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Haliotis virginea Gmelin, 1791 and a new abalone from Aotearoa New Zealand (Mollusca: Gastropoda: Haliotidae)

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ABSTRACT

Several subspecies and forms of *Haliotis virginea* Gmelin, 1791 have been recognised, with intergrading variants between many of them. Published genetic data recovered none of the named subspecies as both monophyletic and significantly divergent from one another. Conversely, specimens previously referred to *H. virginea* from Manawatāwhi Three Kings Islands formed a strongly supported, highly divergent, monophyletic clade, herein described as *Haliotis pirimoana* n. sp. This species differs subtly but consistently in having finer and more numerous spiral threads than *H. virginea* at an equivalent stage of growth. *Haliotis crispata* A. Gould, 1847, *H. gibba* R.A. Philippi, 1846, *H. huttoni* Filhol, 1880, *H. virginea morioria* A.W.B. Powell, 1938, and *H. virginea stewartae* M. Jones & B. Owen, 2004 are interpreted as synonyms of *H. virginea*. Neotypes are designated for *H. crispata* and *H. huttoni*. ZooBank article LSID: urn:lsid:zoobank.org:pub:C0F24F1D-E531-40A7-AAB6-932086847DD7

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Manawatāwhi; Paua; Pāua; systematic; taxonomy; Three Kings Islands; Vetigastropoda

Introduction

Haliotidae ('abalone' or 'ormers', and, in Aotearoa New Zealand, 'pāua') are a group of herbivorous marine gastropods that occupy hard substrates in shallow non-polar regions worldwide (Geiger and Owen 2012). Several haliotids are the basis of wild-caught and/or aquaculture fisheries (McCormick 2000; Prince 2004). Additionally, haliotid shells are often prized for art, cultural practices, jewellery, and by shell collectors (Geiger and Owen 2012).

Presently, 67 species (MolluscaBase, accessed May 2024) and many subspecies and forms are recognised (Geiger and Owen 2012), all in the genus *Haliotis* Linnaeus, 1758, despite the availability of at least 13 supraspecific haliotid names. Deeper relationships within the family remain poorly resolved due to conserved and/or convergent character states (Estes et al. 2005) coupled with incongruent topologies in published phylogenies (Estes et al. 2005; Degnan et al. 2006; Bester-van der Merwe et al. 2012).

Haliotis virginea Gmelin, 1791 is a medium-sized (to 75 mm, Geiger and Owen 2012) species that occurs throughout much of New Zealand (Figure 1). Five regional variants have been treated as subspecies (Powell 1979; Jones and Owen 2004; Geiger and Owen 2012), and additional forms occur (Walton et al. 2022). Recent molecular work, however, recovered none of these subspecies as both monophyletic and significantly divergent from one another (Walton et al. 2022). Conversely, samples from Manawatāwhi Three Kings Islands (Figure 1), north of mainland New Zealand, formed a highly divergent (~4.4% difference between partial mitochondrial genomes) with strong support (100% support in both maximum-likelihood and Bayesian analyses) clade (Walton et al. 2022), and are here introduced as a new species.

Materials and methods

Specimens examined are in the collections at the Museum of New Zealand Te Papa Tongarewa (NMNZ; specimen lots prefixed 'M.') and the National Institute of Water and Atmospheric Research (NIWA), both in Wellington, New Zealand, and the Auckland War Memorial Museum (AWMM; lots prefixed 'MA'), Auckland, New Zealand. Measurements <10 mm were taken using a Leica M60 stereo microscope with a 10× magnification eyepiece with graticules calibrated against a 1×1 mm grid. Measurements >10 mm were made using Mitutoyo callipers. Images were generated using a Canon EOS-1DX camera and Helicon Focus (v 5.3) image-stacking software. Adobe Photoshop® was used for clearcutting images and plate assembly.

Systematics

Subclass Vetigastropoda Salvini-Plawen, 1980
Order Lepetellida Moskalev, 1971
Superfamily Haliotoidea Rafinesque, 1815
Family Haliotidae Rafinesque, 1815
Genus *Haliotis* Linnaeus, 1758

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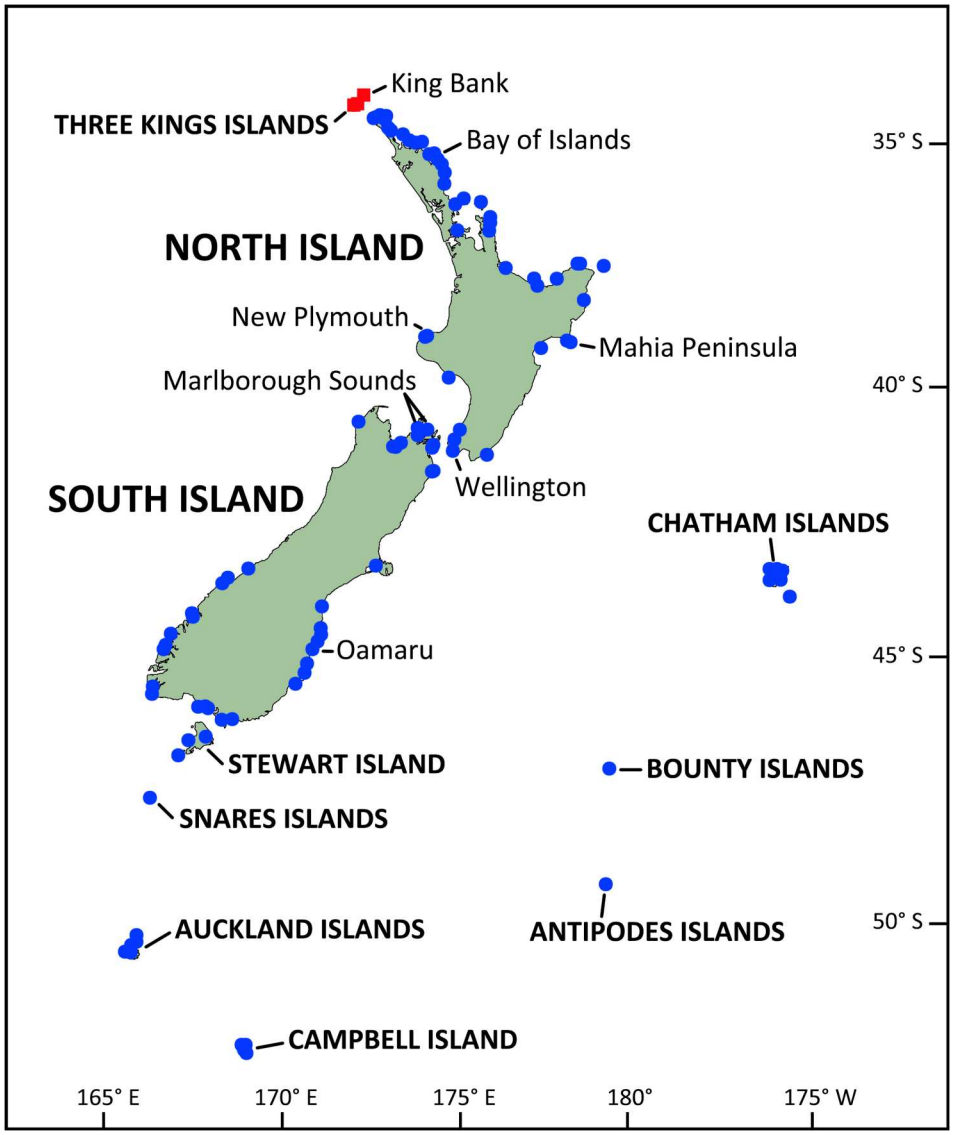

Figure 1. Map of Aotearoa New Zealand with distribution records held at the Museum of New Zealand Te Papa Tongarewa of *Haliotis pirimoana* n. sp. (red squares) and *H. virginea* Gmelin, 1791 (blue circles).

Haliotis Linnaeus, 1758: 779. Type species (by subsequent designation of Montfort 1808–1810: 119): *Haliotis asinina* Linnaeus, 1758: 780, extant, Indian and Pacific Oceans.

Subgenus *Paua* C.A. Fleming, 1952: 230. Type species (by original designation): *Haliotis iris* Gmelin, 1791: 3691; extant, New Zealand.

***Haliotis (Paua) pirimoana* n. sp.**

Figure 1; Figure 2A–D; Table 1.

ZooBank taxon LSID: urn:lsid:zoobank.org:act:292CCC92-6839-49AB-B069-DDFF8406EC5C

Haliotis virginea crispata.— Owen and Kershaw 2014: 59 (in part, not A. Gould, 1847)

Haliotis virginea.— Walton et al. 2022: 118 (in part, not Gmelin, 1791)

Holotype M.333915 and paratypes (13, M.134648; 1, MA 73697; 1, NIWA 172951): South East Bay, Great Island, Three Kings Islands (34°09.5′S, 172°08.8′E), under boulders, alive, 13–15 m, K.W. Burch and D.D. Crosby, 5 Mar. 1997.

Material examined

Type material. See above. *Other material*. **King Bank, NE of Three Kings Islands** 123–128 m (20, M.158063). **Three Kings Islands –** Off West Island, *Elingamite* wreck, 37 m (15, M.158064). W of Tapatu Bay, Great Island, 47–54 m, alive (2, NIWA 73116). North West Bay, Great Island: 24 m, living (16, MA134924); 13–15 m, alive (2, M.335073); 15–21 m, alive (3, M.059511); 18 m, alive (2, soft tissues only, M.333468; shells in A. Howell colln.); 23 m (3, M.109413); 24 m, alive (14, MA134924). South East Bay, Great Island: 10-12 m, alive (1, M.335344); 15 m, alive (2, M.275308); 18 m, alive (5, M.100393); 18–22 m, alive (2, M.117897). Great Island, 15–21 m, alive (2, M.335345). Reef between Great Island and Farmer

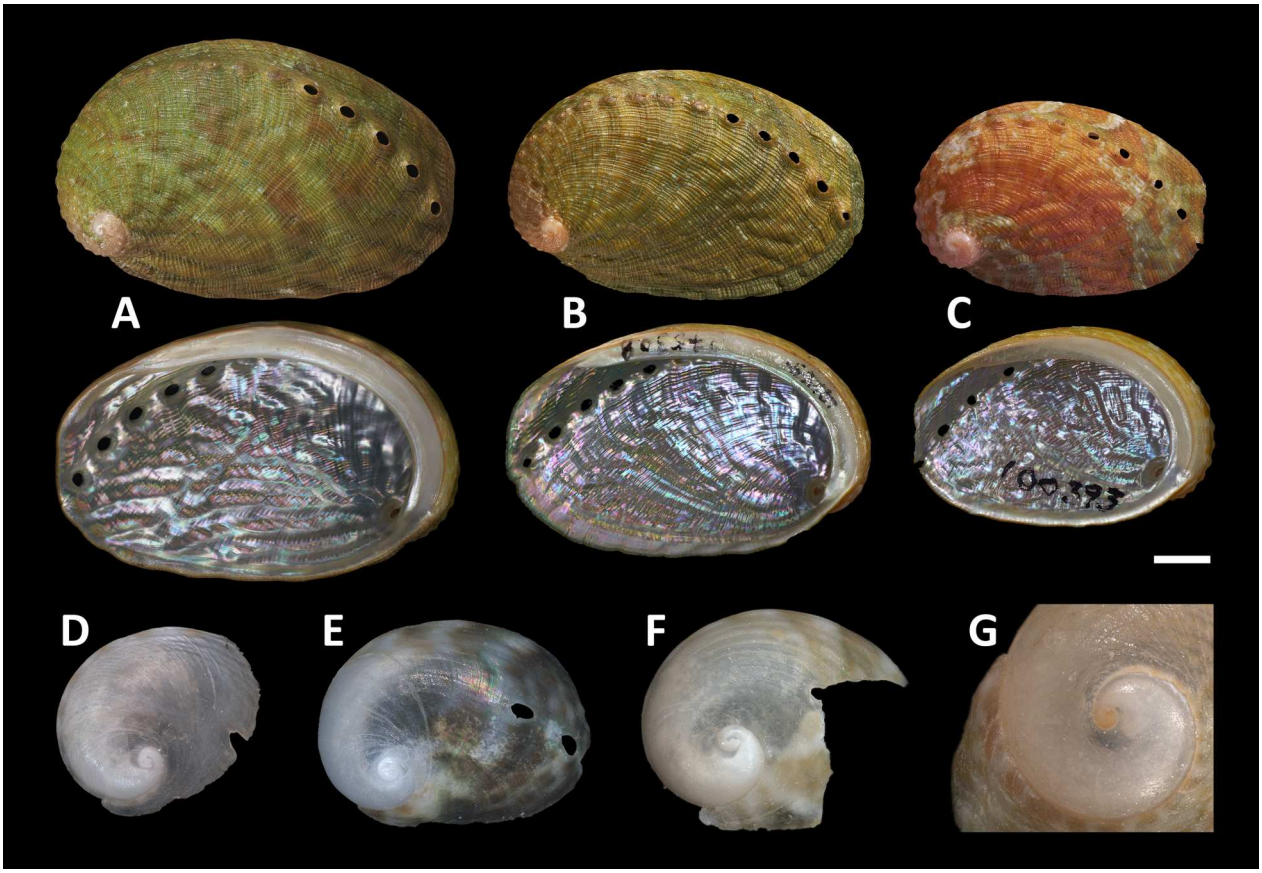

Figure 2. Shells of *Haliotis pirimoana* n. sp. from Manawatāwhi Three Kings Islands (**A**–**D**) and *H. virginea* Gmelin, 1791 (**E**–**G**). **A,** Holotype, South East Bay, Great Island, M.333915; **B,** SW corner of South East Bay, Great Island, M.337867; **C,** E corner of North West Bay, Great Island, M.059511; **D,** South East Bay, Great Island, M.134648; **E,** Two Thumb Bay, N of Caswell Sound entrance, south-western South Island, M.144345; **F,** Northeast Harbour, Campbell Island, M.301663; **G,** Motuhora Island, Bay of Plenty, M.036228. Scale bar 5 mm (**A**–**C**) and 0.5 mm (**D**–**G**). Images generated by Jean-Claude Stahl (Te Papa).

Rocks, 53 m (2, M.093944). Princes Islands: Arch Pinnacle, 38 m (1, M.333417); off N face of Hinemoa Island, 23 m (6, M.112604); NNW side of Princes Pinnacle, 22–32 m, alive (2, M.309580).

Description

Foot cream, with irregular, darker grey and/or green bands on exposed surfaces. Protoconch opaque white, surface rough, lacking strong sculpture, of approximately 0.7 whorls, 0.23 mm width, with a distinctive V-shaped notch indenting the suture just before protoconch/teleoconch boundary.

Shell ovoid, length up to 37.7 mm (31.3–37.7 mm), length/width ratio 1.49–1.56, with 5–7 open tremata.

Table 1. Shell measurements (mm) and open tremata counts for mature specimens of *Haliotis pirimoana* n. sp.

Type status	Registration	Length	Width	Height	Open tremata
Holotype	M.333915	37.1	24.3	8.7	5
Paratype	M.134648a	34.2	22.6	8.5	6.5
Paratype	M.134648b	34.2	23.0	8.0	7
Paratype	M.134648c	30.1	20.2	6.6	5.5
Paratype	M.117897a	36.1	23.9	8.0	6
Paratype	M.117897b	32.6	20.9	7.9	6
Paratype	M.100393a	31.8	20.5	8.5	5
Paratype	M.100393b	31.3	20.6	7.4	5

First half teleoconch whorl opaque white, second half whorl translucent, pale, with faint, similar, commarginal axial lamellae, their spacing increasing slightly with size; fine spiral riblets finer or absent nearer suture. Later whorls with numerous fine spiral threads (width to 0.24 mm) that multiply by intercalation; interspaces about as wide as threads, or slightly narrower; most threads of similar width, but every second or fourth thread usually slightly wider; radial sculpture comprising a series of broad, irregular, rounded, non-commarginal radial wrinkles, numerous fine and similar commarginal primary lamellae, and more numerous, much finer secondary lamellae (5–15 per primary lamella).

Dorsal colouration: apex pale pink; last adult whorl typically uniform light or dark green but some specimens predominantly red or golden, typically with broad, irregular red patches. Each 4th or 8th primary spiral cord in some specimens with regularly alternating brown and paler sectors; some specimens additionally with irregular chevron-shaped colour blotches, their spacing gradually increasing abapically, strongest adapically and near peripheral concavity. Interior brilliantly nacreous. Muscle scar poorly defined. Columella relatively tightly coiled.

Distribution and habitat

King Bank and Manawatāwhi Three Kings Islands, Aotearoa New Zealand (Figure 1); living at 5–47 m depth under rocks and in rock crevices.

Remarks

Haliotis pirimoana n. sp. superficially resembles specimens from North Island (except near Wellington) populations of *H. virginea* (Figure 3A, B) in shell morphology, but, at an equivalent stage of growth differs considerably in having consistently finer spiral threads on the dorsal surface that are more evenly spaced, with narrower interspaces, and a more tightly coiled columella. These differences are particularly evident when shells from the far north of the North Island, closest to the Three Kings Islands, are compared with *H. pirimoana* n. sp.: the former have a distinctly coarser sculpture. *H. pirimoana* n. sp. differs further from mainland populations of *H. virginea* in average shell shape: generally having a lower profile, especially abapically, a more angular abapical margin, and a flatter, broader, and more sharply delimited umbilical margin.

Genetic divergence between *H. pirimoana* n. sp. and *H. virginea* from partial mitogenomes was 4.4% (Walton et al. 2022). From an alignment of just the mitochondrial gene CO1, *H. pirimoana* n. sp. differed from *H. virginea* by 4.3–4.5%. In comparison, the equivalent divergence between any pair of the species *H. kamtschatkana* Jonas, 1845, *H. rufescens* Swainson, 1822, *H. sorenseni* Bartsch, 1940 and *H. walallensis* Stearns, 1899 was 1.1–3.2%, while that for any pair of *H. discus* Reeve, 1846, *H. gigantea* Gmelin, 1791, and *H. madaka* (Habe, 1977) ranged from a mere 0.6% to 2.1% (Walton et al. 2022 table S3).

Etymology

The epithet *pirimoana* (a noun in apposition) stems from the te reo Māori words 'piri' (to cling to) and 'moana' (the sea), and was suggested by Sheridan Waitai with support from Jerry Norman, both of Ngāti Kuri. Ngāti Kuri are Mana i te whenua for the area of Manawatāwhi and surrounding lands and waters.

Haliotis (Paua) virginea **Gmelin, 1791**

Figure 1, Figure 2E–G, Figure 3A–D.

Haliotis virginea Gmelin, 1791: 3690 refers to Chemnitz 1788, p. 314, pl. 166, figs 1607, 1608, "Novam Seelandiam" (= New Zealand); type locality subsequently designated by Powell (1952: 173) as Queen Charlotte Sound (northern South Island, New Zealand); whereabouts of original material unknown.

Haliotis gibba Philippi, 1846 (*in* Philippi 1844–1848), 70 "Nova Hollandia?" (i.e., Australia = inaccurate - correctly from either the Auckland or Campbell islands, New Zealand, more probably the Auckland Islands to judge from the high shell elevation and rounded apertural profile, see below); syntype at Museo Nacional de Historia Natural, Santiago, Chile MNHNS 60037 (formerly '182', Coan and Kabat 2017); Weinkauff 1883: 34, pl. 14, figs 4, 5; Suter 1913: 95, pl. 7, fig. 23.

Haliotis crispata Gould, 1847: 251, "with New Holland shells" (i.e., Australia = inaccurate - correctly from North Island, New Zealand). Type locality subsequently designated by Powell (1952: 173) as 'Bay of Island' (*sic* = Bay of Islands) northern North Island, New Zealand). Original type material presumed lost (not at USNM); neotype (here designated to ensure proper and consistent application of the name): M.337867, live-taken, 10–12 m, under rock slab among kelp, SW of Cape Brett lighthouse, Bay of Islands, New Zealand, K.W. Burch, 31 Mar. 2013 (Figure 3B). **New synonym**.

Haliotis huttoni Filhol, 1880: 1094, "L'île Cambel'l" (Campbell Island). Type material presumed lost (not at MNHN, V. Héros, pers. comm. 30 Nov. 2018); contrary to reports by Geiger and Poppe (2000: 95) and Geiger and Owen (2012: 141), no type material has ever been present at Auckland Museum (S. Hannam, pers. comm. 9 May 2024); neotype (here designated to ensure proper and consistent application of the name): M.337942, between Meteorological Station and Lookout Point, Perseverance Harbour, Campbell Island, New Zealand, F.M. Climo, 12 Nov. 1975 (Figure 3D). **New synonym**.

?Haliotis subvirginea Weinkauff, 1883: 33, pl. 13, figs 7, 8, pl. 17, figs 1, 2) 'Unterguinea (Tams) Loebbecke'sche Sammlung' (= Lower Guinea ([collected by Georg] Tams) [western Africa], Loebbecke collection). Whereabouts of original material and thus taxonomic status unknown.

Haliotis virginea morioria Powell, 1938: 165; pl. 40, figs 1, 2, holotype MA 70350, Owenga, Chatham Islands (collector and date of collecting unknown); Geiger and Poppe 2000: 96; Geiger and Owen 2012: 141. **New synonym**.

Haliotis (*Sulculus*) *virginea virginea*.— Powell, 1979: 37.

Haliotis (*Sulculus*) *virginea crispata*.— Powell, 1979: 37.

Haliotis (*Sulculus*) *virginea huttoni*.— Powell, 1979: 37.

Haliotis (*Sulculus*) *virginea morioria*.— Powell, 1979: 37.

Haliotis virginea crispata.— Geiger and Poppe 2000: 94; Geiger and Owen 2012: 140.

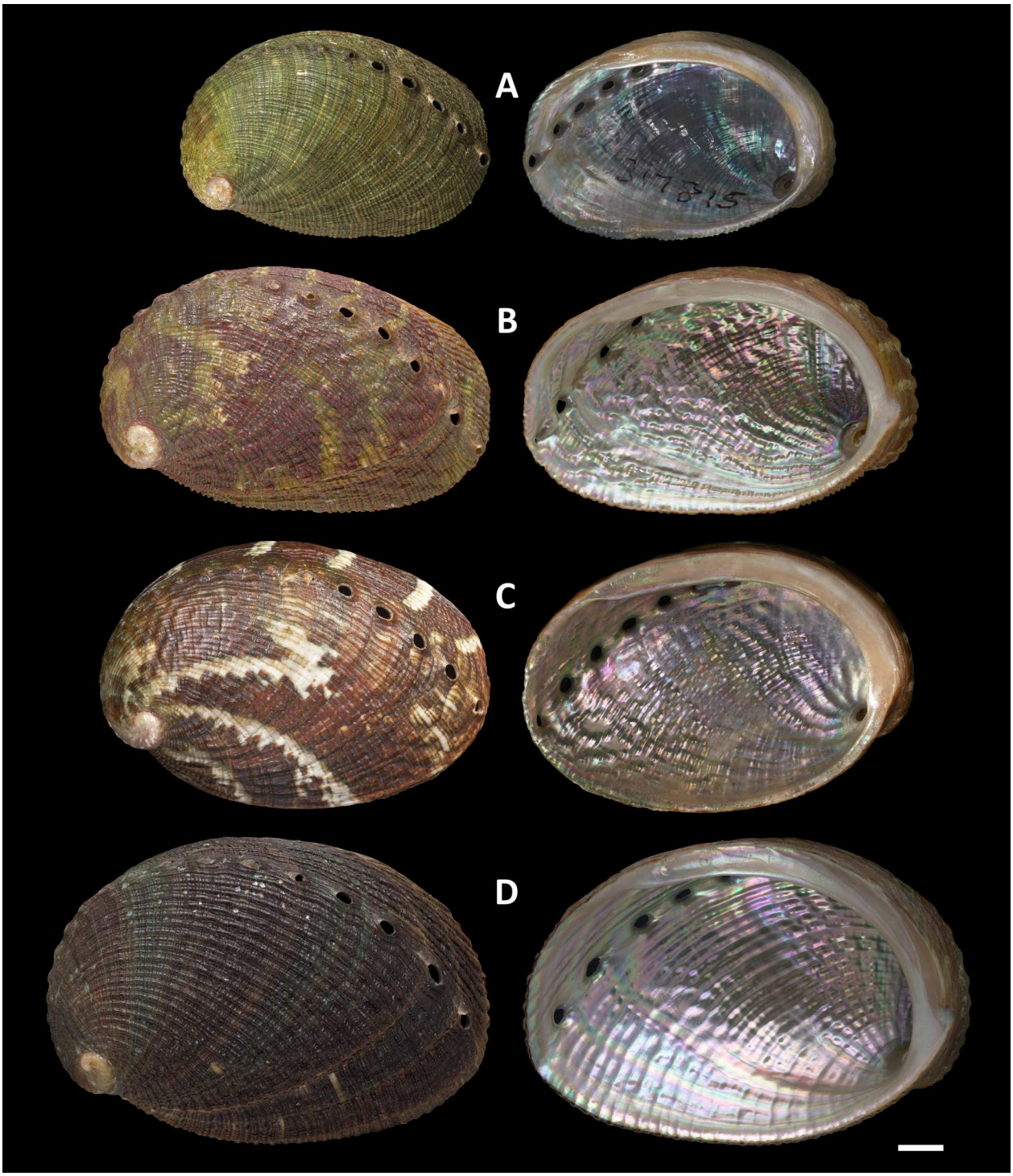

Figure 3. Shells of *Haliotis virginea* Gmelin, 1791. **A,** Ngā Motu Beach, New Plymouth, M.317815; **B,** Neotype of *Haliotis crispata* A. Gould, 1847, rocky gut SW of Cape Brett, Bay of Islands, M.337867; **C,** Lillies Beach, opposite Moioio Island, Tory Channel, M.338233; **D,** Neotype of *Haliotis huttoni* Filhol, 1880, between Met Station and Lookout Point, Perseverance Harbour, Campbell Island, M.337942. Scale bar 5 mm (**A**–**C**) or 6 mm (**D**). Images generated by Jean-Claude Stahl and Melissa Irving (Te Papa).

Haliotis virginea huttoni.— Geiger and Poppe 2000: 95; Geiger and Owen 2012: 141.

Haliotis virginea virginea.— Geiger and Poppe 2000: 93; Geiger and Owen 2012: 138 (both in part = *H. diversicolor* Reeve, 1846, see below).

Haliotis (*Paua*) *virginea virginea*.— Eagle 2002: 35.

Paua (?) *virginea*.— Maxwell 2009: 239.

Haliotis virginea stewartae M. Jones & B. Owen, 2004: 81, holotype M.154176, "Antipodes Island, New Zealand, collected from the extreme northwestern point of the island, latitude 49 degrees 40 minutes, longitude 178 degrees 47 minutes", i.e., North Cape, Antipodes Islands, 49°40′S, 178°47′E (collector and date of collecting unknown). **New synonym.**

NOT *Haliotis marmorata* Reeve, 1846, pl. 13, fig 44 (3 syntypes, NHMUK 1950.3.16.82-84, "Taiwan", ex H. Cuming collection). Geiger and Poppe (2000) and Geiger and Owen (2012) included this taxon in their

synonymy of *H. virginea*, but the syntypes are in fact *H. diversicolor* Reeve, 1846. *Haliotis diversicolor* Reeve, 1846 is here given priority over *H. marmorata* Reeve, 1846 (principle of first reviser, ICZN Art. 24.2.6). **New synonym**.

NOT *Haliotis virginea* Reeve, 1846, pl. 12, fig 36. Reeve referred to Chemnitz 1788, p. 314, pl. 166, figs 1607, 1608 (i.e., *H. virginea* Gmelin, 1791), and his name is a junior homonym of *H. virginea* Gmelin, 1791. Nevertheless, the specimen Reeve illustrated and two additional syntypes (NHMUK 1950.3.16.52-54, no locality data, ex H. Cuming) are *H. marmorata* Linnaeus, 1758.

Material examined

Northern North Island – Cape Maria van Dieman (1, M.275288). Tapotupotu Bay (1, M.275294). Spirits Bay (1, M.003930). Pananehe Island, Spirits Bay (1, M.275291). Waikuku Beach (3, M.011850). Parengarenga Harbour (1, M.275287). Between Paxton Point and Te Kao Stream, Great Exhibition Bay (1, M.275298). Rarawa Beach, Great Exhibition Bay (1, M.275290; 3, M.025635; 1, M.275304). Henderson Bay (5, M.275297). Taemaro Bay (1, M.275303; 1, M.275307). Matai Bay, Karikari Peninsula (2, M.275299; 1, M.275296; 2, M.275289). Whangaroa Heads (12, M.145093; 4, M.145095). Tauranga Bay, Whangaroa Harbour (2, M.083938). Bay of Islands: Tapeka Point (5, M.091023; 2, M.145096); Russell (9, M.004673); Pahi Beach (8, M.025721). Elliot Bay 4, M.275293). Bland Bay (2, M.158061; 2, M.025669). Whangaruru (1, M.091026). Taupiri Bay (1, M.039580; 6, M.275301; 5, M.275295; 3, M.275292). Tutukaka (5, M.275283). Matapouri Bay (2, M.275284). Busby Head, Whangarei (1, M.083939).

Eastern North Island – Oruawharo, Great Barrier Island (22, M.083940). Little Barrier Island, 12 m, alive (2, M.059510). Leigh (18, M.083941). Mission Bay Beach, Auckland (1, M.018535). Tauranga-Kawau Point (5, M.025611). NE of Whitianga, Opito Bay (1, M.275286). N of Whitianga, Kuaotunu (1, M.275285). Whitianga (6, M.083937). Whitianga Bay, SW of Te Kaha, 6 m, alive (3, M.110731). E side of Great Mercury Island, 15 m (1, M.178095). Mount Maunganui, low-tide level, alive (2, M.039845). Mount Maunganui (2, M.083942). Ohope, fossil (Castlecliffian) (1, M.043126). Boulder Bay, Whale Island (27, M.036228). Off Whale Island, 24–29 m (6, M.061267). Ranfurly Bank, 35–37 m (2, M.074931). Reef off Anaura Bay, 12 m, alive (1, M.110723). Lottin Point, 9–12 m, alive (6, M.090240; 6, M.110735). Between Lottin and Matakaoa points (18, M.275282). Mahia Peninsula: Opoutama Beach (1, M.023964); Mahia Beach (7, M.275281); Auroa Point (6, M.275300; 12, M.338236; 10, M.156146). Auroa Point, 6–12 m, alive (5, M.090241; 1, M.110722). NE of Napier, 27 m (1, M.006334). SE of Pahaoa, low-tide level, alive (1, M.318759).

Western North Island – Ngamotu Beach, New Plymouth (~50, M.317815). Seal Rocks, 30 m (2, M.112472). SW of Waitotara, 33–35 m (1, M.050422). Kapiti Island (3, M.001110; 2, M.018534). Onehunga Bay, opposite Plimmerton (12, M.317827).

Southern North Island – Wellington southern coastline: Island Bay, low-tide level, alive (4, M.011946); Lyall Bay (4, M.001982); Houghton Bay (4, M.001983).

Northern South Island – Cable Bay, 4 m, alive (12, M.158062). W of Nelson, Rabbit Island (2, M.275280). Nelson, Tahunanui Beach (1, M.025703). D'Urville: S of French Pass (8, M.338234); Greville Harbour (4, M.011964); between Lucky and Woodsman bays, 9–15 m, alive (3, M.100415); attached to buoy, 18 m, alive (1, M.003901). Chetwode Island (2, M.018541). Pelorus Sound: Te Towaka Bay, low-tide, alive (1, M.318580); Cissy Bay, low-tide, alive (11, M.129796). Arapawa Island, beside Patten Passage, Queen Charlotte Sound, 0.5 m, alive (3, M.134105). Tory Channel: Lillies Beach (5, M.338233); Erie Bay (4, M.017937); outside entrance to Deep Bay (1, M.134015); Tapapaweka Pt (4, M.134010).

Eastern South Island – W of Cape Campbell, Marfells Beach (2, M.062862; 1, M.338338). Off Cape Campbell (1, M.008734). Cape Campbell (7, M.321186). Taylors Mistake (2, M.016512). Timaru (1, M.011363). N of Waitaki River mouth, 24 m, alive (1, M.110512). SE of Waitaki River Mouth: 18 m, alive (3, M.110513); 23 m, alive (1, M.110511). Shelf off Oamaru, 18 m, alive (22, M.110505). Oamaru (3, M.011610; 6, M.013513). Bushy Beach, Oamaru (19, M.110509). Shag Point (1, M.002841). Katiki Beach (1, M.275279). Warrington Beach (15, M.160664). Otago Harbour, Dowling Bay, low-tide, alive (3, M.338337; 2, M.333472). Otago Peninsula, Sandfly Bay (1, M.011846). Karitane Peninsula (1, M.158181).

Western South Island – Paturau, low-tide, alive (1, M.333418). Kahurangi Point (1, M.025992). Abbey Rocks (1, M.152496). Abbey Rocks, 7–11 m (2, M.152285). NE side of Jackson Head, 8–12 m (1, M.183574). Open Bay Islands (3, M.003899). Jackson Bay (~50, M.275328; 6, M.275277; 14, M.276276; 3, M.275278).

Southern South Island – St Anne Bay, entrance to Milford Sound, 10–14 m (1, M.142880). Pater Point, Milford Sound, 10–15 m (1, M.142793). Off Lieutenant Head, Thompson Sound, 15 m (3, M.140301). S of Leg Head, Nancy Sound, 24 m (1, M.141826). S side of Cunaris Sound, Chalky Inlet, 20–30 m (1, M.140487). Two Thumb Bay, 15 m (4, M.144345). Preservation Inlet, 15–20 m (1, M.140746). Kawakaputa Bay (5, M.111345). Riverton (1, M.309676); 5 m, alive (7, M.320224). Oreti Beach (3, M.018533). S of lighthouse, Waipapa Point, low-tide level, alive (6, M.317709; 6, M.057917).

Foveaux Strait – Oyster beds, alive (4, M.004787; 6, M.019486).

Stewart Island – Ringaringa Bay (1, M.001596). Bathing Beach (1, M.019569). The Gutter, Mason Bay (2, M.038358). Murderers Bay, Big South Cape Island (1, M.038826).

Auckland Islands – Rose Island (8, M.016749; 11, M.001988). Hanfield Inlet (21, M.001986). W side of Auckland Islands, alive (8, M.036507). Grafton Point, Adams Island, alive (6, M.117605). Upper reach of Carnley Harbour (8, M.081510). Monumental Island, western entrance to Carnley Harbour (1, M.338334). Carnley Harbour (2, M.001990). Erebus Cove (8, M.001595). Derry Castle Reef (5, M.008374). Enderby Island (3, M.038554; 3, M.117603). Inside Tucker Point (1, M.016796). Beehive Rock, 21 m, alive (1, M.275305). French Island (1, M.021727; 1, M.008395). No other locality data (2, M.000288; 2, M.001987; 1, M.016513; 15, M.001989).

Campbell Island – Monument Harbour (12, M.008403). Shoal Point (3, M.043430); 5 m, alive (5, M.117476). Meteorological Station Beach, Perseverance Harbour (37, M.117609). Between Meteorological Station and Lookout Point, Perseverance Harbour (22, M.047419). Shag Point, 17 m, alive (5, M.117486). E of De la Vire Point, 3 m, alive (4, M.117478). Monument Harbour (1, M.275306). Northeast Harbour, 8–10 m (8, M.301663). S of South Point, 20 m, alive (4, M.117477). Tucker Cove (1, M.042277). Smoothwater Bay: 10 m, alive (2, M.117485); 19 m, alive (4, M.117495). Ramp Point (3, M.275237). "Off wharf, Campbell Island", 7 m, alive (5, M.117496). Off Davis Point, 3 m (2, M.131008). No other locality data (2, M.001985); 6 m, alive (2, M.038549).

Chatham Islands – Waitangi (1, M.012301; 1, M.102505; 7, M.110420; 2, M.145097; 2, M.011947; 2, M.275302). Hansons Point, 2–3 m, alive (1, M.118057). Owenga (1, M.275229; 1, M.338254; 1, M.338235). Off Cape Pattison, 27 m, alive (2, M.012304). N of wharf, Kaingaroa, intertidal, alive (1, M.315654). Taupeka Beach (1, M.042311). Off Pitt Island (1, M.023271). Ocean Bay, 12–15 m, alive (1, M.183573). NNE of Okawa Point (5, M.333470). No other locality data (3, M.004172; 4, M.007073; 5, M.001991; 20, M.003815).

Antipodes Islands – NE side of Bollons Island, 9–18 m, alive (6, M.284140). S side of Reef Point (2, M.338237; 1, M.338238). Reef Point (2, M.029177). N side of Leeward Island (4, M.029181). NW point of Leeward Island, 13 m, alive (1, M.064428). Clio Bay, 15 m, alive (1, M.081452). Northern embayment of Crater Bay, 10 m, alive (1, M.064423). Boat landing site, Anchorage Bay, alive (16, M.100325). N side of Archway Island, 15 m, alive (1, M.284207).

Bounty Islands – Proclamation Island: 10–20 m, alive (1, M.064422); 18-20 m, alive (3, M.064429). Gut between Depot and Proclamation islands, 13 m, alive (6, M.059533). NE side of Tunnel Island, 14 m, alive (4, M.284141). No other locality data, alive (7, M.089934).

Distribution and habitat

Late Pleistocene (Castlecliffian; Ohope Beach, OIS 15?, M.043126) to present; North, South, Stewart, Snares, Auckland, Campbell, Chatham, Bounty, and Antipodes Islands, Aotearoa New Zealand (Figure 1); living from low tide to at least 27 m, under rocks and in crevices.

Remarks

Haliotis virginea is the most widely distributed of the four haliotid species living in the New Zealand region (Walton et al. 2022). Nevertheless, it is not known from the Three Kings Islands, and nor does it occur at Rangitāhua Kermadec Islands, contrary to Suter's (1913) erroneous record.

Partial-mitogenomic evidence revealed a significant genetic disjunction within *H. virginea*: a strongly supported clade comprising samples from the Chatham, Antipodes, and Auckland Islands differed by 1.4–1.5% from a clade comprising both mainland and Campbell Island samples (Walton et al. 2022). This geographic split does not coincide with known biogeographic patterns or morphological evidence (see below), and nor does it support retention of the existing subspecific names. This reported divergence may represent an evolutionary artefact and/or the result of limited molecular sampling from each island group.

Several publications (Geiger and Poppe 2000; Jones and Owen 2004; Geiger and Owen 2012; Owen and Kershaw 2014) have emphasised differences between the previously recognised *H. virginea* subspecies, without depicting intergrading morphological variants between the various mainland and Chatham Islands populations. Even so, there is clear geographic structure within *H. virginea*.

The *crispata* form, as here interpreted, is generally reported as ranging from Northland (Figure 3B) to Mahia Peninsula (Raven and Bracegirdle 2010, 2020; Geiger and Owen 2012; Owen and Kershaw 2014) and is characterised by small, elongate shells (to 40 mm, Powell 1979) with fine dorsal and ventral spiral cords and pronounced radial wrinkles. However, both *crispata* and forms intermediate with southern mainland populations (see below) occur at Mahia Peninsula (Jones and Owen 2004), New Plymouth (Walton 2014) and in western parts of Wellington (e.g., M.317827; Geiger and Owen 2012: 298).

Some specimens from New Plymouth (Figure 3A) closely resemble *H. pirimoana* n. sp. in having weaker and finer sculpture than in other *H. virginea* populations. Monophyly of the *crispata* form reported by Walton et al. (2022) probably reflects their inclusion

of only two specimens from a single location - the genetic distances between them and the nominate (Marlborough) form were minimal.

The southern distribution boundary of the *crispata* form at Mahia Peninsula coincides with commonly reported phylogeographic and biogeographic 'disjunctions' (Ross et al. 2009; Arranz et al. 2021) that result from convergent currents (Chiswell 2000; Chiswell et al. 2015; Stevens et al. 2021). On the west coast, the northern and southern forms intergrade at New Plymouth and Wellington.

Specimens of the supposedly nominate form (see below) of *H. virginea* are generally (Raven and Bracegirdle 2010, 2020; Jones and Owen 2004; Geiger and Owen 2012) but not always (Owen and Kershaw 2014) depicted as having relatively large (to 75 mm; Powell 1979), predominantly green, and weakly-patterned shells that have weak radial wrinkles (Jones and Owen 2004; Geiger and Owen 2012; Owen and Kershaw 2014). Specimens with these characteristics range along the Wairarapa coast of the south-eastern North Island, and, with exceptions (see below), from Cape Campbell southward to Stewart Island. Shells from the southern coast of Wellington share many of these characteristics, but are smaller, seldom exceeding 40 mm (e.g., M.001982, M.001983).

Shells of the true nominate form from Marlborough Sounds are usually very small for the species, seldom exceeding 50 mm, and particularly strongly patterned (Figure 3C; Lakeman et al. 2021), approaching the *crispata* form. Nevertheless, shells from the Marlborough Sounds generally have fewer and weaker radial wrinkles than northern North Island shells (i.e., typical *crispata*). Available specimens from Pelorus Sound (M.129796) and Queen Charlotte Sound (M.134105), the type locality, do not exceed 30.4 mm in length (those populations reported as reaching 38 mm: Raven 2015). The specimen illustrated by Chemnitz (1788, p. 314, pl. 166, figs 1607, 1608) closely resembles Tory Channel specimens (Figure 3C). No specimens matching Chemnitz's illustration are currently available from Queen Charlotte Sound.

With one exception (41.2 mm), shells from two lots (6, M.013513 and 22, M.110505) from the J. Graham collection supposedly from off Oamaru (southeastern South Island), where the species is common (Graham 1962), strongly resemble Marlborough Sounds shells in having small size (smallest mature specimen: 21.7 mm), relatively fine sculpture, and colouration. Size biases in these and other lots may reflect collection from fish-guts and/or microhabitats.

Shells reputedly from the Snares Islands recorded by Owen and Kershaw (2014: 59; none illustrated) were described as the 'nominate' form with strong radial wrinkles, unlike shells from Stewart Island and Auckland Islands to the north and south. We suspect that they are mislocalised shells from the northeastern North Island. The sole confirmed Snares Island record (M.048738), a specimen collected at 7 metres depth off Seal Point by Department of Conservation staff and identified for databasing by one of us (BAM) is unaccountably no longer present in the national collection.

The *huttoni* form is restricted to the Auckland and Campbell Islands (Powell 1979; Jones and Owen 2004; Geiger and Owen 2012; Owen and Kershaw 2014) and most closely resembles specimens from the South Island and Stewart Island, differing principally in having coarser sculpture and darker, unpatterned shells. Auckland and Campbell Islands shells resemble each other in sculpture and colouration, although most Auckland Islands shells are considerably less elongate and more inflated than any specimens from Campbell Island. Given this pattern, it would not have been surprising had Auckland and Campbell Island populations formed distinct genetic clades. Nevertheless, paraphyly of the *huttoni* form with other *H. virginea* populations, as reported by Walton et al. (2022), was unexpected.

Chatham Islands samples of *H. virginea* (*morioria* form) closely resemble mainland shells from the Marlborough Sounds and the North Island, in colouration and pattern, and South Island shells (except Marlborough Sounds) in size at maturity (to 75 mm, Geiger and Owen 2012; average size ~ 48 mm, n=18). Presence of strong radial wrinkles is reported to be the primary distinguishing feature of Chatham Islands shells from mainland ones (Powell 1938; Geiger and Owen 2012), but wrinkle prominence varies significantly within both Chatham Islands (e.g., M.338235 and M.110420) and mainland populations, and there is complete intergradation between strongly and weakly wrinkled specimens. The coastal marine mollusc fauna of the Chatham Islands has low levels of regional endemism despite their distance from the mainland (Walton et al. 2018).

Some Chatham Islands shells also superficially resemble those from the highly distinctive Bounty Plateau populations (*stewartae* form) in having silvery internal nacre, in dorsal colouration (red or very dark brown), in shape (more rounded, and higher in profile) and in being relatively strongly sculptured (e.g., M. 338235 and M.338254). Nevertheless, there is no overlap in strength of dorsal sculpture between Chatham Islands (moderate) and Antipodes/Bounty (extreme) populations. Neither Chatham or Antipodes Islands sequences formed significantly divergent clades warranting continued maintenance of subspecies (Walton et al. 2022).

Absence of continuous suitable habitat connecting the southern islands of New Zealand, and possible ecophenotypic differences (Laferriere 2016) due to rougher and cooler seas around the more southerly islands (Kang et al. 2019) and/or differing algal (food and shelter) communities (Cho and Kim 2012) and

densities, may explain some of the discrete morphological differences between southern island populations of *H. virginea*.

Rafting of benthic organisms associated with the large, abundant, buoyant alga *Durvillaea antarctica* (Chamisso) Hariot, 1892 has resulted in connectivity over long distances between the South, Chatham, and New Zealand subantarctic islands by species with otherwise poor dispersal potential (Fraser et al. 2011; Nikula et al. 2011a, 2011b). Holdfasts have been reported to transport rocks of over seven kilograms in mass (Craw and Waters 2018; Garden and Smith 2011). Although *H. virginea* is not normally directly associated with kelp holdfasts, those taxa co-occur in high abundance, so infrequent rafting events are inevitable.

Discussion

Over its wide distribution, the endemic New Zealand abalone *Haliotis virginea* varies considerably in shell size, morphology, colour and colour pattern. This variation has long been viewed as having taxonomic significance, with up to five subspecies recognised (Jones and Owen 2004; Geiger and Owen 2012). Genetic data (Walton et al. 2022) does not support such a classification, with negligible genetic distances reported between some subspecies, and non-monophyly of others. Here, we extend these findings to include reinterpretation of shell characters, showing that many of the allegedly diagnostic features are inconsistent and intergrade among subspecies and forms. Consequentially, we do not recognise distinct subspecies within *H. virginea*.

Conversely, we show that populations from Manawatāwhi Three Kings Islands, hitherto referred to *H. virginea*, are genetically distinct (Walton et al. 2022) and morphologically separable. We describe these populations as a new species, *Haliotis pirimoana* n. sp. Whether *H. pirimoana* n. sp. now has a relictual distribution at Three Kings Islands or diverged there from *H. virginea* following a period of isolation is unknown.

Contemporary conditions in the ~40 km wide strait between Three Kings Islands and the North Island evidently present a strong barrier to the dispersal of many marine species. This barrier must have existed, at least intermittently, since the Miocene (Hayward and Moore 1987). The shallowest benthic connection between them is cut by the Karetu Trough, a channel over 200 m deep (Nelson 1982; Nelson et al. 1982, 1988; Nelson and Hancock 1984). This channel has, at least in part, a current-scoured sandy bottom, and the floor of the southern part of the strait is mostly worn, current swept detrital bryozoa and shell (Nelson 1982; Nelson et al. 1982). The strait supports far lower diversity and densities of living benthic marine invertebrates compared to the Three Kings Islands and the northern North Island (Nelson et al. 1982; comprehensive collections of Mollusca NMNZ). Neither the channel nor most of the floor of the strait is a suitable habitat for haliotids.

The occurrence of strong eastward-moving currents and upwelling (Stanton 1973; Stevens et al. 2021) at the Three Kings Islands has resulted in a highly productive marine region (Bradford and Roberts 1978) with noticeably cooler surface and shallow subsurface water temperatures (Garner 1959; Stanton 1973) than in nearby North Island coastal areas. Several shallow sublittoral marine species that are rare or patchily distributed off the northern North Island, and that are normally associated with cooler, southern parts of New Zealand, occur in high abundance at the Three Kings Islands (Fleming 1944; Hardy et al. 1987), such as the large brown kelp *Durvillaea antarctica*.

The shallow sublittoral fauna at the Three Kings Islands has extremely high regional endemism (Willan 1978; Marshall 1995, 1998a, 1998b; Marshall et al. 2018; Marshall and Marrow 2021). The drivers of high, localised levels of endemism at the Three Kings Islands remain unclear, but this phenomenon is no doubt influenced by successive periods of connectivity and isolation during glacial cycles since the Miocene. The strong upwelling may result in more stable water conditions during glacial cycles. Given the small size of the Three Kings region, its accessibility from mainland New Zealand, its proximity to major shipping routes, and the extreme degree of regional endemism, the region could benefit from addition of greater marine protection.

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Author contributions

KW, BAM, NJR, and HGS conceptualised the study; KW and BAM examined the specimens and addressed the

synonymies; KW drafted the manuscript; all authors contributed substantively to the writing and editing of the manuscript.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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