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The Recent Cypraeidae of Northern New Zealand from the Kermadec Islands to the Poor Knights Islands, Southwest Pacific Ocean (Mollusca: Gastropoda: Cypraeidae)

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ABSTRACT For researchers, isolated regions at the periphery of species' distributions hold a peculiar fascination. The causes of their remoteness vary based on: distance (*e.g.* the Tropical Eastern Pacific), distance and countervailing currents (*e.g.* the Marquesas), location in a present day gyre (*e.g.* the Pitcairn Group) or the absence of present day means of veliger transport (*e.g.* the Vema Seamount). (Daughenbaugh & Beals 2013; Daughenbaugh 2015a & b, 2017). The northern New Zealand Region from the Kermadec Islands (Kermadecs) to the coastal and shelf areas in the northernmost part of New Zealand's North Island (Northland), including the Poor Knights Islands (PKI), constitute the distributional boundaries for a number of Cypraeidae species. The boundaries are the result of the absence of coastal shelves along the east side of the Kermadec Ridge (Ridge) and precipitous drops to abyssal depths along Northland's east coast continental shelf. Tropical waters, with their potential to transport Cypraeidae larvae, flow eastward from southern Queensland, Australia, entrained in the Tasman Front which terminates when reaching North Cape, the northernmost tip of Northland. There, the North Cape Eddy captures most of this flow while the remainder, the East Auckland Current (EAUC), flows intermittently southward along the eastern coastal, shelf and offshore areas of Northland into waters incapable of supporting Cypraeidae populations.

KEY WORDS Bay of Islands, Bay of Plenty, Cavalli Islands, East Australian Current, East Auckland Current, East Cape Eddy, *Erosaria cernica cernica*, *Erosaria cernica kermadecensis*, *Erosaria cernica tomlini*, Kermadec Islands, New Zealand, Northland, Poor Knights Islands, Raoul Island, Tasman Front.

INTRODUCTION While Cypraeidae species have been reported from the Kermadecs, Northland and PKI, the numbers are small. As with other end of range regions, this raises questions of the origin, timing and means of invasions, endemism and, in this region, possible connectivity between the Kermadec populations and Northland/PKI populations. The validity of *Erosaria cernica kermadecensis* (Powell 1958), currently considered a synonym of the nominate species, *Erosaria cernica cernica* (Sowerby III 1870), is also assessed. While the isolation of the population and an examination of a limited number of specimens suggest the validity of the subspecies, an examination of additional specimens is needed to confirm their taxonomic features and their relationship to other populations.

Published and Other Reports of Northern New Zealand Cypraeidae Species

Published Kermadecs Reports

The largely uninhabited Kermadecs represent an imposing challenge to any prospective collector due to their distance from mainland New Zealand (NZ) as well as any other land mass, and the consequent lack of support facilities. In 1990, the NZ Government placed the Kermadecs within a marine reserve, extending 12 nautical miles out to the territorial limits, further restricting access.

Nevertheless, several major expeditions have resulted in the identification of 302 gastropod species in the coastal marine faunas, intertidal to < 50 m, at the Kermadecs. However, virtually all collecting activity has been restricted to the northern Kermadecs where there are a number of anchorages and onshore locations at or near Raoul Island (Raoul) available for extended expeditions. There are a limited number of easily accessed intertidal sites at Raoul as well as more gradually inclined rocky slopes and rock walls on large boulders to about 20-30 m at Raoul as well as Chanter and Meyer Islands, northeast of Raoul. The southern Kermadecs are not included in the reports. Their molluscan fauna has not been comprehensively studied and is, therefore, poorly known. (Brook 1998a).

The first reports of Cypraeidae species at the Kermadecs were published in 1915 by W. R. B. Oliver based on collections made in 1908-10, which included 261 gastropod taxa. Five Cypraeidae species were documented, all from the northernmost island, Raoul, with three of the five records coming from beach collected specimens. The two live taken species were collected intertidally among rocks. The species collected were:

1. *Erosaria cernica cernica* (Sowerby III 1870)
2. *Erosaria poraria* (Linnaeus 1758) – live collected
3. *Luria isabella isabella* (Linnaeus 1758)
4. *Lyncina vitellus* (Linnaeus 1758)
5. *Monetaria caputserpentis caputserpentis* (Linnaeus 1758) – live collected.

Iredale (1939) recorded an *E. c. cernica* specimen from the Kermadecs. Subsequently, based on a specimen dredged off Raoul in March, 1952 between 58-85 m by the Danish Research Vessel, *Galathea*, Powell described *Ravitrona tomlini kermadecensis* (1958), subsequently referred to as *E. c. kermadecensis* (Powell 1958). This will be discussed further below.

These and subsequent reports were confirmed and summarized by Brook (1998a). The number of reported gastropod species was raised to 302, many of which are undescribed. Three additional Cypraeidae species were included, all dead collected, bringing the total number of reported species there to eight. The species collected were:

1. *Monetaria moneta* (Linnaeus 1758) – intertidally
2. *Talparia talpa* (Linnaeus 1758) – 10-30 meters
3. *Talostolida teres teres* (Gmelin 1791) – 20-30 meters.

In addition, fossil *E .c. cernica* were collected at Napier and Dayrell Islands, northeast and east northeast of Raoul respectively, from uplifted Early Pleistocene deposits from inferred mid-shelf depths. (Brook 1998a & b).

There have been no further published reports of additional Cypraeidae species at the Kermadecs. (Duffy & Ahyong 2015).

NOTE: The validity of the genus *Erosaria* is unclear at present. Meyer (2004) reclassified *Naria irrorata* (Gray 1828) as *E. irrorata*, although it formed a poorly supported sister clade to a strongly supported clade that included *E. albuginosa* and *E. poraria*. Some authors

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have treated *Erosaria* as a synonym of *Naria* as the latter was introduced 26 years prior to *Erosaria*. As the generic status remains to be resolved, in the interest of continuity of the literature, *Erosaria* is here retained for all species presently classified in that genus. This is in accordance with the World Register of Marine Species (WoRMS) (Moretzsohn 2013).

Other Kermadec Reports

Over a number of decades, Allen Howell, a retired New Zealand crayfish fisherman, has undertaken annual months-long voyages around the Southwest Pacific. Sailing and diving from his yacht, he would stop at a number of islands and island chains, including Raoul. He probably has more experience observing Raoul marine fauna than any other person. He considers *E. c. cernica* to be moderately common there.

In total, about 200 specimens have been collected off Raoul by scientists and recreational divers, most in 15-35 m of water, on or at the base of rock walls covered with sponges, bryozoans, algae and sparse corals. (K. Walton, pers. comm. 2017).

Caledonian Shells dealer, Vincent Crayssac, was able to obtain a number of *E. c. cernica* from the Kermadecs, some of which were subsequently sold to collectors worldwide. A 26.4 mm specimen was acquired from Crayssac and resides in the author's collection. An additional two specimens were made available to the author for this study.

Published Northland Coastal/PKI Reports

While the number of reported Cypraeidae species from the Kermadecs is few, even fewer are known from Northland Coastal Areas (CA)/PKI. In addition, PKI, from which most mainland records originated, was declared a marine reserve in 1981, making collecting off limits to recreational divers. Both *E. cernica* and *L. vitellus*, the only species reliably known from Northland CA, are still reported from PKI every few years by divers, although few active shell collectors dive there regularly or in other northern regions. (K. Walton, pers. comm. 2017).

Several *M. c. caputserpentis* and *E. e. erosa* were found in Northland CA waters in association with a floating oil rig, built in Singapore and towed to Whangarei Heads (Powell 1976), just to the southwest of PKI. These were never established as naturalized components of the fauna.

Powell (1967) reported the presence of *L. vitellus* at Shag Bay, west coast of Tawhiti Rahi Island, PKI. A live specimen was taken at 90 feet, which he illustrated, and dead specimens were taken in the same area at 100 feet. Cernohorsky (1971) reported only that "several specimens have been taken by divers at a depth of 60-100 feet (20-33 m)" at PKI. Elaborating on Powell's report, Grange (1973) reported that "subsequent dives around the same depth produced three well-preserved specimens, the largest being 59.0 mm long". In addition, he reported that two very fresh dead specimens were found elsewhere on Northland's east coast in 15 feet of water. The first was found at Goat Island, Leigh, to the southwest of PKI. Goat Island became a marine reserve in 1977. The second was found near Tutukaka outside an octopus lair. Tutukaka, considered the gateway to PKI, is just west of those islands.

Powell (1958), in describing *E. c. kermadecensis*, did not mention the presence of *E. c. cernica* in Northland CA/PKI waters. Eagle (1993) reports that the first two *E. c. cernica* recorded from New Zealand were collected in 1964 by Bill Palmer, at 30 m at PKI.

Cernohorsky (1971) reports a single, small and slender specimen found in beach debris at Cape Maria van Dieman (CMVD), at the northwestern most point of Northland. He also reports records of specimens from PKI collected at 60-120 feet (20-30 m), ranging in length from 27-31 mm. Elaborating, Powell (1976) reported that the Cape Maria specimen was very well worn and collected in 1933. (Note: The author is not aware of any earlier reports of *E. c. cernica* from mainland NZ waters.) Powell also records a specimen from 23-25 fathoms (42-46 m) off Deep Water Cove, Maunganui Bay, on the east side of Northland's Bay of Islands. Lastly, Powell reports that "more than twenty living examples are known to have been found by skin divers at Poor Knights Islands".

Eagle (1993) reported and illustrated a live collected specimen of *Cribrarula cribraria cribraria* (Linnaeus 1758). The specimen was reportedly collected in December, 1993 by an itinerant diver and fishermen and given to Eagle on a nearby beach when he expressed interest. The "small *Cypraea*" was reported to have been collected "at dusk by scuba, in a situation where there is active, well aerated water" at Motutara Island at the entrance to Whangaruru Harbor. The island lies approximately 5 km north and 35 km west of PKI. However, this record is at best considered spurious and it is unlikely that *C. c. cribraria* has ever lived in Northland CA/PKI waters. (K. Walton, pers. comm. 2017).

Fossil records are sparse. "Cypraeids have a sporadic record from earliest Eocene … to Recent in New Zealand. Their general rarity and low diversity suggest that New Zealand was never fully tropical." Beu & Raine (2009). Aside from *Paleocypraea eripnides* (Darragh 2002), *Bernaya chatamensis* (Cernohorsky 1971) and two other unnamed species from the Paleocene, only two *Notocypraea* species from the Miocene have been described based on fossil specimens. They are *Notadusta clifdenensis* (Cernohorsky 1971) and *Notadusta trelissickensis* (Suter 1917). These became extinct due to the terminal Miocene impoverishment. (Beu & Raine 2009). There are also a number of unnamed fossil species dating to the Miocene or earlier. The author was unable to locate any record of fossil *L. vitellus, E. c. cernica* or any other extant Cypraeidae species from mainland New Zealand.

Other Northland/PKI Reports

A 64.5 mm specimen of *L. vitellus* collected by a diver at 20-30 m in 1986 off Opua, Bay of Islands on the east coast of Northland, resides in the author's collection. Opua is northwest of PKI. The Andrew Spurgeon collection includes a 31 mm specimen collected by Bill Palmer at 90 feet (27 m) on a rock face at PKI.

Two *E.* c. *cernica* specimens from mainland New Zealand reside in the author's collection. The first is a small, slender 22.7 mm specimen, trawled in 120 m in 1984 off the Cavalli Islands, approximately 30 km north of Kerikeri. The second is a fresh dead 27.1 mm specimen, collected by a diver at 25 m in 1975 at PKI ex. Peter Poortman collection. In addition, Andrew Spurgeon's collection contains a 33 mm fresh dead, crabbed specimen collected at 80-100 feet (24-33 m) at the edge of the sand off the northeast point of Aorangi Island, PKI in 1978.

The Museum of New Zealand Te Papa Tongarewa (Wellington) has nine specimens of *E. cernica* from the Poor Knights Islands in six lots (46 m, 1, M.119890; 24 m, 1, M.145008; 37 m, 1, M.018475; 24-77 m, 3, M.020262; 1, M.118110; 2, M.277040). In addition, there are at least four additional PKI, one Cavalli Island and one CMVD specimens in private collections in New Zealand. (K. Walton, pers. comm. 2017).

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Geography

Zealandia

Historically, the offshore ridges and plateaus to the north northwest of New Zealand's North Island have been considered an amalgam of continental islands, fragments and slivers rather than a true continent (*see* Figure 1). However, that view has been evolving over recent decades as more and better mapping of the sea floor has provided an alternative view. The latter posits the continent of Zealandia which covers 4.9M km² and is 94% submerged. Its northwest corner is separated by a mere 25 km from Australia's Queensland coast by the 3,600 m deep Cato Trough. Encompassing the Lord Howe and Norfolk Ridges to the east, with the latter including both New Caledonia and Norfolk Island, Zealandia encompasses both the North and South Islands of New Zealand as well as large areas to the south and east of the South Island. Comprised of very thin, stretched continental crust, the region evidences related elevated bathymetry, diverse and silica rich rocks and a low velocity crustal structure. (Mortimer *et al.* 2017).

Figure 1. Northland Map.

However, the Kermadecs fall outside Zealandia as the southwest trending crust of the latter turns southward into the northeast coast of Northland, rather than northward to encompass the Kermadecs.

Kermadecs

The Kermadecs are a relatively short chain (215 km) of volcanic islands and rocks (*see* Figure 2). They lie in the middle of a long, near linear oceanic ridge, forming a frontal island arc stretching approximately 1,815 km from the southern Tonga Group (Ata Island), south southwest approximately 800 km to the Kermadecs' Raoul Island, continuing south southwest and terminating approximately 640 km north northeast of New Zealand's North Island. The ridge, beginning as the Tonga Ridge and continuing as the Kermadec Ridge, evolved as the result of the subduction of the Pacific Plate in the east beneath the Australian Plate in the west. Beginning in the Eocene (56-33.9 mya), the subduction also produced the Kermadec Trench. The latter trench lies in the center, between the Tonga Trench to the north and the Hikurangi Trench off the northeast coast of New Zealand's North Island. Lying to the east of the Kermadecs, it is one of the deepest oceanic trenches with a maximum depth of approximately 10,000 m. Just to the west of the Kermadecs lies the 2,500-3,000 m deep Havre Trough which is bounded by the Kermadec Ridge on the east and the parallel Colville Ridge, 175-200 km to the west. The latter ridge is considered to have separated from the former, beginning in the Pliocene, as a backarc ridge and forms the eastern boundary of the South Fiji Basin. The basin, with depths ranging from approximately 2,700 to 7,000 m, combined with the Colville Ridge and Havre Trough, acts as a boundary between the Kermadecs and other South Pacific Islands to the west.

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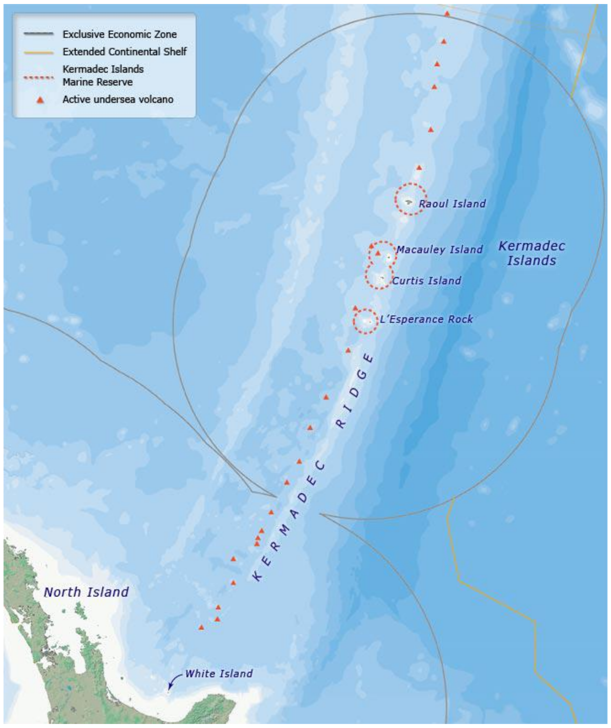

Figure 2. Kermadec Islands and Ridge Map (NIWA: National Institute of Water and Atmospheric Research).

The Kermadecs first appeared as the emergent tops of a chain of largely submarine volcanic mountains from 1,000+ m depths along the crest of the Kermadec Ridge in the Pleistocene and have continued their emergence through to the Holocene (present day). (Brook 1998a & b). They lie in a south southwest trending line from 29.2° S 177.8° W to 31.3° S 178.8° W in three groups separated from each other along the top of the ridge crest. The Northern Group consists of Raoul and a number of small islands and rocks. The Central Group, 100 km south southwest of Raoul, consists of the northern Macauley Island and the adjacent Haszard Islet with Curtis and Cheeseman Islands 35 km to the south southwest, but still within the Central Group. A further 80 km to the south southwest lies the Southern Group consisting of L'Esperance Rock, a tiny rock pinnacle, and the submerged Havre Rock, representing the end of the Kermadecs' chain. The Central and Southern Group islands have very limited, if any, shallow water (< 50 m depth) marine habitats due to the very small size of all but Macauley Island and inshore steeply inclined slopes along most of the coastlines. Further, the absence of suitable anchorage, except for large research vessels, at these islands has meant that almost all scientific expeditions have been conducted near Raoul.

The Northern Group, anchored by Raoul, is the largest and oldest group in the Kermadecs. Raoul represents the summit of a large submerged mountain mass approximately 35 km by 20 km aligned to the southwest, slightly inclined to the south southwest alignment of the Kermadec Ridge (*see* Figure 3). It is flanked off its northeast coast by a compact scattering of seven named islands, plus additional islets and rocks. The islands are Meyer, Napier, Nugent, Dayrell and the three Chanter islands. The seven islands in total cover a land area of approximately 0.51 km². Raoul itself is anvil shaped, with a huge caldera in the center which supports three lakes. Its six km north-south length and 10 km east-west length covers approximately 29.4 km². The island is still active volcanically with the most recent eruption having occurred in 2006.

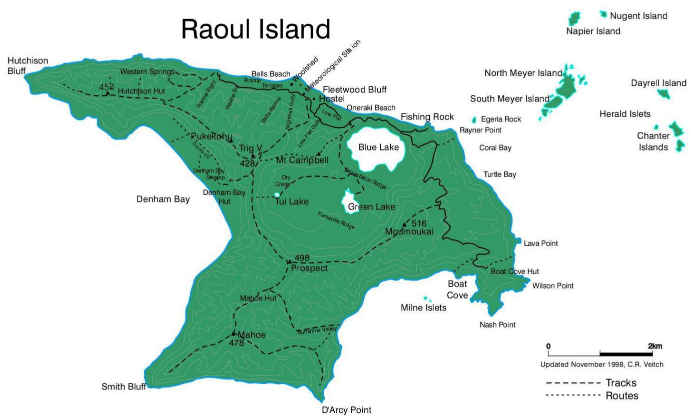

Figure 3. Map of Raoul Island, *in* Kermadec Marine Reserve Map (Department of Conservation, *Te Papa Atawhai*, New Zealand Government).

Stratigraphic studies have centered on the southeast and east coast of Raoul as well as the seven flanking islands. Together they have been designated the Herald Group. The study of early volcanic and sedimentary sequences revealed poorly constrained (uncertain) age estimates within the group. However, the studies have posited a 1.4± 0.8 mya age for the oldest of the three formations studied. The second oldest was posited at 1.1± 0.1 mya age. This places the age of the group in the Early Pleistocene. Subsequently, the group has been subject to further eruptions, uplifting and subsidence and the accumulation of sedimentary surface substances. The study material consisted of submarine lava flows, coral patch reefs, algal limestone and molluscan fossils. These were posited to have accumulated at intertidal to mid shelf depths on the sides of volcanic islands which were subject to subsequent erosion. (Brook 1998a & b). An earlier study indicated that the Northern Group has existed continuously since at least the middle to late Pleistocene. (Lloyd & Nathan 1981).

Brook 1998a wrote:

> *"...there is a limited range of physical habitat types at intertidal and shallow subtidal depths around the northern Kermadec Islands, and all but a very few sites ... are exposed to unrefracted oceanic swell and storm waves. The smaller islands are encircled by rocky reefs, whereas boulder coasts and gravelly sand beaches predominate around Raoul Island. Steeply sloping rocky reefs, commonly with crevices, caves and overhangs, occur to between 10 m and 70 m depth around the smaller islands and rocks, and on parts of the southern and southeastern coasts of Raoul Island. More gently sloping substrata of in situ rock or large boulders are present locally around Meyer, Chanter and Raoul islands to depths of approximately 20-30 m. Volcaniclastic gravel and sand substrata extend offshore from sandy and boulder coasts around Raoul Island, and fringing aprons of mixed ... gravelly and sandy sediments are present below approximately 10-20 m depth to seawards of rocky reefs around Raoul and the smaller islands.... Hermatypic scleractinian [Hard] corals are present at the Kermadec Islands, but there are no coral reefs or Bioherms. Hermatypic coral cover on rocky reefs around the northern Kermadec Islands is typically greatest at 1-6 m depth, constituting up to 40%. Below that, corals generally contribute less than 10% of benthic cover on reefs, but increase in abundance to approximately 15-25% cover between depths of 18 m and 25 m in some areas. Coral cover decreases to less than 1% below 25-30 m depth."*

The Gap

The southern most of the Kermadecs Islands is L'Esperance Rock, while the undersea Ridge continues its south southwest trajectory approximately 200 km further as far as the Bay of Plenty on the east coast of Northland. Numerous submarine volcanoes line the Ridge throughout its entire length.

Northland/PKI

Northland lies over 100 km to the northwest of the Bay of Plenty where remnants of the Kermadec Ridge terminate (*see* Figure 1). The region is a narrow peninsula in the northernmost part of New Zealand's North Island. It stretches approximately 330 km northwest, 85 km at its widest and 7.5 km at its narrowest, from approximately 80 km north of Auckland to North Cape at the northern most tip of Northland. Underlain mostly by hard compressed sandstone (greywacke) formed on the seabed between 280 and 135 mya, the

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region was shaped by uplifting greywacke and volcanic rock. Ancient volcanoes have formed many of the region's mountain ranges while more recent volcanic activity and erosion helped shape the coast and its near shore islands.

The Northland's 1,700 km coastline encompasses the west, north and east coasts. The relatively straight west coast is indented with several broad, shallow bays. The far north coast features three prominent capes and many smaller capes along a very short coastline, from west to east: Cape Maria van Dieman, Cape Reinga and North Cape. The more irregular east coast features rocky headlands, deep water harbors and sandy bays. One of the largest of these sandy bays, the Bay of Islands, is a drowned river valley with numerous tributaries, with resultant estuaries, small embayments and a sprinkling of 150 islands. The bay is at its deepest at its exposed entrance where depths range from 50-60 m. Prominent offshore island groups include the Cavalli Islands (eroded mainland remnants), the Hen and Chicken Islands and PKI. The latter two are volcanic remnants.

The Poor Knights Islands, lie 24 km off Northland's east coast and 50 km northeast of Whangarei at 35.28° S 174.44° E. PKI consist of two large islands and numerous small islets and stacks between and adjacent to the two islands (*see* Figure 4). Tawhiti Rahi, at 1.51^2 km, is the larger of the two while Aorangi, at 1.0^2 km, lies immediately to the south of the former. Located in the open ocean, PKI experience very strong wave attacks from all directions, but primarily from the north and northeast. These have resulted in high cliffs, continuing below the surface of the ocean, around the north end of Tawhiti Rahi and along the east coasts of both islands. Erosion caused by wave action along perimeter fractures has resulted in cuts, caves, arches and land slides with the base levels of the majority of coastal and subsurface caves and arches carved out during the second to last glacial period. (Hayward 1991).

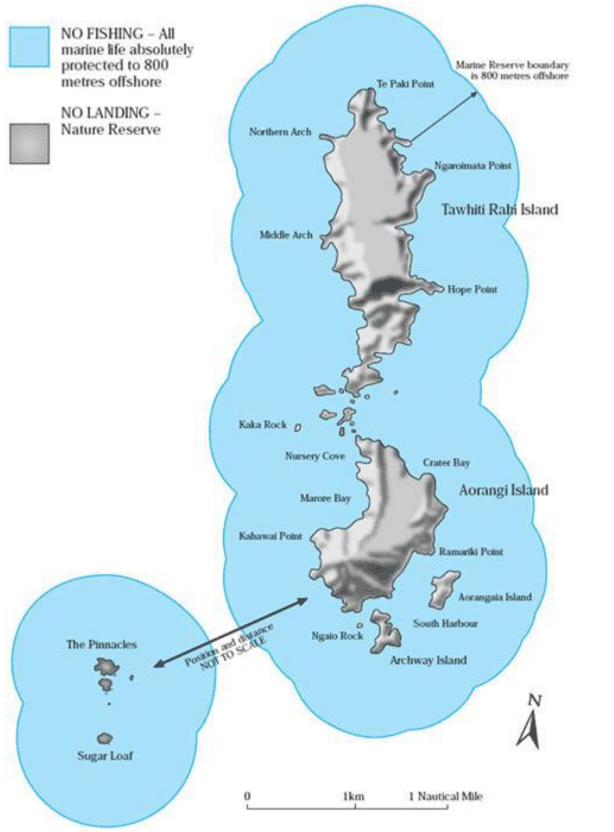

Figure 4. Poor Knights Islands Marine Reserve Map (Department of Conservation, *Te Papa Atawhai*, New Zealand Government).

Over a basement of greywacke, the PKI are composed of volcanic debris, probably on the western slopes of an active volcano. In the late Miocene, the present PKI were buried under about 500 m of this debris. Volcanic activity ceased approximately nine mya. Since then, extensive erosion, primarily during the last million years of the Pleistocene, has led to the present size and configuration of the islands. The PKI have probably not have had any connection to the mainland since approximately two mya. At present, the islands rise rapidly from 100-125 m from the floor of the outer continental shelf. (Hayward 1991).

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"At the peak of the last glacial period about 23,000 years ago, the oceans were a different place. Sea level fell by about 120 m as water was retained within expanding polar ice caps. Most of the continental shelf – the submarine plain surrounding New Zealand – was exposed.… The entire coastal current system was forced 20-200 km offshore by the exposed shelf." (Carter 2001). Cooler water temperatures and greatly reduced viable habitats makes it is doubtful that any Cypraeidae species were present in mainland NZ waters during the Otiran glacial cycle, 23-12 mya. While most present day local temperate species survived the transition, it is unlikely that any subtropical Cypraeidae species would have survived through the glacial period.

Subsequent to the peak of the last glacial period approximately 23 mya, sea levels began to rise as the planet gradually warmed. Northland's continental shelf and offshore islands were once again submerged with ocean levels rising to their current level approximately 12 thousand years ago ("kya'). The Tasman Front gradually shifted south to its present day position approximately 10 kya. Winds were reduced, seas became less turbulent and currents slowed. (Carter 2001). In time, this produced the conditions which would result in subtropical waters being transported to the temperate waters of Northland's east coastal areas and offshore islands, including PKI, via the Tasman Front and the EAUC.

Oceanic Currents

Northland CA/PKI

An understanding of the oceanic currents and conditions which impact Northland CA/PKI begins with an understanding of the East Australian Current (EAC), the tributary Tasman Front and the off shooting East Auckland Current (EAUC). The EAC represents the western boundary current of the South Pacific Subtropical Gyre. It flows from the Coral Sea southward along the Queensland coast and onward to Sugarloaf Point (32.5° S), New South Wales, 275 km north northeast of Sydney. From there, part of the current separates from the coast and begins a north-south undulating flow eastward as the Tasman Front. (Tilburg *et al.* 2001).

The Tasman Front is the connection between the subtropical EAC western boundary current and the EAUC eastern boundary current off Northland's eastern coast. The EAC, acting as a zonal jet across the Tasman Sea, captures subtropical water from the southern flowing waters of the Tasman Sea. It then flows eastward to Northland's North Cape, undulating generally north and south in response to the ridges and troughs in its paths with anticyclonic eddies and meanders as an integral part of the front. The meanders are influenced by several subsurface ridge systems, *i.e.* the Dampier Ridge, Lord Howe Rise and Norfolk Ridge. Measurements have shown that the waters of the Tasman Front are shallower than those of the EAC which extends below 2,000 m. Rather, Tasman Front flows encompass the upper 800 m. In addition, Tasman Front flows are narrower than those of the EAC, coupled with the meanders and instances of anticyclonic flow reversal, constitutes a weaker connection between the EAC and the EAUC than that of a contiguous western boundary system. (Sutton & Bowen 2014).

The EAC/Tasman Front flows present the potential for the transport of Cypraeidae larvae from several locations from the west to the east coast of Northland CA/PKI. The closest potential sources are Lord Howe Island and New Caledonia/Norfolk Island. The former is just north of the Tasman Front which is fed from currents from the north, making the transport of larvae into the front almost certain. The distance from Lord Howe to NZ's North Cape is approximately 1,340 km.

Owing to the complicated nature of the Tasman Front, it is not possible to calculate a reliable distance or transit time for larvae originating from Lord Howe Island. However, tracking of transit times for rock lobster larvae (*Sagmariasus verreauxi* H. Milne Edwards 1851), released from the east Australia coast just to the west of Lord Howe, resulted in a median transit time of 838 days. However, 3% of the drifters took less than a year (one larval life time) to cross to New Zealand. These larvae were entrained in the Tasman Front. (Chiswell 2014).

While that timeframe may work for long lived rock lobster larvae, it is unlikely to work for lesser numbers of Cypraeidae larvae originating from Lord Howe. While precise larvae life spans for *L. vitellus* and *E. c. cernica*, as well as other Cypraeidae species, are not known due to a variety of complicating factors, they are estimated to have only moderate life spans (Paulay & Meyer 2006). As a result, Lord Howe is an unlikely source of larvae.

NOTE: During times of La Niña, the EAC flows along the east coast of Australia extend farther south, allowing tropical species from Queensland to migrate into areas they are not normally found, *i.e.* New South Wales and eastern Victoria. Likewise, the Tasman Front extends further south. These extensions are reversed with the return of El Niño. The west to east flow rates of the EAC do not appear to be significantly impacted by either.

New Caledonia and Norfolk Island, which lies south of the former, lie approximately 1,270 km and 370 km north of the Tasman Front respectively. The coastline at Norfolk is characterized by cliff faces, similar to Raoul and PKI, and is unlikely to host significant Cypraeidae populations. However, it does hold the potential to act as a source of migrants from local Cypraeidae populations or as a stepping stone for migrants from New Caledonia. Currents flow to the south into the Tasman Front from these islands, leaving approximately 550 km to reach the North Cape.

The author is not aware of any studies on currents flowing from New Caledonia/Norfolk Island to the Tasman Front. However, the route south does not possess the geological obstacles existing along the front to the west. South of the Norfolk Ridge, the front does begin a more direct flow toward the North Cape. For larvae reaching the front, the remaining 550 km would not likely pose a significant obstacle. As a result, the trajectory from New Caledonia/Norfolk Island is a more likely potential source of any immigrant veligers.

However, as the eastward subtropical flow of the Tasman Front approaches Northland's North Cape the majority of the flow enters the North Cape Eddy. The latter is a topographically constrained, anticyclonic eddy whose center lies approximately 150 km northeast of North Cape. As the eddy contracts, southernmost Tasman Front waters not captured in the eddy as well as water from the edge of the eddy form the intermittent EAUC. By its nature, the eddy prevents the formation of a continuous EAUC. The EAUC flows closest to the shore from the North Cape to 35°S, around the Bay of Plenty, where it begins to move over the shelf and father offshore to the Bay of Plenty where its flows either joint the East Cape Eddy or the East Cape Current. The EAUC is normally stronger in the spring and summer (*see* Figure 5). (Stanton *et al.* 1997).

As noted, the nature of the North Cape Eddy precludes a continuous EAUC and can act as a limit or an obstacle to the transport of larvae to Northland CA and its offshore islands.

Northland CA/PKI Cypraeidae Origins

Two hypotheses which could account for the two Cypraeidae species extant in Northland/PKI waters are examined below. Neither has sufficient evidence to support a definitive conclusion. Genetic analysis, when it becomes available, would likely provide support for one of the two hypotheses.

Present Day Migration

Powell (1976) first hypothesized "Natural causes contributing to greatly increased influx of warm water molluscs and other invertebrates to our shores could be accounted for by a small increase in water temperature coupled with possible fluctuations in surface water currents, which would enable an increasing number of warm water species to colonize Northland waters. … It would appear that some molluscs arriving here in their larval stage in massive strength manage to grow to adults but are unable to reproduce because of lower temperatures than their normal requirement". Morley and Hayward (1999) echoed Powell's comments, but added "three such [warm water] species that have been introduced to the Bay of Islands by warm currents, and that have bred for a season or two and established small populations, now appear to have died out". The three species are *Perirhoe circumcincta* (Deshayes 1857), *Phenacovolva wakayamaensis* (Cate & Azuma 1973) and *Natica lemniscata* (Philippi 1852). However, two of those three species have been collected alive this year (2017) and the third, *P. circumcincta*, is only known from a small remote area that hasn't been re-sampled since that initial survey in which they were recorded. There is no evidence that it is not still extant there. (K. Walton, pers. comm., 2017).

Temporary, significant retractions of the North Cape Eddy, would allow the EAUC to facilitate temporary, greatly increased influxes of warm water into Northland CA to the Bay of Islands and the offshore island groups, including PKI. However, while these warm water influxes represent a possible hypothesis for the presence of *L. vitellus* and *E. c. cernica* at the Bay of Islands and PKI, it does not provide support for:

1. The presence of *L. vitellus* in coastal areas south of the Bay of Islands, nor does it
2. Explain the presence of only two Cypraeidae species in these waters, despite the presence of many other Cypraeidae species in areas to the west and northwest, particularly New Caledonia and Norfolk Island, nor does it
3. Explain the presence of these two particular species, nor does it
4. Explain the wide variation in the shell features of *E. c. cernica* found at PKI, (K. Walton, pers. comm. 2017), potentially indicating possible larval dispersal from multiple source populations.

The continued presence of these two Cypraeidae species as well as several other warm water species, suggests that these are ongoing, breeding populations rather than just present day migrants.

Pleistocene Invasion

An alternative hypothesis would consider them as relictual self sustaining populations from earlier invasions that may or may not be supplemented by on-going sporadic migrant dispersal.

As sea water levels lowered during the ice ages, the habitat for shallow water specimens was severely reduced and, particularly in the Western and Central Pacific, populations became isolated and extinctions occurred in lagoon and other shallow water habitats. Current flows were also reduced during these glacial events, thereby reducing larval dispersal. Subsequent flooding as each glacial maximum receded, restored connectivity between many populations and resulted in the repopulation of these habitats. Despite these extremes, few marine species became extinct. Pelagic larval duration (PLD) was not a strong indicator of population dispersal and range in the Pleistocene. (Ludt & Rocha 2015).

Northland CA and offshore islands would not have been immune from these events. It is probable that, as sea levels rose to present day levels and the Tasman Front shifted to its southern position 12-10 kya, at least two Cypraeidae species from multiple populations invaded the area. This also marked the beginning of more stable, predictable oceanic currents, limiting the potential sources for further migration.

Subsequent variations in oceanic conditions, such as occurred during NZ's Little Ice Age (LIA: 1450-1850 CE), were much less extreme than during Pleistocene Ice Ages, but would have produced challenging conditions for any Cypraeidae populations. Studies "suggest both colder- and wetter-than-normal conditions were a pervasive component of the base climate state across New Zealand during the LIA, as were colder-than-normal Tasman Sea surface temperatures". (Lorrey *et al.* 2013). This period, coupled with the region's temperate ocean temperatures would have been a challenge for any subtropical or tropical Cypraeidae populations and most of these populations would have gone extinct over time.

The Two Cypraeidae Survivors

Of the two surviving Cypreaidae species, *E. c. cernica* is the least surprising. This is a wide ranging Indo-Pacific species which "is one of the most widely distributed species among cowries. The species is often found in deeper waters throughout the IWP and is found at shallower depths only in subtropical areas where water temperature is lower". (Meyer 2004). It has been trawled in deep water, 120 m, just north of the Bay of Islands and over 20 specimens have been reported from PKI, at depths similar to and deeper than at Raoul. This suggests that there may be populations extant in deeper water offshore Northland CA north of PKI. It is likely that larvae from such populations would occasionally flow south to shallower waters at PKI as the intermittent flows of the EAUC permitted.

While *L. vitellus* is not considered a deep water Cypraeidae as is *E. c. cernica*, it has adapted to such depths (*see* Plate 3). The author personally collected a specimen at 34 m off the wreck of the *Augustina* in the Java Sea and acquired a specimen trapped at 80-100 m from a fishing boat in Wanli Harbor, northern Taiwan. It is also one of the most wide ranging and hardiest species. *Lyncina vitellus* was collected at 20-30 m off the Bay of Islands and in coastal areas south of there as shallow as 4.5 m. Specimens were collected at PKI from 20-33m. As with *E. c. cernica*, the presence of *L. vitellus* at PKI is likely the result of flows from the north. The presence of *L. vitellus* in shallower waters in coastal areas just west of PKI could represent either larvae carried by expanded, eastward EAUC flows from the north or relictual populations extant in areas not often frequented by shell collectors.

Both Cypraeidae species, as well as others with low diversity clades, share certain characteristics: "(1) They have large geographical ranges with little population structure, indicating good dispersal ability. (2) They exhibit morphological stasis based on fossil first occurrences. (3) They have never experienced pulses of diversification, but instead appear to hover just above the perilous extinction boundary for their duration. … and if they have more than one species, additional ones are all peripheral endemics". (Meyer 2003). Their survival would not be unexpected.

Kermadecs

The Kermadecs, including Raoul, occupy a peripheral region which is isolated in the approximate middle of the South Pacific Subtropical Gyre, unconnected with any other subtropical or tropical region by present day predictable regional or boundary currents (*see* Figure 5).

However, a study of the connectivity between the Kermadecs and the mainland was made based on simulations of larval transport using virtually generated larvae seeded in the Kermadecs and Northland's east coast and the Bay of Plenty. Virtual larvae were seeded at five locations in the Kermadecs and 12 locations along the northeast coast of New Zealand. One hundred larvae were seeded at each location every 25 days between January, 1993 and November, 2007. (Sutton *et al.* 2012).

The results showed that the mean surface currents in the region are weak and dominated by eddies. Larvae spread over a wide area with a slight eastward bias. Within the Kermadecs, possible transport to the other islands was in the order of 3-10 days. Exchange from the Kermadecs to Northland would take 50 days from Raoul and 20 days from L'Esperance Rock. However, the study showed that larvae from the Kermadecs were transported well offshore to the east of the uppermost part of Northland, *i.e.* north of 35° S where the Bay of Islands is situated. No larvae reached Northland CA or the Northland shelf. (Sutton *et al.* 2012).

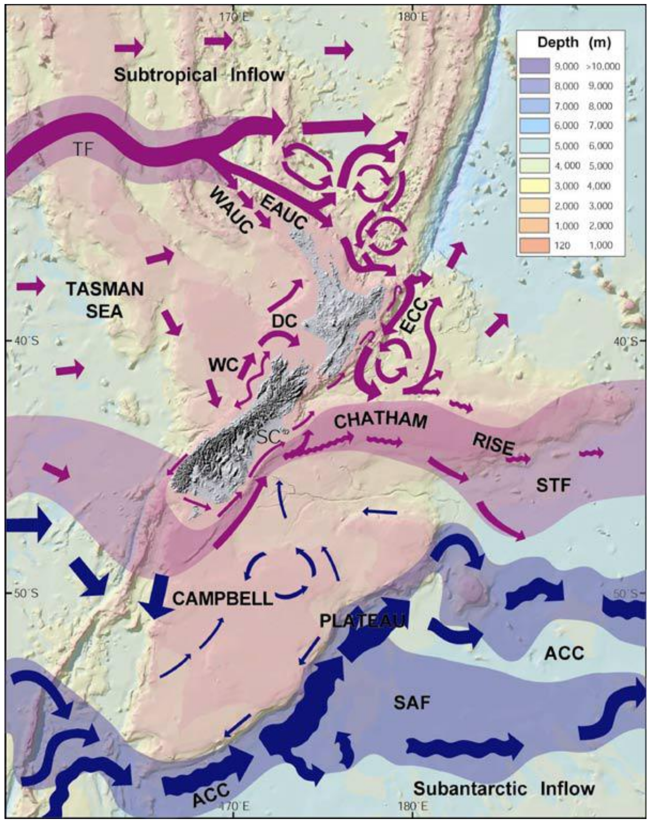

Figure 5. Ocean Currents Map. Craig Stevens and Stephen Chiswell, 'Ocean currents and tides - Currents', Te Ara - the Encyclopedia of New Zealand, http://www.TeAra.govt.nz/en/map/5912/ ocean-currents-around-new-zealand (accessed 22 January 2018)

Most of the larvae released from the mainland were largely contained within the EAUC and trended southward along the continental shelf. The remaining larvae scattered northeast over a wide arc with some larvae reaching the Kermadecs after 30 days. Even allowing for longer larval life cycles, the study concluded

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there is limited connectivity between mainland New Zealand and the Kermadecs. (Sutton *et al.* 2012).

Kermadec/Raoul Cypraeidae

Remote from any border currents, the origin of the molluscan species at Raoul is not definitely known. Rather, hypothetical affinity areas have been posited where Kermadec species are also found. These range from areas to the west (eastern Australia, Elizabeth and Middleton reefs, Lord Howe Island, and Norfolk Island), New Zealand and the Central and Eastern Pacific, including Pitcairn and Easter Island. (Brook 1998a). However, no support has been offered for any of these areas.

All eight Cypraeidae species reported from Raoul are among the widest ranging and most prolific of all species. They range from the East African coast, across the Indian Ocean to Australia, across the Pacific Ocean, some as far as Hawaii, French Polynesia and the TEP. They have also adapted to a variety of habitats. Studies of such wide ranging species at periphery regions have resulted in the central marginal hypothesis, a.k.a. the core periphery hypothesis. These hypotheses posit that end of range populations exhibit "low genetic diversity and high genetic differentiation relative to populations within the core of a species range.… These genetic patterns … are a consequence of reduced population size and

Plate 1, Figures 1-2. *Erosaria cernica*: **1a-d** *E. cernica*, Dumbea Pass, Noumea, New Caledonia, diver at 20-30 m. 31.9 mm.SBMHN 163933 **2 a-d** *E. cernica*, Raoul Island, Kermadec Islands, diver at 25 m, 26.4 mm. SBMNH 163934. Both ex- Vincent Crayssac. Compare the collumellar dentition of **1a** with **2a**, illustrating the features described by Powell for **(1)** *E. c. tomlini* from New Caledonia vs. **(2)** *E. c. kermadecensis* from Raoul. Also, note the more numerous columelllar and labral teeth of **(1)**. It should be noted that the New Caledonia specimen represents only one population of *E. cernica* among a number of other New Caledonian (and its surrounds) populations with significantly different features.

connectivity toward a species range periphery." While no such studies have been performed on Kermadec Cypraeidae, a study was conducted on two wide ranging species found in the Kermadecs. These are the Crown of Thorns star fish, *Acanthaster planci* (Linnaeus 1758) and the sea urchin *Tripneustes gratilla* (Linnaeus 1758). "The haplotypic composition of both populations suggests they have been founded by a small number of colonists with little subsequent immigration. Thus, local reproduction and self-recruitment appear to maintain these populations despite the ecologically marginal conditions of the Kermadec Islands for these tropical species." (Liggins *et al.* 2014).

While this study is narrow in scope and subject to subsequent revision, the Cypraeidae at Raoul are in the same region and subject to the same oceanic and habitat conditions as the Crown of Thorns and urchins in the Kermadecs. Self recruitment is probably relatively high and the majority of Cypraeidae veligers produced at Raoul are probably retained locally. Similar invasions have occurred in the Marquesas where genetic studies have shown that six endemic Cypraeidae species were the result of Pleistocene invasions approximately 1.58 million years ago ("mya") (Daughenbaugh 2015a). As above, flooding subsequent to glacial maximums resulted in the spread of molluscan populations. This suggests that the Raoul Cypraeidae populations are possibly, if not probably, the result of such Pleistocene invasions. The finding of *E. c. cernica* fossils in Early Pleistocene deposits in the Raoul's Herald Group is supportive.

Erosaria cernica kermadecensis

A fossil history that dates to the Early Pleistocene and the collection of a significant number of specimens in recent times supports the status of *E. c. cernica* as an extant population at Raoul. Has time and isolation allowed the Raoul population to evolve into a distinct subspecies? Powell, in 1958, named the population *Ravitrona tomlini kermadecensis*, about a decade ago reclassified as *Erosaria cernica kermadecensis* (Powell 1958) and today placed into synonymy with *E. c. cernica* by most authors.

The Holotype was trawled at 58-60 m off Raoul on March 3, 1952. Powell's description reads "Shell shining but not highly polished. Dorsum dull orange marked with evenly distributed but irregularly sized white spots. Sides, base, teeth and interior porcellanous white. Margins coarsely pitted, a few dark reddish-brown spots in the anterior and posterior series of pits and others sparsely and irregularly distributed along the sides, more numerous along the labial side. Labial teeth 19, Columellar teeth, 18, exclusive of the anterior and posterior ridges and two strong denticles on the fossula." The length of the Holotype is 24 mm, width 15 mm and height 11.75 mm.

In his discussion, Powell stated that the Kermadec population should be regarded as a subspecies of *Erosaria tomlini* (Iredale 1939), choosing Iredale's treatment of the New Caledonia population over *E. c. tomlini* (Schilder 1930). The latter included all southern Melanesian populations. He also compared the Kermadec shell to *Ravitrona [Erosaria] tomlini prodiga* (Allan 1956), type locality Newcastle, New South Wales. Allan (1956) also included Queensland, Lord Howe Island, Norfolk Island, and the Kermadecs in the distribution, excluding New Caledonia, presumably retaining it in Schilder's southern Melanesian population.

Powell's separation of the Kermadec population was based upon differences in the columellar teeth of the three populations. He separated *E. c. kermadecensis* from the "*E. tomlini prodiga*" populations stating the latter's "teeth are short and evenly graded throughout". Tarrant, in his comprehensive book on the Cowries of New South Wales, contains a plate of specimens from NSW which supports this aspect of Powell's assessment.

The columellar dentition differences between the New Caledonia population and the Kermadec population are more nuanced (*see* Plate 1). Powell noted that New Caledonian shells "are long at the posterior end but short over the anterior end, not graded but suddenly stepped just posterior to the middle. … The Kermadec subspecies has evenly graded teeth also but they are long, extending medially almost a third of the way across the basal callus." The Holotype was figured at the end of the article and it accurately reflects Powell's description.

Various authors have proposed at least eight subspecies and to date, all but two have been placed into synonymy (*see* Plate 2). The species exhibits very variable shape, callosity, color and dentition features within most regional populations. This is true of both *E. c. prodiga* and *E. c. tomlini*. The latter's dentition in particular includes specimens aligning with Powell's comparative description. As such, both populations are appropriately considered *E. c. cernica*, the nominate species.

The one subspecies relevant to this study which has been generally accepted is *Erosaria cernica leforti* (Senders & P. Martin 1987) from remote, end of range Easter Island. There, the population has developed distinct, consistent features indicative of a self recruiting population. These include fusing anterior columellar teeth, dense postulate marginal spotting and excess callous along the margins and the ends of the shell. These features allow the subspecies to be easily recognized.

The three Raoul specimens on hand also exhibit distinct, consistent features indicative of a self recruiting population. These include the columellar teeth as described by Powell, an ovate, slightly inflated shape with rounded margins and a white spotted, orange dorsal coloration. While these features are more nuanced than *E. c. leforti*, the three specimens at hand all exhibit them. However, while it is likely that the Raoul population represents a valid subspecies, additional specimens are needed to garner the support necessary to propose removing it from synonymy. Genetic analysis, should it become available, would also shed light on the origin(s) and the timing of the population's invasion. As such, the population will remain classified as *E. c. cernica* for the purposes of this paper.

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Plate 3, Figures 16-17. *Lyncina vitellus*: **16.** PKI, on a rock face at 90', < 1996-1997, leg. W. Palmer, 31 mm. **17.** Off Opua, Bay of Islands, Northland, N. Z., diver at 20-30 m, 1986, 64.5 mm. SBMNH 163937.

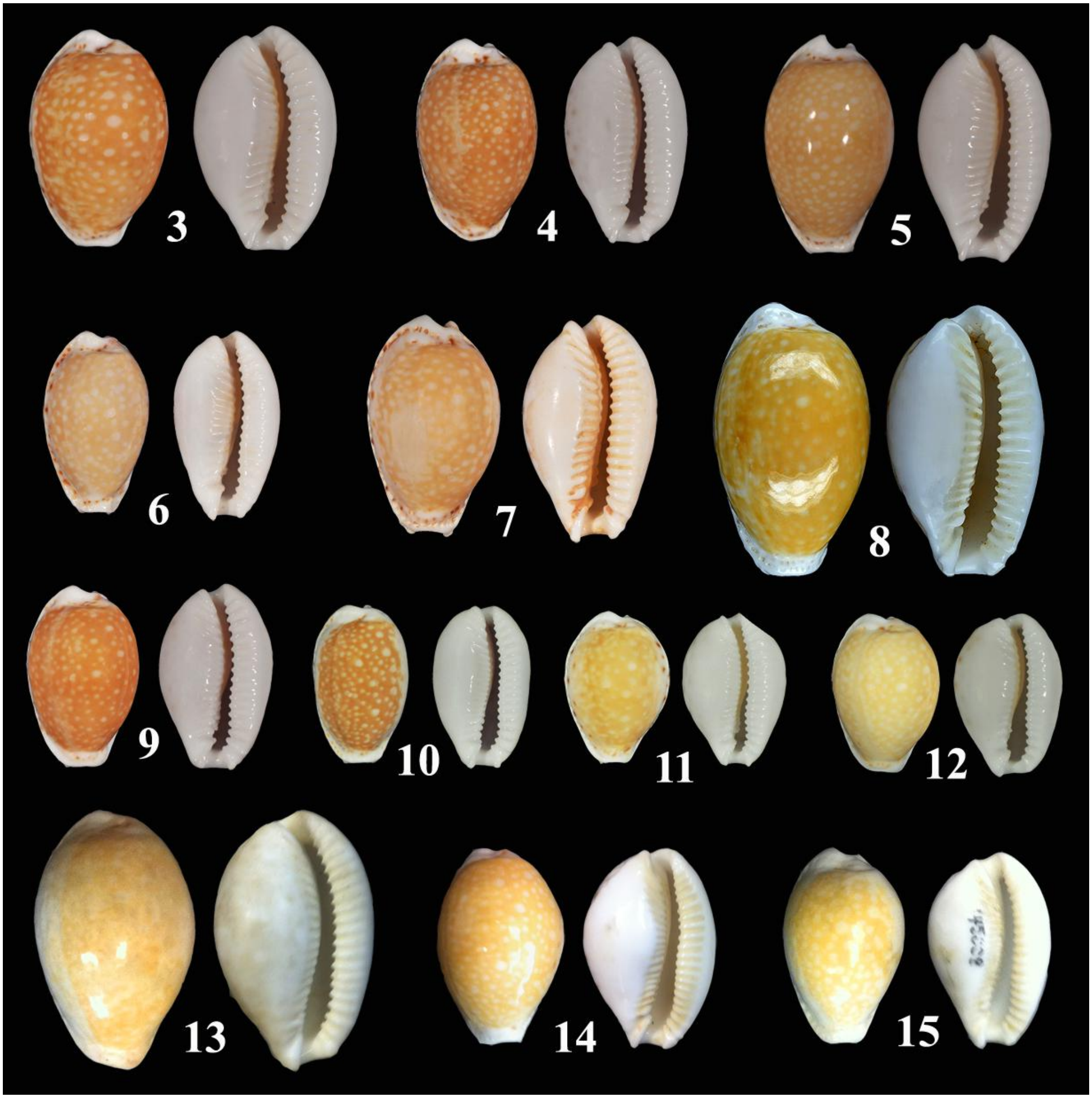

Plate 2, Figures 3-15. *Erosaria cernica*: **3**. Same as 2a-b, 26.4 mm. **4**, **5**. Kermadec Islands, scuba at 15-20 m, 26.9 & 24.7 mm respectively. Both ex- Vincent Crayssac. **6**. Cavalli Islands, Northland, N.Z., trawled at 120 m, 1984, 22.7 mm.SBMHN 163935 **7**. Poor Knights Islands (PKI), N. Z., diver at 25m, 1975, 27.1 mm. SBMHN 163936. **8**. PKI, off the NE point of Aorangi Island, diver at 80-100', 1978, 33 mm. SBMHN 163937. **9**. North side Noddy Island, off north coast, Lord Howe Island, SCUBA at 20 m, 1999, 22.1 mm. **10**. Bellona Reefs, southern Coral Sea, west of New Caledonia, diver at 2-3 m on hard reef, 2001, 18.1 mm. **11**. Sournois Reef, Boulari Passage, Noumea, New Caledonia, SCUBA at 3-5 m under coral rubble, 1987, 19.7 mm. **12**. Ilot Maitre, Noumea, New Caledonia, diver at 20-25 m in algae on sand, 1978, 18.2 mm. **13**. PKI, North Island, 37 m, 1975, leg. W. Palmer. M.018475*. **14**. PKI, 1975, ex. JR Penniket, 32.5 mm. M.118110*. **15**. PKI, North Island, Northern Arch, S side, 24 m, 1984, Dunning, JR. M.145008*. * Accession numbers. Museum of New Zealand, Te Papa Tongarewa, Wellington, New Zealand.