magn. × 760).

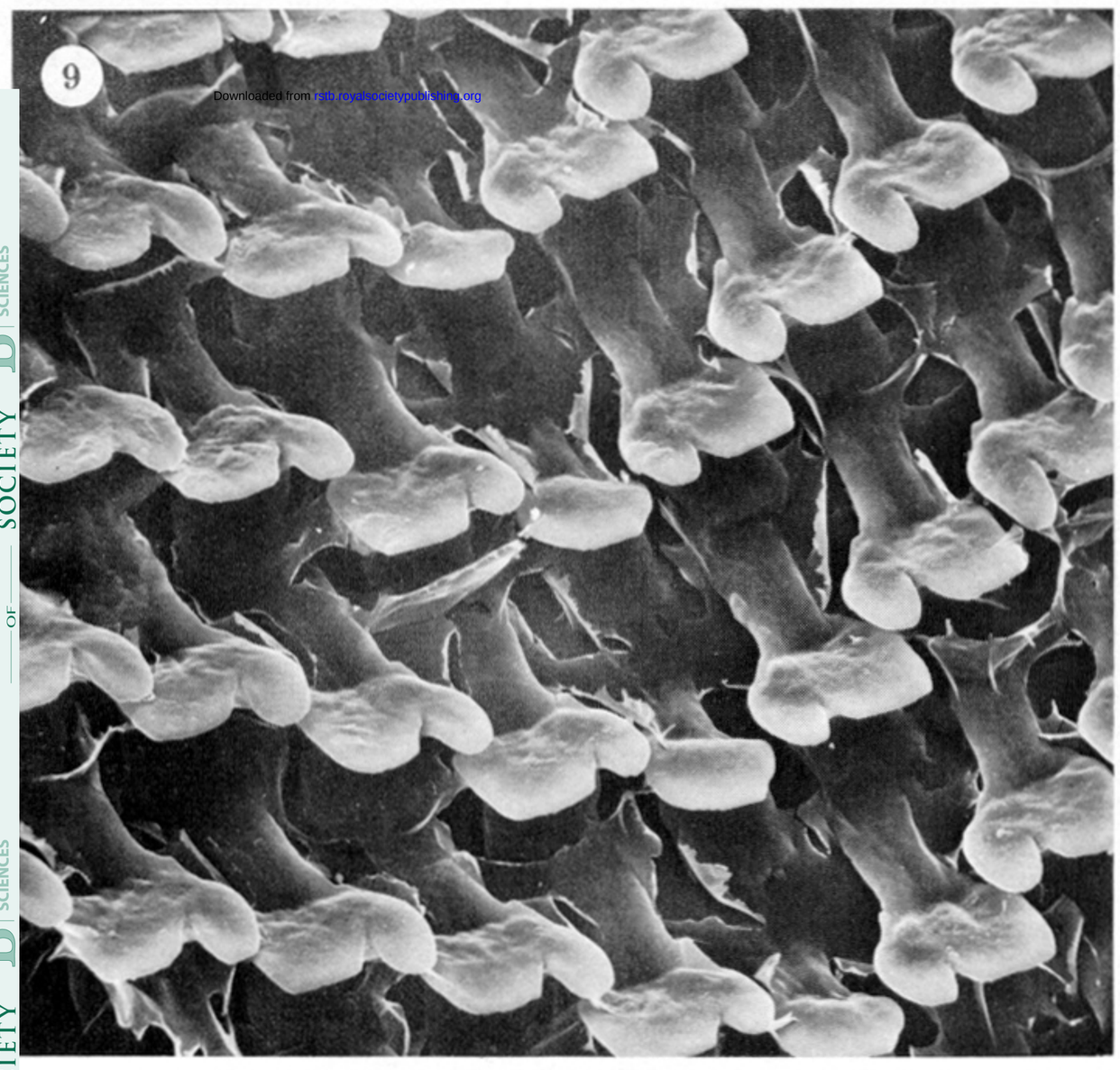
FIGURE 4. Radula of *Pupisoma orcula* from the summit of Rakata (magn. × 1700).

FIGURE 5. Radula of *Elasmias sundanum* from the summit of Rakata (magn. × 6000).

FIGURE 6. Radula of *Coneuplecta sitaliformis* from the summit of Rakata (magn. × 2100).







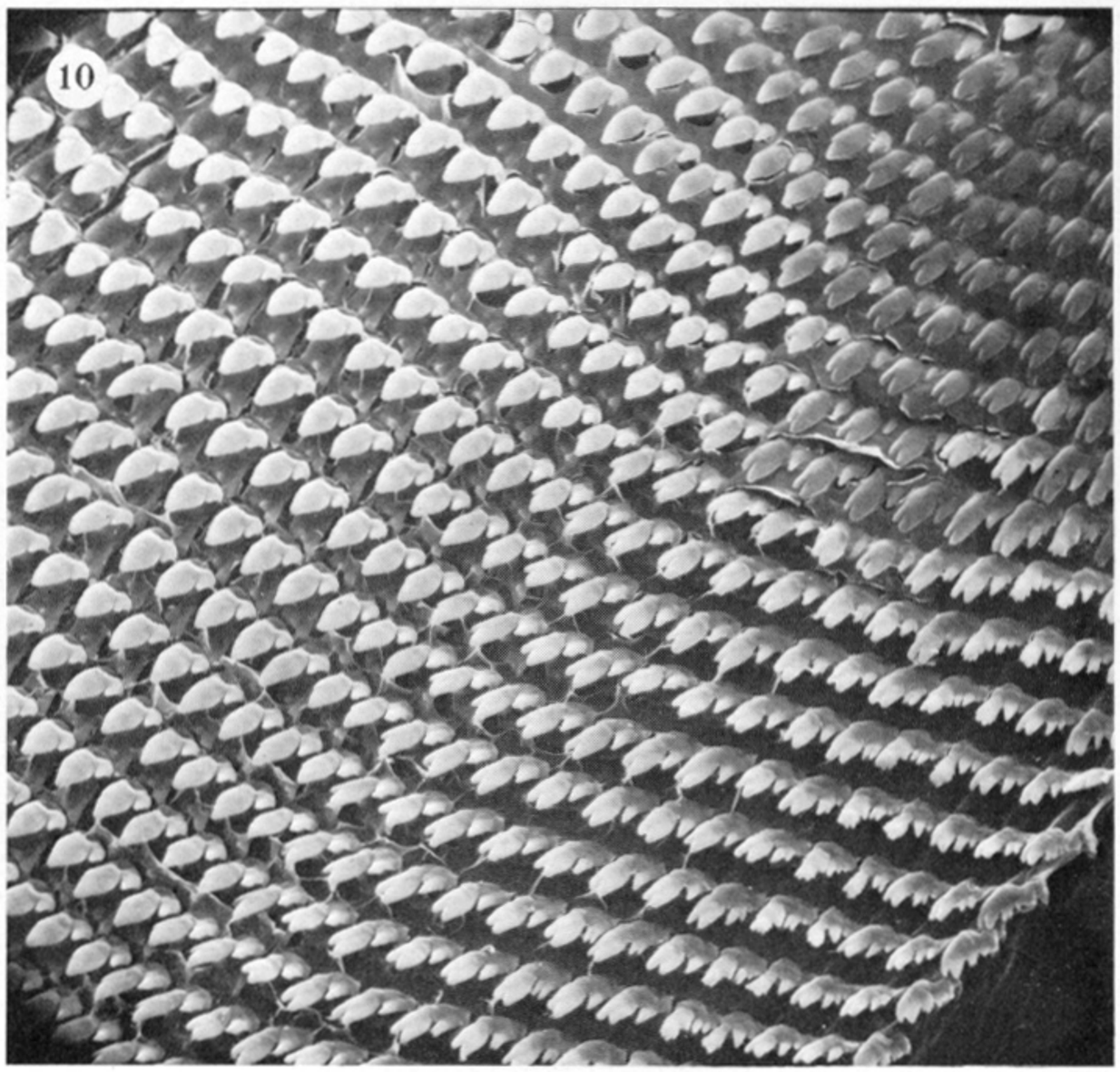


FIGURE 7. Radula of *Liardetia doliolum* from Sertung showing the central teeth (magn. × 1760).

FIGURE 8. Radula of *Liardetia doliolum* from Sertung showing the central and lateral teeth (magn. × 880).

FIGURE 9. Radula of *Amphidromus* (*Syndromus*) *porcellanus* from Zwarte Hoek, Rakata (magn. × 560).

FIGURE 10. Radula of *Landouria rotatoria* from Zwarte Hoek, Rakata (magn. × 300).