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The phylogeny and taxonomy of New Zealand *Notoacmea* and *Patelloida* species (Mollusca: Patellogastropoda: Lottiidae) inferred from DNA sequences

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Abstract

The systematics of *Notoacmea* Iredale, 1915 have been confused because of their highly variable shells. We used DNA sequences from a mitochondrial gene (COI) and a nuclear gene (ITS1) to define the species boundaries among New Zealand *Notoacmea* species, using the allied genus *Patelloida* Quoy & Gaimard, 1834 as outgroup. Phylogenetic trees of 195 individuals showed 14 well-supported, reciprocally monophyletic clades, which we treat as species: *N. badia* Oliver, 1926, *N. cellanoides* Oliver, 1926, *N. daedala* (Suter, 1907), *N. elongata* (Quoy & Gaimard, 1834), *N. parviconoidea* (Suter, 1907), *N. pileopsis* (Quoy & Gaimard, 1834), *N. scapha* (Suter, 1907), *N. scopulina* Oliver, 1926, *N. sturnus* (Hombron & Jacquinot, 1841), *N. subantarctica* Oliver, 1926, *Patelloida cortica* (Hutton, 1880) and three new *Notoacmea* species, *N. potae*, *N. rapida*, and *N. turbatrix*, which are described here. Of the above names, *N. daedala* and *N. subantarctica* are resurrected from synonymy. *Notoacmea helmsi* (E.A. Smith, 1894) and *N. virescens* Oliver, 1926 are interpreted as synonyms of *N. elongata*.

Key words: Gastropoda, limpet, new taxa, species boundaries, COI, ITS1, intertidal.

Introduction

Limpets are a diverse and ecologically important group of molluscs. They are found throughout the world's oceans, from tropical to polar regions, and from the deep-sea to well above the high tide line. The lottiid limpet genus *Notoacmea* Iredale, 1915 has long been considered to exhibit an antitropical distribution, with representative species from temperate waters of both the southern and northern Pacific (Kira 1961; Habe and Kosuge 1967; Keen 1971; Abbott 1974; Habe and Okutani 1975; Ponder and Creese 1980; Powell 1979). More recently, however, Lindberg (1986) transferred all the North American species to *Tectura* Gray, 1847, and Sasaki and Okutani (1993) erected a new genus, *Nipponacmea* Sasaki & Okutani, 1993, for the Japanese species. Nakano and Ozawa (2004) subsequently confirmed the monophyly of *Nipponacmea*, but restricted *Tectura* to one northeastern Atlantic species, *T. virginea* (Müller, 1776), and removed the American Pacific species to *Lottia* G.B. Sowerby I, 1834. As the result of these revisions, *Notoacmea* now consists solely of species from New Zealand and Australian waters. In New Zealand eight *Notoacmea* species and two subspecies are currently recognized (Powell 1979; Spencer *et al*. 2006); additionally two species and two subspecies have been treated as synonyms.

Historically, taxonomic studies of these limpets have been based on shell morphology and radular characters (e.g., Suter 1907; Oliver 1926; Powell 1973; Ponder and Creese 1980), but the highly variable shell morphology of limpets has led to taxonomic confusion and the failure to recognize species complexes (Sasaki 1999; Nakano and Spencer 2007). Molecular techniques have recently proved very useful in limpet systematics, both for estimating phylogenetic trees (e.g., Koufopanou *et al*. 1999; Nakano and Ozawa 2004; Kirkendale and Meyer 2004; Goldstien *et al*. 2006), as well as for clarifying species complexes that are difficult to distinguish on morphological characters alone (Simison and Lindberg 1999, 2003; Kirkendale and Meyer 2004; Nakano and Ozawa 2005). In the case of *Notoacmea*, Nakano and Ozawa (2007) showed the monophyly of the genus using three mitochondrial genes and Nakano and Spencer (2007) utilized both mitochondrial and nuclear genes to discover that there are five distinct species within the taxon *N. helmsi* as currently interpreted. The goal of the present study is to elucidate the species boundaries among the New Zealand species of *Notoacmea* using sequences from the mitochondrial cytochrome c oxidase subunit I gene (COI) and the nuclear internal transcribed spacer 1 (ITS1), and to rectify the nomenclature to reflect this phylogeny. The two genera dealt with in this paper are readily distinguished on radular characters; *Notoacmea* by lack of marginal teeth (radular formula 0-2-0-2-0), *Patelloida* Quoy & Gaimard, 1834 by presence of two marginal teeth on each side of each cross row (2-2-0-2-2).

Materials and Methods

Field observation and collection of samples

Table 1 lists the species and collection data (localities and habitats) of specimens used in this study, representing eight of the nine currently recognized New Zealand species and subspecies of *Notoacmea*, as well as one distinctive named form. In addition, a species of *Patelloida* was also collected to use as an outgroup. Sampling was carried out at 39 intertidal shore sites in mainland New Zealand between the Bay of Islands in the North Island and Southland in the South Island, as well as three additional sites from the subantarctic Auckland and Campbell Islands, with type localities of different species included if possible. All localities of individuals genetically analyzed are plotted on maps (Figs 1, 2). Living specimens were preserved in 70% ethanol and returned the laboratory where they were stored at 4 ˚C. In total, 145 individuals were newly sequenced, and combined with published sequences of 50 individuals from Nakano and Spencer (2007). All voucher specimens are deposited (database linked to GenBank numbers) in the Museum of New Zealand Te Papa Tongarewa (NMNZ). Table 1 also shows both the revised species name (the result of this study) along with the NMNZ lot numbers and GenBank accession numbers for all specimens genetically analyzed in this study.

TABLE 1. Species identification, localities, detailed habitats, NMNZ lot numbers and GenBank accession numbers for specimens genetically analyzed in this study. Type localities are indicated with *.

Species	Locality	Habitat	NMNZ Lot No.	GenBank Accession No.	
				COI	ITS1
N. badia	St. Clair, Dunedin*	middle shore, medium exposure tide pool	184115-A	AB287009	AB287128
	St. Clair, Dunedin*	middle shore, medium exposure tide pool	184115-B	AB287010	AB287129
	Oamaru	under rocks on lower shore, medium exposure	184116	AB287011	AB287130
	Oamaru	under rocks on lower shore, medium exposure	184117	AB287012	AB287131
	Katiki	under rocks on lower shore, medium exposure	184118	AB287013	AB287132
N. cellanoides	South of Cape Campbell	on rocks on upper shore	184119	AB287014	AB287133
	Kaikoura	on rocks on upper shore	184120	AB287015	AB287134
	Island Bay, Wellington	on rocks on upper shore	184121	AB287016	AB287135
	Castlepoint	on rocks on upper shore	184122	AB287017	AB287136
	Ocean Beach, Whangarei	on rocks on upper shore	184123	AB287018	AB287137
N. daedala	Vauxhall, Otago Harbour	under rocks on lower sheltered shore	184284	AB287037	AB287156
	Kaikoura	under rocks on lower shore, medium exposure	184290	AB287038	AB287157
	Titahi Bay	under rocks on lower shore, medium exposure	184289	AB287039	AB287158
	Mahia	under rocks on lower shore, medium exposure	184286	AB287040	AB287159
	Tatapouri, Gisborne	under rocks on lower shore, medium exposure	184287	AB287041	AB287160
	McLeod Bay, Whangarei Harbour	under rocks on middle sheltered shore	184288	AB287042	AB287161
	Halls Beach, Waitemata Harbour*	under rocks on middle sheltered shore	184285	AB287043	AB287162
N. elongata	Harington Point, Otago Harbour	under rocks on lower shore, medium exposure	184124-A	AB287019	AB287138
	Harington Point, Otago Harbour	under rocks on lower shore, medium exposure	184124-B	AB287020	AB287139
	Vauxhall, Otago Harbour	on rocks on lower sheltered shore	184125	AB287021	AB287140
	Bluff	under rocks on lower sheltered shore	184126	AB287022	AB287141
	Jackson Bay	under rocks on lower shore, medium exposure	184127	AB287023	AB287142
	Nelson Haven	under rocks on lower sheltered shore	184128	AB287024	AB287143
	French Pass*	under rocks on lower shore, medium exposure	184129	AB287025	AB287144
	Lyttelton Harbour, Christchurch	under rocks on lower shore, medium exposure	184130	AB287026	AB287145
	Port Levy	on rocks on lower sheltered shore	184131	AB287027	AB287146
	Pigeon Bay	under rocks on lower sheltered shore	184132	AB287028	AB287147
	Island Bay, Wellington	under rocks, exposed shore	184133	AB287029	AB287148
	Castlepoint	under rocks, exposed shore	184134	AB287030	AB287149
	Maketu	under rocks, medium exposure	184135	AB287031	AB287150
	North of Cape Egmont	under rocks on exposed shore	184136	AB287032	AB287151
	Cornwallis, Manukau Harbour	under rocks, sheltered shore	184137	AB287033	AB287152
	Tapeka Point, Bay of Islands	under rocks, medium exposure	184138	AB287034	AB287153
	Opononi, Hokianga Harbour	under rocks, sheltered shore	184139	AB287035	AB287154
	Halls Beach, Waitemata Harbour	under rocks on sheltered middle shore	184140-A	AB287036	AB287155

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TABLE 1 (contnued)

Species	Locality	Habitat	NMNZ Lot No.	GenBank Accession No. COI	ITS1
N. parviconoidea	Greymouth	on rocks, high intertidal, exposed shore	184145-A	AB284884	AB284938
	Greymouth	on rocks, high intertidal, exposed shore	184145-B	AB284885	AB284939
	Heathcote Estuary, Christchurch	on sheltered rocks in barnacle zone	184146-A	AB287044	AB287163
	Heathcote Estuary, Christchurch	on sheltered rocks in barnacle zone	184146-B	AB287045	AB287164
	Sumner*	on *Mytilus* on lower shore, semi-exposed	184147-A	AB287046	AB287165
	Sumner*	on *Mytilus* on lower shore, semi-exposed	184147-B	AB287047	AB287166
	Sumner*	in barnacle zone, semi-sheltered shore	184148-A	AB287048	AB287167
	Sumner*	in barnacle zone, semi-exposed shore	184148-B	AB287049	AB287168
	Oamaru	On rocks, middle intertidal, moderate exposure	184149-A	AB287050	AB287169
	Oamaru	On rocks, middle intertidal, moderate exposure	184149-B	AB287051	AB287170
	St. Clair, Dunedin	on medium-exposure rocks in barnacle zone	184150	AB287052	AB287171
	Jackson Bay	in barnacle zone, moderate exposure	184151	AB287053	AB287172
	Jackson Bay	on rocks, middle intertidal, moderate exposure	184152	AB287054	AB287266
	Tauranga Bay	on *Mytilus* on lower shore, moderate exposure	184153	AB287055	AB287173
	Tauranga Bay	in barnacle zone, moderate exposure	184154	AB287056	AB287174
	West Port	on *Mytilus*, on lower shore, moderate exposure	184155	AB287057	AB287175
	West Port	in barnacle zone, moderate exposure	184156	AB287058	AB287176
	The Blowhole, Kahurangi	in barnacle zone, middle intertidal, moderate exposure	184157	AB287059	AB287177
	South of Cape Campbell	on rocks, middle intertidal, moderate exposure	184158	AB287060	AB287178
	Kaikoura	in barnacle zone, moderate exposure	184159	AB287061	AB287179
	Lyttelton Harbour, Christchurch	on rocks, middle intertidal, moderate exposure	184160	AB287062	AB287180
	Little Akaloa Bay	on *Mytilus*, lower shore, semi-sheltered shore	184161	AB287063	AB287181
	Caroline Bay, Timaru	on rocks, medium exposure	184162	AB287064	AB287182
	Katiki	on rocks, exposed shore	184163	AB287065	AB287183
	Island Bay, Wellington	in barnacle zone, exposed shore	184164	AB287066	AB287184
	Titahi Bay	in barnacle zone, medium exposure	184165-A	AB287067	AB287185
	Titahi Bay	in barnacle zone medium exposure	184165-B	AB287068	AB287186
	Castlepoint	high intertidal, exposed shore	184166	AB287069	AB287187
	Mahia	in barnacle zone, medium exposure	184167	AB287070	AB287188
	Tatapouri, Gisborne	in barnacle zone, medium exposure	184168	AB287071	AB287189
	Sponge Bay	in barnacle zone medium exposure	184169	AB287072	AB287190
	Maketu, Bay of Plenty	in barnacle zone medium exposure	184170	AB287073	AB287191
	Maketu, Bay of Plenty	on *Mytilus* on lower shore, medium exposure	184171	AB287074	AB287192
	Whale Bay	in barnacle zone, medium exposure	184172	AB287075	AB287193
	North of Cape Egmont	in barnacle zone, exposed shore	184173	AB287076	AB287194
	Motutara	in barnacle zone, exposed shore	184174	AB287077	AB287195
	Motutara	on mussels, exposed shore	184175	AB287078	AB287196
	Ocean Beach, Whangarei	in barnacle zone, exposed shore	184176	AB287079	AB287197
	Ocean Beach, Whangarei	on mussels, exposed shore	184177	AB287080	AB287198
	Tapeka Point, Bay of Islands	in barnacle zone, moderate exposure	184178	AB287081	AB287199
	Opononi, Hokianga Harbour	in barnacle zone, sheltered shore	184179	AB287082	AB287200
	Maunganui Bluff	in barnacle zone, exposed shore	184180	AB287083	AB287201
	Maunganui Bluff	on mussels, exposed shore	184181	AB287084	AB287202

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TABLE 1 (contnued)

Species	Locality	Habitat	NMNZ Lot No.	GenBank Accession No. COI	GenBank Accession No. ITS1
N. pileopsis	French Pass*	high intertidal rocks, medium exposure	184183-A	AB287087	AB287205
	French Pass*	high intertidal rocks, medium exposure	184183-B	AB287088	AB287206
	Greymouth	high intertidal rocks, exposed shore	184184	AB287089	AB287207
	Tauranga Bay,	high intertidal rocks, medium exposure	184185	AB287090	AB287208
	Titahi Bay	high intertidal rocks, medium exposure	184186	AB287091	AB287209
	Mahia	high intertidal rocks, medium exposure	184187	AB287092	AB287210
	Maketu, Bay of Plenty	high intertidal rocks, medium exposure	184188	AB287093	AB287211
	Whale Bay	high intertidal rocks, exposed shore	184189	AB287094	AB287212
	North of Cape Egmont	high intertidal rocks, exposed shore	184190	AB287095	AB287213
	Motutara	high intertidal rocks, exposed shore	184191	AB287096	AB287214
	Tapeka Point, Bay of Islands	high intertidal rocks, medium exposure	184192	AB287097	AB287215
	Maunganui Blaff	high intertidal rocks, exposed shore	184193	AB287098	AB287216
N. potae n. sp.	Green Point, Bluff Harbour	on oyster shell, in mud	184207	AB284873	AB284927
	Motueka, Tasman Bay	on rocks, in mud	184208	AB284874	AB284928
	Parapara, Golden Bay	on rocks, in mud	184209	AB284875	AB284929
	Nelson Haven, Nelson*	on rocks, in mud	184210	AB284876	AB284930
	Heathcote Estuary, Christchurch	on rocks, in mud	184211	AB284877	AB284931
	Head of the Bay, Lytteleton Harbour	on rocks, in mud	184212	AB284878	AB284932
	Porirua Harbour	on shells, in mud	184213	AB284879	AB284933
	Maketu, Bay of Plenty	on rocks, in mud	184214	AB284880	AB284934
	Cornwallis, Manukau Harbour	on bivalve, in mud	184215	AB284881	AB284935
	Kerikeri Inlet, Bay of Islands	on rocks, in mud	184216	AB284882	AB284936
	Whanganui Inlet	on rocks, in mud	184217	AB284883	AB284937
N. rapida n. sp.	Napier	on shells, in mud	184204	AB284847	AB284901
	McLeod Bay, Whangarei Harbour	on bivalve, in mud	184205	AB284848	AB284902
	Halls Beach, Waitemata Harbour*	on bivalve, in mud	184206	AB284849	AB284903
	Halls Beach, Waitemata Harbour*	on bivalve, in mud	275439	AB284850	AB284904
N. scapha	Harwood, Otago Harbour*	on *Zostera*, in mud	184194-A	AB284836	AB284890
	Harwood, Otago Harbour*	on *Zostera*, in mud	184194-B	AB284837	AB284891
	Vauxhall, Otago Harbour	on *Austrovenus* shell, in mud	184195	AB284838	AB284892
	Harwood, Otago Harbour*	on bivalve, in mud	184196	AB284839	AB284893
	Whanganui Inlet	on shell, in mud	184197	AB284840	AB284894
	Whanganui Inlet	on *Zostera*, in mud	184198	AB284841	AB284895
	Porirua Harbour	on *Zostera*, in mud	184199	AB284842	AB284896
	Raglan Harbour	on *Zostera*, in mud	184200	AB284843	AB284897
	Raglan Harbour	on bivalve, in mud	184201	AB284844	AB284898
	Cornwallis, Manukau Harbour	on *Zostera*, in mud	184202	AB284845	AB284899
	Cornwallis, Manukau Harbour	on *Diloma*, in mud	184203	AB284846	AB284900
N. scopulina	Castlepoint	in barnacle zone, exposed shore	184218	AB287099	AB287217
	Mahia	in barnacle zone, moderate exposure	184219	AB287100	AB287218
	Sponge Bay	in barnacle zone, moderate exposure	184220	AB287101	AB287219
N. sturnus	St. Clair, Dunedin	on rocks, exposed shore	184221	AB287102	AB287220
	Stirling Point	high intertidal, exposed shore	184222	AB287103	AB287221
	Oamaru	high intertidal, moderate exposure	184223	AB287104	AB287222
	Auckland Island	on rocks, upper shore	190279	AB353900	AB358905

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TABLE 1 (contnued)

Species	Locality	Habitat	NMNZ Lot No.	GenBank Accession No. COI	GenBank Accession No. ITS1
N. subantarctica	Enderby Island	on rocks, upper shore	190276	AB353896	AB353901
	Campbell Island	on rocks, upper shore	190277-A	AB353897	AB353902
	Campbell Island	on rocks, upper shore	190277-B	AB353898	AB353903
	Auckland Island	on rocks, upper shore	190278	AB353899	AB353904
N. turbatrix n. sp.	Kaikoura*	on rocks, middle shore, moderate exposure	184224	AB284851	AB284905
	Kaikoura*	on rocks, middle shore, moderate exposure	275226	AB284852	AB284906
	The Blowhole, Kahurangi	tide pool, middle shore, moderate exposure	184225-A	AB284853	AB284907
	The Blowhole, Kahurangi	tide pool, middle shore, moderate exposure	184225-B	AB284854	AB284908
	Kaikoura	On *Cellana* limpets, moderate exposure	184227	AB284855	AB284909
	Oamaru	tide pool, middle shore, moderate exposure	184228	AB284856	AB284910
	Castlepoint	tide pool, exposed shore	184229	AB284857	AB284911
	Castlepoint	in barnacle zone, exposed shore	184230	AB284858	AB284912
	Mahia	tide pool, moderate exposure	184231-A	AB284859	AB284913
	Mahia	tide pool, moderate exposure	184231-B	AB284860	AB284914
	Tatapouri, Gisborne	tide pool, moderate exposure	184233	AB284861	AB284915
	Maketu, Bay of Plenty	on rocks, moderate exposure	184234	AB284862	AB284916
	Whale Bay	tide pool, exposed shore	184235	AB284863	AB284917
	Whale Bay	under rocks, exposed shore	184236	AB284864	AB284918
	North of Cape Egmont	tide pool, exposed shore	184237	AB284865	AB284919
	Motutara	tide pool, exposed shore	184238	AB284866	AB284920
	Motutara	on smooth rocks, exposed shore	184239	AB284867	AB284921
	Ocean Beach, Whangarei	on cat's eye shell, exposed shore	184240	AB284868	AB284922
	Tapeka Point, Bay of Islands	rocky middle-shore slope, moderate exposure	184241	AB284869	AB284923
	Opononi, Hokianga Harbour	on cat's eye shell, sheltered shore	184242	AB284870	AB284924
	Maunganui Bluff	tide pool, exposed shore	184243	AB284871	AB284925
	Maunganui Bluff	on smooth rocks, exposed shore	184244	AB284872	AB284926
P. corticata	St. Clair, Dunedin	amongst lower shore coralline algae	184245-A	AB287105	AB287223
	St. Clair, Dunedin	amongst lower shore coralline algae	184245-B	–	AB287224
	Lyttelton Harbour, Christchurch	high intertidal, moderate exposure	184246-A	AB287106	AB287225
	Lyttelton Harbour, Christchurch	high intertidal, moderate exposure	184246-B	–	AB287226
	Jackson Bay	amongst lower shore coralline algae, moderate exposure	184247-A	AB287107	AB287227
	Jackson Bay	amongst lower shore coralline algae, moderate exposure	184247-B	–	AB287228
	Oamaru	on rocks, middle intertidal, moderate exposure	184248	AB287108	AB287229
	St. Clair, Dunedin	on exposed rocks, lower shore	184249	AB287109	AB287230
	Stirling Point	on rocks, exposed shore	184250	AB287110	AB287231
	Stirling Point	amongst exposed lower shore coralline algae	184251	–	AB287232
	Tauranga Bay	amongst lower shore coralline algae, moderate exposure	184252	AB287111	AB287233
	Tauranga Bay	in barnacle zone, middle intertidal, moderate exposure	184253	AB287112	AB287234
	South of Cape Campbell	amongst lower shore, coralline algae, moderate exposure	184254	AB287113	AB287235
	Kaikoura	tide pool, middle intertidal, moderate exposure	184255	AB287114	AB287236
	Castlepoint	high intertidal, moderate exposure	184261	–	AB287242

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TABLE 1 (contnued)

Species	Locality	Habitat	NMNZ Lot No.	GenBank Accession No. COI	GenBank Accession No. ITS1
	Lyttelton Harbour, Christchurch	amongst lower shore, coralline algae, moderate exposure	184256	–	AB287237
	Little Akaloa Bay	amongst lower shore, coralline algae, moderate exposure	184257	–	AB287238
	Little Akaloa Bay	in barnacle zone, moderate exposure	184258	–	AB287239
	Katiki	amongst lower shore coralline algae, moderate exposure	184259	–	AB287240
	Island Bay, Wellington	amongst exposed lower shore coralline algae	184260	–	AB287241
	Castlepoint	tide pool, exposed shore	184262	–	AB287243
	Mahia	amongst lower shore coralline algae, moderate exposure	184263	–	AB287244
	Tatapouri, Gisborne	tide pool, moderate exposure	184264	–	AB287245
	Sponge Bay	in barnacle zone, moderate exposure	184265	AB287115	AB287246
	Sponge Bay	tide pool, moderate exposure	184266	–	AB287247
	Whale Bay	tide pool, exposed shore	184267	–	AB287248
	Whale Bay	in barnacle zone, exposed shore	184268	AB287116	AB287249
	Ruapuke	in barnacle zone, exposed shore	184269	AB287117	AB287250
	Ruapuke	in barnacle zone, exposed shore	184270	–	AB287251
	North of Cape Egmont	tide pool, exposed shore	184271	–	AB287252
	Motutara	in barnacle zone, exposed shore	184272-A	AB287118	AB287253
	Motutara	tide pool, exposed shore	184273	–	AB287254
	Ocean Beach, Whangarei	tide pool, exposed shore	184274	–	AB287255
	Ocean Beach, Whangarei	in barnacle zone, exposed shore	184275	AB287119	AB287256
	Tapeka Point, Bay of Islands	tide pool, moderate exposure	184276	AB287120	AB287257
	Opononi, Hokianga Harbour	in barnacle zone, sheltered shore	184277	–	AB287258
	Motutara	in barnacle zone, exposed shore	184272-B	AB287121	AB287259

Selection of Markers

We chose to sequence two genes, mitochondrial cytochrome *c* oxidase subunit I (COI) and the nuclear rRNA internal transcribed spacer I (ITS1). Mitochondrial COI and 16S are known to be informative for molluscan phylogeny (e.g. Williams *et al*. 2003; Williams and Reid 2004; Donald *et al.* 2005, Meyer *et al*. 2005, Nakano and Ozawa 2005). We selected COI as a representative of mitochondrial gene. We also chose the nuclear ITS1 gene to compare the results between mitochondrial and nuclear markers. ITS1 evolves faster than other ribosomal DNA (18S, 5.8S and 28S) and so is useful in estimating phylogenies of closely related taxa (Anderson and Adlard 1994; Armbruster *et al*. 2000). Both genes, therefore, could be informative about the phylogeny of a group with extensive variation in shell morphology such as *Notoacmea*.

DNA Extraction, PCR Amplification and DNA sequencing

The procedures described in Nakano and Spencer (2007) were used to extract DNA, amplify it using PCR and determine the sequence of the COI and ITS1 genes. All new sequences determined in this study have been deposited in DDBJ (see Table 1).

Phylogenetic analyses

As in Nakano and Spencer (2007), COI sequences were manually aligned using MacClade 4.03 (Maddison and Maddison 2002), with reference to the translated amino acid sequence. Third-codon positions of COI sequences were retained in all analyses. ITS1 sequence was aligned using ClustalX alignment program, run at default parameters (Thompson *et al*. 1997). Further manual adjustments to improve alignments were made by eye. All edited sequences used for phylogenetics analysis have been deposited in TREEBASE. The models of nucleotide substitution for the Bayesian analyses were selected using Modeltest (Posada and Crandall 1998), giving GTR + I + G for COI and TVM + I + G for ITS1, and these models were then used to calculate pairwise molecular distances among individuals. The partition-homogeneity test (Swofford 2002; the ILD test Farris *et al*. 1995) was performed to test whether the COI and ITS1 sequences contained the same phylogenetic signal and could thus be analysed as a single data-set. Taxa for which a gene region was unable to be sequenced were excluded from this last analysis.

Phylogenetic analyses were performed with PAUP* version 4b10 (Swofford 2002). Equally weighted maximum parsimony (MP) bootstrap values (Felsenstein 1985, 1988) were calculated from 1,000 replicates using a heuristic search (with 10 random addition sequence replicates and TBR branch-swapping). MrBayes v.3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003) was used for the Bayesian analysis.

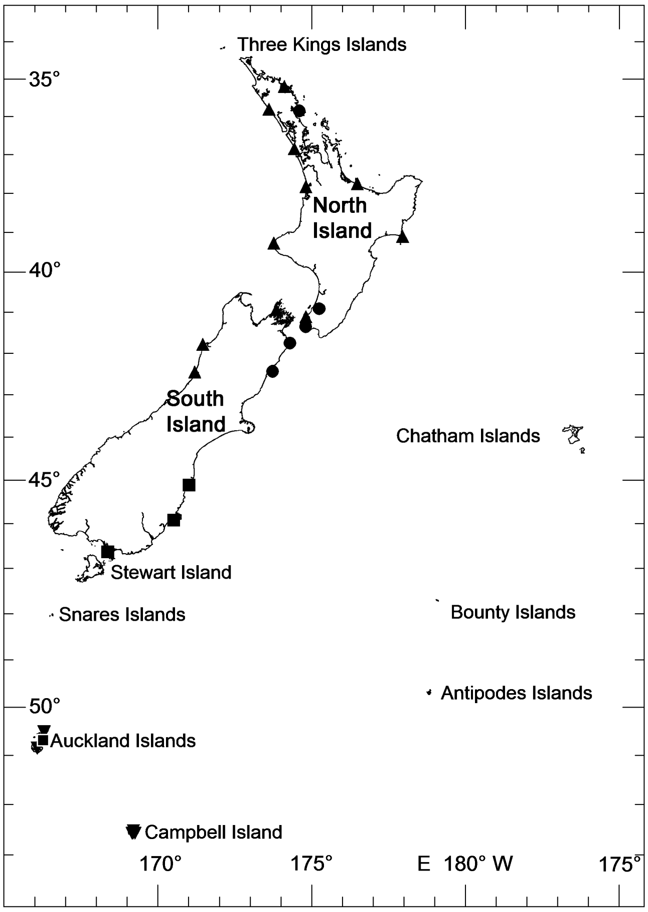

FIGURE 1. Map of New Zealand showing localities for sequenced specimens used in the present study: *Notoacmea cellanoides* Oliver, 1926 (●), *N. pileopsis* (Quoy & Gaimard, 1834) (▲), *N. sturnus* (Hombron & Jacquinot, 1841) (■), *N. subantarctica* Oliver, 1926 (▼). The range of most species will be greater than the locations shown on the map, because we may not have found all species present at some locations and we did not genetically analyze all individuals collected.

MrBayes was run with the following settings for the two partitions (i.e., genes): the maximum-likelihood model employed six substitution types (nst=6); rate variation across sites was modeled using a gamma distribution, with a proportion of the sites being invariant (rate=invgamma); the shape, proportion of invariable sites, state frequencies, and substitution rate parameters were estimated for each partition separately. The Markov-chain Monte-Carlo search was run twice with four chains for 5,000,000 generations, with trees being sampled every 100 generations and the first 5,000 trees (i.e., 500,000 generations) were discarded as burnin.

Results

Molecular data

PCR amplification of COI gave a product of approximately 660 bp, and subsequent sequencing of this product routinely yielded approximately 621 bp of readable sequence. The ITS1 product was usually 550–600 bp long, and sequencing routinely gave a 530–580 bp read. The partition-homogeneity test confirmed that there was no significant difference in the phylogenetic signal between the COI and ITS1 gene sequences (1,000 replicates, $P = 0.50$), and thus the two genes were subsequently concatenated and also analyzed as a single dataset. The COI data set of 621 characters, including the outgroup taxon (*Patelloida corticata*), had 329 variable and 324 parsimony-informative characters. The ITS1 data set of 429 characters had 230 variable and 206 parsimony-informative sites.

Molecular phylogeny

All the phylogenetic trees, whether based on COI, ITS1 or both genes concatenated (Figs 3, 4), gave 14 well-supported clades: MP bootstrap support was consistently 100% and the Bayesian analysis gave posterior probabilities of 0.99 to 1.00. There are some differences concerning interspecific relationships in the trees between COI and ITS1. Although ITS1 is valuable in separating closely related taxa, it may not be as useful for elucidating deeper relationships, a property manifested in the low bootstrap support and posterior probabilities of deep branches in the ITS1 tree. In the combined COI and ITS1 tree (Fig. 4), the interspecific relationships became clearer and supported with higher bootstrap and posterior probabilities than those of the separate gene trees.

Genetic distances between the 14 clades ranged from 3.94 to 48.3% (for COI), and 1.18 to 38.8% (for ITS1), whereas distances within species were from 0.00 to 2.96% (for COI) and 0.00 to 3.68% (for ITS1) (Table 2).

Systematics

The present study using molecular techniques revealed both polyphenism and cryptic species in New Zealand lottiids, and established species boundaries that were difficult to distinguish on morphological characters alone. The resultant trees showed a well-resolved phylogeny of New Zealand *Notoacmea*, and, as a consequence, it is necessary to revise the taxonomy of the genus. Nevertheless, further work is doubtless required, as anatomies of the different species remain to be compared, and precise species distributions have yet to be established. Moreover, the relationships with the Australian species (see Ponder and Creese 1980) are not clear, nor are the limits and relationships of *Notoacmea* resolved.

Family **Lottiidae** Gray, 1840

Genus ***Notoacmea*** Iredale, 1915

Notoacmea Iredale, 1915: 428. Type species (by original designation) *Patelloida pileopsis* Quoy & Gaimard, 1834;

Recent, New Zealand.

Parvacmea Iredale, 1915: 428. Type species (by original designation) *Acmaea daedala* Suter, 1907; Recent, New Zealand.

Conacmea Oliver, 1926: 577. Type species (by original designation) *Acmaea parviconoidea* Suter, 1907; Recent, New Zealand.

Thalassacmea Oliver, 1926: 579. Type species (by original designation) *Notoacmea badia* Oliver, 1926; Recent, New Zealand. New synonymy.

Subacmea Oliver, 1926: 580. Type species (by original designation) *Notoacmea scopulina* Oliver, 1926; Recent, New Zealand.

Remarks: The genetic distances among the types of the various subgenera recognized by Oliver (1926) and Powell (1979) do not suggest that these distinctions need be taxonomically recognized. Moreover, the assignment of various taxa to these subgenera on morphological grounds does not match the genetic phylogeny. Consequently, we view all of these names as synonyms of *Notoacmea*, adding *Thalassacmea* to the list of synonyms given in the morphological study of Ponder and Creese (1980). An evaluation of the relationships of *Notoacmea* within Lottiidae is beyond the scope of this study. Outside of New Zealand, *Notoacmea*, as currently recognized, occurs only in Australia, where the species were revised most recently by Ponder and Creese (1980).

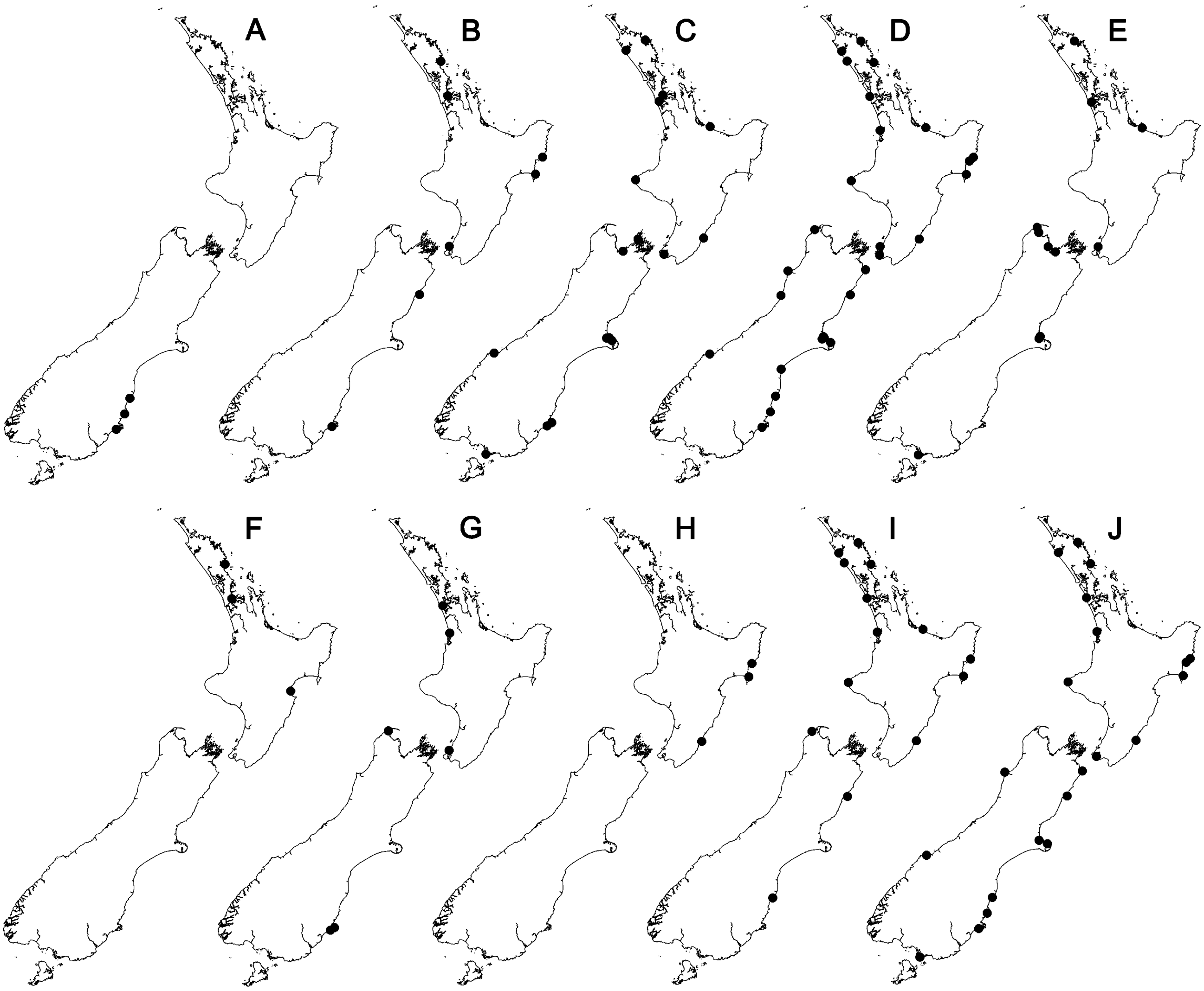

FIGURE 2. Maps of New Zealand showing localities for sequenced specimens used in the present study: **A**. *Notoacmea badia* Oliver, 1926. **B**. *N. daedala* (Suter, 1907). **C**. *N. elongata* (Quoy & Gaimard, 1834). **D**. *N. parviconoidea* (Suter, 1907). **E**. *N. potae* n. sp. **F**. *N. rapida* n. sp. **G**. *N. scapha* (Suter, 1907). **H**. *N. scopulina* Oliver, 1926. **I**. *N. turbatrix* n. sp. **J**. *Patelloida corticata* (Hutton, 1880). The range of most species will be greater than the locations shown on the map, because we may not have found all species present at some locations and we did not genetically analyze all individuals collected.

Notoacmea badia Oliver, 1926
Figs 2A, 5A–D, 9M

Notoacmea (*Thalassacmea*) *badia* Oliver, 1926: 579, pl. 99, fig. 7; Powell 1937: 67; Powell 1946: 68; Powell 1957: 86; Powell 1962: 78; Powell 1976: 82; Powell 1979: 49, figs 4–13.

Type material

Holotype NMNZ M.1562, St. Clair, Dunedin, New Zealand.

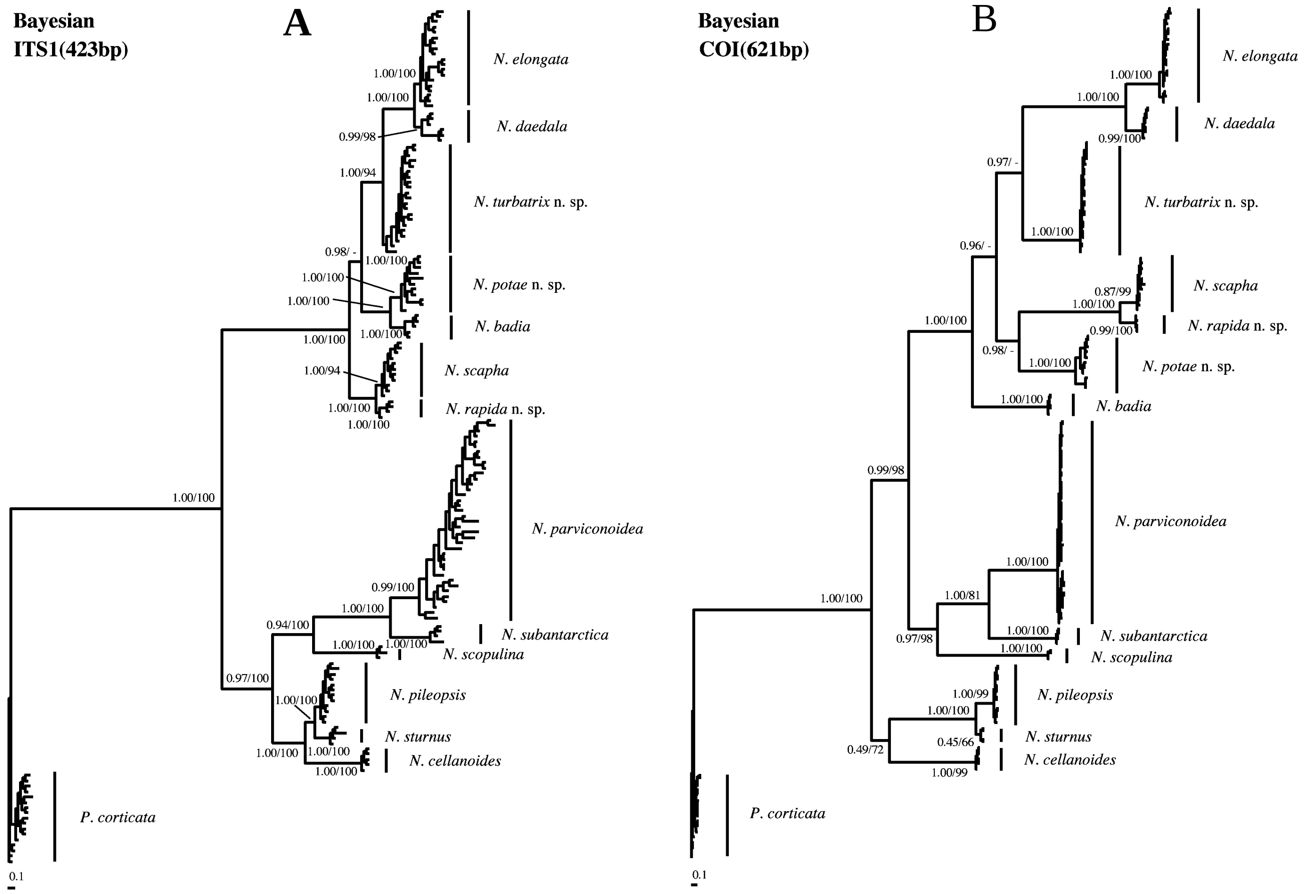

FIGURE 3. Bayesian phylograms, showing Bayesian posterior probabilities and equally weighted MP bootstrap values, generated from **A** ITS1 and **B** COI sequences.

Material examined

Type material (see above); Table 1.

Distribution

South-eastern South Island, from Oamaru to Balclutha and possibly Stewart Island (e.g. M.133836), New Zealand (Fig. 2A).

Habitat

Notoacmea badia lives in clean tide pools on exposed shores.

Remarks

According to the original description of this species, the shell is black and broadly depressed, with its apex usually eroded (Oliver 1926). Our molecular analysis includes topotypes, which are perfectly accordant with the holotype in shell morphology. In our study, a few individuals were genetically this species but looked like *N. subtilis* (Suter, 1907), which has an elongate oval, whitish shell with thin brown radial lines, similar to forms of *N. elongata* (Fig. 5C, D). Radially banded forms of *N. badia* could be distinguished from *N. elongata* by the lack of a netted pattern. Conversely, Nakano and Spencer (2007) found individuals with black shells similar to *N. badia* from a North Island locality (Castlepoint), but genetic analysis showed them to be a form of *N. turbatrix* n. sp. This species should not be confused with dark forms of *N. potae* n. sp. of similar size, which lack the dark irregular marking on the pale central area of the interior, and other *Notoacmaea* species. The largest specimen confirmed as *N. badia* in our study has a shell length of 7.35 mm. The holotype, however, is 10.5 mm long (Oliver 1926).

Notoacmea cellanoides Oliver, 1926
Figs 1, 6A–E, 9N

Notoacmea (*Notoacmea*) *pileopsis cellanoides* Oliver, 1926: 570, pl. 99, fig. 2; Powell 1937: 66; Powell 1946: 68; Powell 1957: 85; Powell 1962: 78; Powell 1976: 82; Powell 1979: 47, pl.16, figs 5, 6; Spencer *et al*. 2006.

Type material

Holotype NMNZ M.1560, Little Barrier Island, New Zealand (Fig. 6A).

Material examined

Type material (see above); Table 1.

Distribution

North Island and northern South Island as far south as Katiki Beach (41°44.5’S), New Zealand (Fig. 1).

FIGURE 4. Bayesian phylogram generated from the 1,050bp combined COI and ITS1 data, showing Bayesian posterior probabilities and equally weighted MP bootstrap values.

TABLE 2. Genetic distances: intraspecific (in bold on diagonals) and interspecific pairwise comparisons. Figures are the minimum and maximum of the sequence differences among different individuals calculated using the models selected by Modeltest: GTR + I + G for COI and TVM + I + G for ITS1.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
COI														
1. *N. elongata*	**0.00–1.30**													
2. *N. daedala*	9.91–10.5	**0.00–0.16**												
3. *N. turbatrix* n. sp.	29.7–31.1	27.9–28.2	**0.00–0.16**											
4. *N. potae* n. sp.	32.1–33.0	31.0–31.9	23.8–24.9	**0.00–2.96**										
5. *N. badia*	30.3–31.1	32.5–32.8	28.2–28.5	26.4–27.1	**0.00**									
6. *N. scapha*	34.7–35.4	34.0–34.8	28.6–29.6	27.0–27.8	29.9–30.4	**0.00–0.80**								
7. *N. rapida* n. sp.	35.6–36.2	34.1–34.9	27.2–27.5	27.1–28.1	28.9–29.4	5.70–6.38	**0.00–0.48**							
8. *N. parviconoidea*	37.0–37.8	37.0–37.4	36.4–36.7	34.9–35.3	32.4–32.8	35.8–36.1	36.0–36.4	**0.00–0.16**						
9. *N. scopulina*	41.7–42.5	40.3–41.0	40.0–40.6	34.9–35.3	36.0–36.3	39.6–40.5	39.3–40.2	32.5–33.0	**0.00–0.65**					
10. *N. pileopsis*	40.1–41.8	38.6–39.0	34.2–34.7	38.6–39.0	36.0–36.5	36.0–37.2	34.9–35.6	32.1–32.6	35.0–35.5	**0.00–0.48**				
11. *N. sturnus*	40.4–41.0	38.6–39.0	34.0–34.8	37.0–37.8	34.7–35.2	36.8–37.8	36.0–36.3	31.2–31.5	34.2–34.7	3.94–4.11	**0.00–0.32**			
12. *N. cellanoides*	43.6–44.4	42.1–43.4	36.0–36.6	37.5–38.4	39.5–39.8	36.0–37.0	37.0–37.7	37.9–38.2	32.3–32.5	29.8–30.0	28.5–28.8	**0.00–0.16**		
13. *N. subantarctica*	37.9–38.7	38.8–39.2	34.5–34.9	35.9–36.4	31.7–32.1	37.2–32.8	37.1–37.4	23.1–23.7	30.9–31.7	35.6–36.1	35.9–36.1	34.3–34.6	**0.00–0.16**	
14. *P. corticata*	46.7–47.8	45.7–46.5	45.8–46.5	45.8–46.3	47.7–48.3	44.1–46.0	45.5–46.5	45.4–46.0	44.7–46.4	42.2–43.0	41.4–42.4	40.4–40.9	40.6–41.4	**0.00–0.49**
ITS1														
1. *N. elongata*	**0.00–0.17**													
2. *N. daedala*	1.44–2.70	**0.00–1.44**												
3. *N. turbatrix* n. sp.	4.68–5.22	4.16–5.22	**0.00–1.43**											
4. *N. potae* n. sp.	7.31–8.40	6.24–8.12	5.68–6.98	**0.00–1.20**										
5. *N. badia*	6.77–7.60	5.70–7.32	5.16–6.20	2.17–3.39	**0.00–0.47**									
6. *N. scapha*	8.07–8.67	7.52–8.97	5.13–6.45	6.16–7.47	5.90–6.71	**0.00–0.24**								
7. *N. rapida* n. sp.	7.81–8.36	7.26–8.65	4.87–6.44	6.17–6.95	5.65–6.68	0.47–0.95	**0.00–0.47**							
8. *N. helmsi*	25.2–29.3	24.3–28.5	24.0–28.2	23.0–27.4	23.2–27.6	22.8–26.9	22.2–26.2	**0.00–3.68**						
9. *N. scopulina*	27.2–28.6	26.8–28.4	25.7–26.8	25.4–27.2	25.9–26.6	24.4–25.6	23.8–24.8	16.6–20.4	**0.00–0.47**					
10. *N. pileopsis*	21.0–21.4	20.3–21.1	19.5–20.5	20.8–21.7	20.4–20.7	19.2–19.6	18.9–19.2	15.3–19.6	12.1–13.2	**0.00–0.47**				
11. *N. sturnus*	22.2–22.5	21.4–22.2	20.6–21.6	21.1–22.1	20.7–21.0	19.9–20.3	19.6–19.9	15.7–20.1	12.7–13.2	1.18–1.66	**0.00–0.47**			
12. *N. cellanoides*	24.9–25.1	24.2–25.0	23.0–24.0	24.3–25.3	23.5–23.9	22.3–22.8	22.1–22.4	18.5–22.6	15.0–15.7	6.14–6.67	6.43–6.90	**0.00–0.47**		
13. *N. subantarctica*	24.9–25.3	25.4–26.3	24.1–25.1	23.1–24.2	24.6–25.0	23.9–24.7	23.3–23.9	7.02–11.2	13.1–14.5	15.9–16.9	16.2–16.7	15.3–15.8	**0.00–0.94**	
14. *P. corticata*	37.9–38.7	37.3–38.3	35.6–36.3	36.1–36.9	36.3–36.7	36.3–37.2	35.6–36.3	31.7–35.2	32.4–34.0	28.6–29.6	29.1–29.8	32.0–32.6	29.4–32.4	**0.00–0.96**


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FIGURE 5. Shells of *Notoacmea* species (* = sequenced voucher material). **A–D.** *Notoacmea badia* Oliver, 1926. A, B. St Clair, Dunedin, M.184115* (A, 7.35 × 6.00 mm; B, 9.45 × 7.85 mm). C. Oamaru, M.184116* (6.90 × 5.00 mm). D. Katiki Beach, S of Oamaru, M.184118* (7.90 × 5.75 mm). **E**–**I**. *Notoacmea daedala* (Suter, 1907). E. Auckland Harbour, lectotype, CM 2802 (7.05 × 5.55 mm). F. Titahi Bay, N of Wellington, M.184289* (7.50 × 5.00 mm). G. Mahia, M.184286* (5.15 × 3.70 mm). H. McLeod Bay, Whangarei Harbour, M.184288* (5.40 × 4.20 mm). I. Vauxhall, Otago Harbour, M.184284* (5.55 × 4.05 mm). **J–Y**. *Notoacmea elongata* (Quoy & Gaimard, 1834). J. French Pass, Marlborough Sounds, lectotype, MNHN 20782 (6.35 × 4.60 mm). K, L. Greymouth, lectotype of *Acmaea helmsi* E.A. Smith, 1894, BMNH 1893.5.27.22a (11.48 × 9.27 mm). M, N. Kekerengu, NE of Kaikoura, holotype of *Notoacmea virescens* Oliver, 1926, M.1561 (8.55 × 6.80 mm). O. New Brighton, Christchurch (juvenile from sample of adults that are indistinguishable from holotype of *N. virescens*), M.2249 (4.75 × 3.40 mm). P, Q. Fossil Point, N of Collingwood, M.71264 (12.30 × 9.55 mm). R, S. Bluff, M.184126* (8.80 × 6.35 mm). T. Castlepoint, M.184134* (9.05 × 7.25 mm). U. Tapeka Point, Bay of Islands, M.184138* (6.05 × 4.30 mm). V. Pigeon Bay, Banks Peninsula, M.184132* (8.30 × 6.65 mm). W. Lyttelton Harbour, Christchurch, M.184130* (5.50 × 4.20 mm). X, Y. Harrington Point, Otago Harbour, M.184124* (X, 8.25 × 6.25 mm; Y, 7.50 × 5.60 mm).

Habitat

Notoacmea cellanoides inhabits the high intertidal splash zone on exposed shores.

Remarks

Specimens used in our molecular analysis are perfectly accordant with the holotype in shell morphology. *Notoacmea cellanoides* can be found at the same localities as *N. pileopsis*, although it tends to be in more exposed situations and also lower down on the shore (sympatric but asyntopic). *Notoacmea cellanoides* attains similar size to *N. pileopsis* (length up to 24.6 mm), but is readily distinguishable by its prominent radial sculpture.

Notoacmea daedala (Suter, 1907)
Figs 2B, 5E–I, 9K

?*Acmaea flammea*.—Hutton 1883: 132; Hutton 1884: 373. Not Quoy & Gaimard, 1834. Probably in part = *N. elongata*.
Acmaea daedala Suter, 1907: 328, pl. 27, figs 30–32.
Notoacmea (*Parvacmea*) *daedala*.—Iredale 1915: 428, 430; Oliver 1926: 575; Powell 1937: 66, pl. 9, fig. 5; Powell 1946: 68, pl. 9, fig. 5; Powell 1962: 78, pl. 9, fig. 10; Powell 1976: 82, pl. 16, fig. 5; Powell 1979: 48. Probably in part = *N. elongata*.
Notoacmea elongata.—Ponder and Creese 1980: 192, pl. 3, figs 16–19; Spencer *et al*. 2006. In part of Quoy & Gaimard, 1834.

Type material

Lectotype (here selected, 7.05 × 5.55 mm; Figs 5E, 9K) CM 2802 and paralectotypes CM M2803 (5), NZGS TM 568 (1), Auckland Harbour, New Zealand.

Material examined

Type material (see above); Table 1.

Distribution

North and South Islands, New Zealand (Fig. 2B).

Habitat

Notoacmea daedala lives under boulders resting on clean sand, from intertidal flats to exposed shores.

Remarks

Until Ponder and Creese (1980) pointed out that the name *N. elongata* Quoy & Gaimard, 1834 applied to New Zealand animals, both *N. daedala* and *N. elongata* as here interpreted were known under the name *N. daedala*. All our phylogenetic trees, however, show two closely related, reciprocally monophyletic clades, with a mean genetic distance at the COI locus of more than 9.9%. Since these two clades are sympatric—indeed, we found individuals from both under a single rock at Halls Beach, Auckland (essentially topotypes of *N. daedala*)—and the clades for the mitochondrial COI and the nuclear ITS1 are identical, hybridization seems unlikely. Hence, we consider the two clades to be specifically distinct, even though we have been unable to separate them using shell shape and size, colour and colour pattern, or sculpture with the limited (sequenced) material at hand. The shells of both species may be either smooth or have radial rows of fine nodules. Since it seems impossible to tell from their shells, our association of the lectotypes of *N. daedala* and *N. elongata* with the sequenced specimens is purely pragmatic, to avoid having to rename both taxa. Further work will be required to ascertain if the species differ in details of internal or external soft anatomy, radula or micro-habitat. The largest specimen identified as *N. daedala* in our study has a shell length of 7.50 mm (Titahi Bay; Fig. 5F).

Notoacmea elongata (Quoy & Gaimard, 1834)
Figs 2C, 5J–Y, 9L

Patelloida elongata Quoy & Gaimard, 1834: 358, pl. 71, figs 12–14.
? *Acmaea flammea*.—Hutton 1883: 132; Hutton 1884: 373. Not Quoy & Gaimard, 1834. Probably in part = *N. daedala* (Suter, 1907).
Acmaea helmsi E.A. Smith, 1894: 58, pl. 7, figs 4–5; Suter 1907: 324; Suter 1913: 69, pl. 7, fig. 3. Probably in part = *N. potae* n. sp., *N. rapida* n. sp., *N. parviconoidea* (Suter, 1907) and *N. scapha* (Suter, 1907). New synonymy
Notoacmea (*Parvacmea*) *helmsi*.—Iredale 1915: 428, 430. Probably in part = *N. potae*, *N. rapida*, *N. parviconoidea* and *N. scapha*.
Notoacmea (*Parvacmea*) *daedala*.—Oliver 1926: 575; Powell 1937: 66; 1946: 68, pl. 9, fig. 5; Powell 1962: 78, pl. 9, fig. 5; Powell 1979: 48, fig. 4/6. Probably in part = *N. potae*, *N. rapida*, *N. parviconoidea* and *N. scapha*.
Notoacmea (*Parvacmea*) *helmsi*.—Oliver 1926: 576; Powell 1937: 66; Powell 1946: 68, pl. 9, fig. 7; Powell 1976: 82, pl. 16, fig. 7. Probably in part = *N. potae*, *N. rapida*, *N. parviconoidea* and *N. scapha*.
Notoacmea (*Parvacmea*) *virescens* Oliver, 1926: 577. pl. 99, fig. 4; Powell 1937: 66; Powell 1946: 68; Powell 1957: 86; Powell 1962: 78. New synonymy
Notoacmea (*Parvacmea*) *helmsi helmsi*.—Powell 1957: 86, pl. 9,

fig. 7; Powell 1962: 78, pl. 9, fig. 7. Probably in part = *N. potae*, *N. rapida*, *N. parviconoidea* and *N. scapha*.

Notoacmea elongata.—Ponder and Creese 1980: 192, pl. 3, figs 16–19; Spencer *et al*. 2006. In part = *N. daedala*.

NOT *Acmaea helmsi*.—Odhner 1924: 10 = *N. subantarctica* Oliver, 1926

NOT *Notoacmea* (*Parvacmea*) *helmsi*.—Powell 1979: 48, fig. 4/3, 4 = *N. scapha* (Suter, 1907).

NOT *Notoacmea helmsi*.—Nakano and Spencer 2007: 471, figs 4H, 5F = *N. parviconoidea*.

Type material

Patelloida elongata—lectotype (here selected, Figs 5J, 9L) MNHN 20782 and 3 paralectotypes MNHN 4941(3 MNHN). The type locality was originally given as "King George Sound", Australia, which is an error (Ponder and Creese 1980). Type locality here selected as French Pass, Marlborough Sounds, northern South Island, where the *Astrolabe* made landfall (Hombron and Jacquinot 1854).

Acmaea helmsi—lectotype (here selected, Fig. 5K, L) BMNH 1893.5.27.22a and 1 paralectotype BMNH 1893.5.27.22b, Greymouth, New Zealand.

Notoacmea virescens—holotype NMNZ M.1561 (Fig. 5M, N), Kekerengu, NE of Kaikoura, New Zealand.

Material examined

Type material (see above); Table 1.

Distribution

North and South Islands, New Zealand (Fig. 2C).

Habitat

Like *N. daedala*, *N. elongata* also lives under boulders from mud flats to exposed shores, sometimes even the very same boulders (see above).

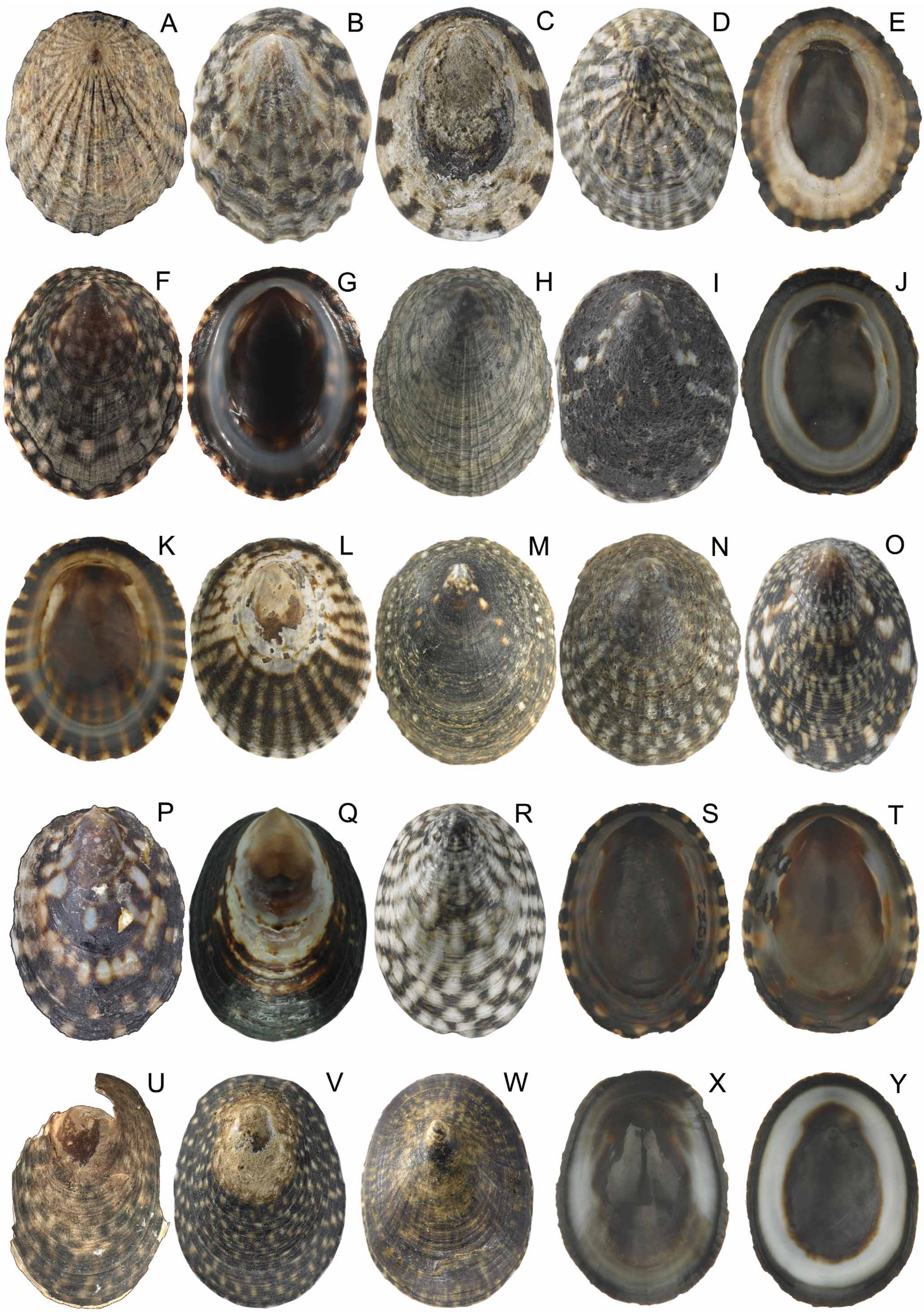
Remarks

Our molecular analysis includes topotypes of *N. elongata*, which are perfectly accordant with the holotype in shell morphology, but as indicated below *N. elongata* appears to be indistinguishable from *N. daedala* on shell morphology. The lectotype of *Acmaea helmsi* (Fig. 5K, L) is highly distinctive in combining rather large size (length 11.48 mm) with a colour pattern of thin, dark bands on a whitish ground. Regrettably we were unable to locate similar specimens at the type locality, Greymouth, during the present study. The supposition of Nakano and Spencer (2007) was that *N. helmsi* was based on a form of *N. parviconoidea*, but the lectotype of *N. helmsi* is unlike any confirmed specimen of *N. parviconoidea* in colour pattern. A clue to its affinities is suggested by closely similar specimens from Fossil Point (Fig. 5P, Q), on the same coast some 220 km to the north-east, some of which retain remnants of dark green tissue bordering the muscle scar (regrettably too old and degraded for genetic analysis) as in *N. elongata*, *N. daedala* and *N. badia*, but unlike *N. parviconoidea* in which it is predominantly cream or reddish brown. Our conclusion that it is not a form of (or rather, an earlier name for) *N. badia* is influenced primarily by the disjunct distributions (Figs 2A, D), but also by the absence of uniformly darkly pigmented shells resembling the holotype of *N. badia* from the west coast of the South Island.

The holotype of *N. virescens* resembles some specimens of *N. parviconoidea* in external shell colour pattern on the mid- to late teleoconch (Figs 5M, 7C), but we consider them unlikely to be conspecific because well preserved juveniles of specimens from a population that includes adults indistinguishable from the holotype of *N. virescens* (Fig. 5O), show splitting and converging of the radial bands on the early teleoconch and fine radial threads and nodules characteristic of *N. elongata* and *N. daedala*, but unknown in *N. parviconoidea*.

As stated above, we are unable to say if, or how, *N. daedala* and *N. elongata* may be distinguished using shell characteristics, and further work will be required to ascertain if the species differ in details of internal or external soft anatomy, body colour or colour pattern, radula or microhabitat. Our conclusion that *N. virescens* and *N. helmsi* are synonyms of *N. elongata* rather than *N. daedala* is thus somewhat arbitrarily based on closer similarity of shell colour and pattern to sequenced specimens deemed to represent the former (compare Figs 5M–O and 45K, L, R–T). It is noteworthy that no individuals currently classified as *N. helmsi* are that species as interpreted here (i.e., as a junior synonym of *N. elongata*). As shown by Nakano and Spencer (2007) these individuals fall into five distinct species: *N. scapha* (Suter, 1907), *N. parviconoidea* (Suter, 1907)—labelled by Nakano and Spencer as *N. helmsi*—, *N. potae* n. sp., *N. rapida* n. sp. and *N. turbatrix* n. sp.

FIGURE 6. Shells of *Notoacmea* species (* = sequenced voucher material). **A–E**. *Notoacmea cellanoides* Oliver, 1926. A. Little Barrier Island, holotype, M.1560 (17.4 × 14.2 mm). B. Ocean beach, Whangarei, M.184123* (10.65 × 8.15 mm). C. Kaikoura, M.184120* (16.0 × 12.0 mm). D, E. Bay E of Taupiri Island, Cape Maria van Diemen, M.174303* (24.6 × 20.0 mm). **F–N**. *Notoacmea pileopsis* (Quoy & Gaimard, 1834). F, G. French Pass, Marlborough, neotype, MNHN 20779* (14.7 × 11.7 mm). H. Titahi Bay, N of Wellington, M.184186* (15.5 × 12.3 mm). I, J. Maketu, SE of Tauranga, M.184188* (18.4 × 14.0 mm). K, L. Mahia, M.184187* (19.0 × 15.9 mm). M. N of Cape Egmont Lighthouse, M.184190* (28.0 × 22.5 mm). N. Maunganui Bluff, NW of Dargaville, M.184193* (18.3 ×14.0 mm). **O–T**. *Notoacmea sturnus* (Hombron & Jacquinot, 1841). O. Thule Bay, Paterson Inlet, Stewart Island, M.19767 (18.2 × 13.5). P. Southern South Island or Stewart Island, lectotype of *Patella cantharus* Reeve, 1855, BMNH 19750615a (15.5 × 11.7 mm). Q. Auckland Islands, lectotype of *Patelloides antarctica* Hombron & Jacquinot, 1841, MNHN 20781 (31.3 × 23.8 mm). R, S. Leask's Bay, Stewart Island, neotype of *Patella sturnus* Hombron & Jacquinot, 1841, MNHN 20780 (20.0 ×14.3 mm). T. Warrington, N of Dunedin, M.174301* (15.0 × 12.0 mm). **U–Y**. *Notoacmea subantarctica* Oliver, 1926. U. Campbell Island, holotype, CM M12834 (8.60 × 5.80 mm). V, X. Hanfield Inlet, Auckland Islands, M.8348 (13.5 × 10.0 mm). W, Y. Perseverance Harbour, Campbell Island, M.47423 (17.8 × 13.0 mm).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The largest specimen identified as *N. elongata* in our study has a shell length of 9.05 mm (Castlepoint; Fig. 5T), but assuming *N. helmsi* is indeed a junior synonym, it attains considerably larger size (lectotype 11.48 mm long).

Notoacmea parviconoidea (Suter, 1907)
Figs 2D, 7A–L, 9R, S

Acmaea parviconoidea Suter, 1907: 321, pl. 27, figs 22–25; Suter 1913: 69, pl. 5, fig. 13.
Acmaea parviconoidea var. *nigrostella* Suter, 1907: 322, pl. 27, figs 27–29. In part: paralectotypes and fig. 26 = *Asteracmea suteri* (Iredale, 1915). New synonymy.
Notoacmea parviconoidea.—Iredale 1915: 430.
Notoacmea parviconoidea nigrostella.—Iredale 1915: 430.
Notoacmea (*Conacmea*) *parviconoidea*.—Oliver 1926: 577; Powell 1937: 67, pl. 9, fig. 6; Powell 1946: 68, pl. 9, fig. 6; Powell 1957: 86, pl. 9, fig. 6; Powell 1962: 78, pl. 9, fig. 6; Powell 1979: 48, fig. 4/8,9; Spencer *et al*. 2006.
Notoacmea helmsi.—Nakano and Spencer 2007: 471, figs 4H, 5F (not E.A. Smith, 1894).

Type material

Acmaea parviconoidea—lectotype (here selected, Figs 7A, 9R) CM2804, paralectotypes CM M2805 (11), Sumner, New Zealand.

Acmaea parviconoidea nigrostella—lectotype (Boreham 1959: 24, Suter 1907, figs 27–29; Figs 7B, 9S) NZGS TM 572, Titahi Bay, N of Wellington, New Zealand. The paralectotypes (14, NZGS TM573–582; 11, M.70265) are the lottiid *Asteracmea suteri* (Iredale, 1915).

Material examined

Type material (see above); Table 1.

Distribution

North and South Islands, New Zealand (Fig. 2D).

Habitat

Notoacmea parviconoidea occurs on exposed coasts on rocks from the low tide level, among the mytilids *Mytilus galloprovincialis* Lamarck, 1819 and *Perna canaliculus* (Gmelin, 1791) to the mid-tidal barnacle zone and above.

Remarks

Specimens we collected from the type localities of *N. parviconoidea* and *N. parviconoidea nigrostella* correspond well to their type material in shell characteristics, and are genetically identical. Hence, we consider them to be synonyms.

The shell is remarkably variable in height and size, as well as markings. Those found among *P. canaliculus*, for example, have a highly conical dark brown to black shell, whereas those from vertical rocks in the high tide zone are depressed and usually eroded, with radial markings on the edge of the shell.

Compared with other *Notoacmea* species occurring on non-estuarine shores, *N. parviconoidea* is characterised by the combination of small size (maximum length of sequenced specimens 11.3 mm) and the typical exterior colour pattern of dark, solid, marginal rays, often with the addition of an interior calligraphy-like pattern. The tissue bordering the muscle scar is cream or brown or rather than green as in the similar coastal species *N. daedala*, *N. elongata* and *N. turbatrix*.

Notoacmea pileopsis (Quoy & Gaimard, 1834)
Figs 1, 6F–N, 9O

Patelloida pileopsis Quoy & Gaimard, 1834: 359, pl. 71, figs 25–27.
Lottia pileopsis.—Gray 1843: 240.
Tectura pileopsis.—Hutton 1873: 43; Hutton 1878: 36.
Acmaea pileopsis.—Hutton 1880: 88; Suter 1907: 319; Suter 1909: 5; Suter 1913: 71, pl. 7, fig. 4; Odhner 1924: 10. In part = *N. sturnus* (Hombron & Jacquinot, 1841) and *N. subantarctica* Oliver, 1926.
Acmaea (*Collisella*) *pileopsis*.—Hutton 1884: 373. In part = *N. sturnus*.
Acmaea septiformis.—Suter 1907: 318; Suter 1909: 5; Suter, 1913: 72. Not Quoy & Gaimard, 1834; in part = *N. sturnus* and *N. subantarctica*.
Notoacmea pileopsis.—Iredale 1915: 428, 429. In part = *N. sturnus*.
Notoacmea (*Notoacmea*) *pileopsis pileopsis*.—Oliver 1926: 568; Powell 1937: 66, pl. 9, fig. 4; Powell 1946: 68, pl. 9, fig. 4; Powell 1957: 85, pl. 9, fig. 4; Powell 1962: 78, pl. 9, fig. 4; Powell 1976: 82, pl. 16, fig. 4; Powell 1979: 47, pl.16, figs 1, 2; Spencer *et al*. 2006.

FIGURE 7. Shells of *Notoacmea* species (* = sequenced voucher material). **A–L**. *Notoacmea parviconoidea* (Suter, 1907). A. Sumner, Christchurch, lectotype of *Acmaea parviconoidea*, CM2804 (5.85 × 4.85 mm). B. Titahi Bay, N of Wellington, lectotype of *Acmaea parviconoidea nigrostella* Suter, 1907, NZGS TM 572 (9.80 × 7.10 mm). C–E. Greymouth, M.184145* (C, D, 11.0 × 8.50 mm; E, 10.75 × 8.50 mm). F, G. Jackson Bay, Southland, M.184152* (7.50 × 5.50 mm). H, I. Oamaru, M.184149* (H, 11.30 × 8.40 mm; I, 7.30 × 5.50 mm). J. Motutara, W of Auckland, M.184175* (6.30 × 4.45 mm). K. Kaikoura, M.184159* (6.50 × 5.00 mm). L. Tauranga Bay, W of Westport, M.184155* (5.35 × 4.30 mm). **M–S**. *Notoacmea potae* n. sp. M, N. Nelson Haven, Nelson, holotype, M.184210* (8.80 × 7.41 mm). O. Green Point, Bluff Harbour, M.184207* (5.85 × 4.50 mm). P. Kerikeri Inlet, Bay of Islands, M.184216* (8.80 × 7.55 mm). Q. Porirua Harbour, N of Wellington, M.184213* (8.20 × 6.90 mm). R. Heathcote Estuary, Christchurch, M.184211* (9.85 × 8.35 mm). S. Whanganui Inlet, W of Collingwood, M.184217* (3.91 × 2.78 mm). **T–X**. *Notoacmea rapida* n. sp. T, U. Halls Beach, Northcote, Waitemata Harbour, holotype, M.184206* (4.42 × 3.39 mm). V. McLeod Bay, Whangarei Harbour, M.184205* (6.30 × 5.00 mm). W. Halls Beach, paratype, M.274539* (6.80 × 5.20 mm). X. Napier, M.184204* (8.00 × 6.80 mm).


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Type material

Original material apparently no longer extant (not at MNHN, V. Héros, 29 Jun. 2007); neotype (here selected, 14.7 × 11.7 mm; Fig. 6F, G) MNHN 20779, French Pass, Marlborough, New Zealand, on high intertidal rocks, T. Nakano & J. Irwin, 6 Aug. 2006.

Material examined

Type material (see above); Table 1.

Distribution

Three Kings Islands, North Island, and Marlborough, northern South Island (34°09'S–41°11'S), New Zealand (Fig. 1).

Habitat

Notoacmea pileopsis inhabits the high intertidal zone to splash zone on exposed shores.

Remarks

Three subspecies are currently recognized within *N. pileopsis*: *N. p. pileopsis, N. p. sturnus* and *N. p. cellanoides* (Powell 1979; Spencer *et al*. 2006), including a '*subantarctica* form' of *N. pileopsis sturnus* (Powell 1979), but our results show that they are morphologically and genetically distinct from each other. *Notoacmea pileopsis* and *N. cellanoides* are sympatric (asyntopic), *N. pileopsis* and *N. sturnus* have closely adjacent and non-overlapping distributional limits (allopatric), and *N. sturnus* and *N. subantarctica* are sympatric at the Auckland Islands. Consequently, we treat these taxa as specifically distinct.

Among *Notoacmea* species, *N. pileopsis* is distinctive in the combination of large shell (length up to 32 mm) internally with dark spatula and typically solid, dark peripheral band.

Notoacmea potae n. sp.
Figs 2E, 7M–S, 9V, 10A, B

Notoacmea helmsi of authors in part—includes *N. scapha* (Suter, 1907) and *N. rapida* n. sp.
Notoacmea sp. C Nakano & Spencer, 2007: 472, figs 4G, 5E.

Type material

Holotype NMNZ M.184210, Nelson Haven, Nelson, New Zealand, T. Nakano & J. Irwin, 6 Aug. 2006 (8.80 × 7.41 mm; Figs 7M, N, 9V, 10C, D).

Material examined

Type material (see above); Table 1.

Description

Shell (holotype) 8.80 mm long, apex at about anterior sixth, height 40% of length, rather thin. Anterior slope slightly concave, lateral and posterior slopes broadly convex, aperture broadly and evenly ovate. Dull cream with brown radial colour pattern: at first narrow, divaricating and converging bands, then transforming to broader and darker bands after about 6.5 mm shell length. Exterior with fine radial threads.

Animal: Dorsal surface of mantle fringe green, a thin, darker green median line and another bordering shell muscle, edge white. Head-foot cream.

Radula: First and Second lateral teeth long and pointed. Third lateral teeth reduced, rounded triangular, separated from second lateral teeth except at bases.

Distribution

North and South Islands, New Zealand (Fig. 2E).

Habitat

Notoacmea potae n. sp. is commonly found on rocks in sheltered inlets, but also attached to dead bivalve shells.

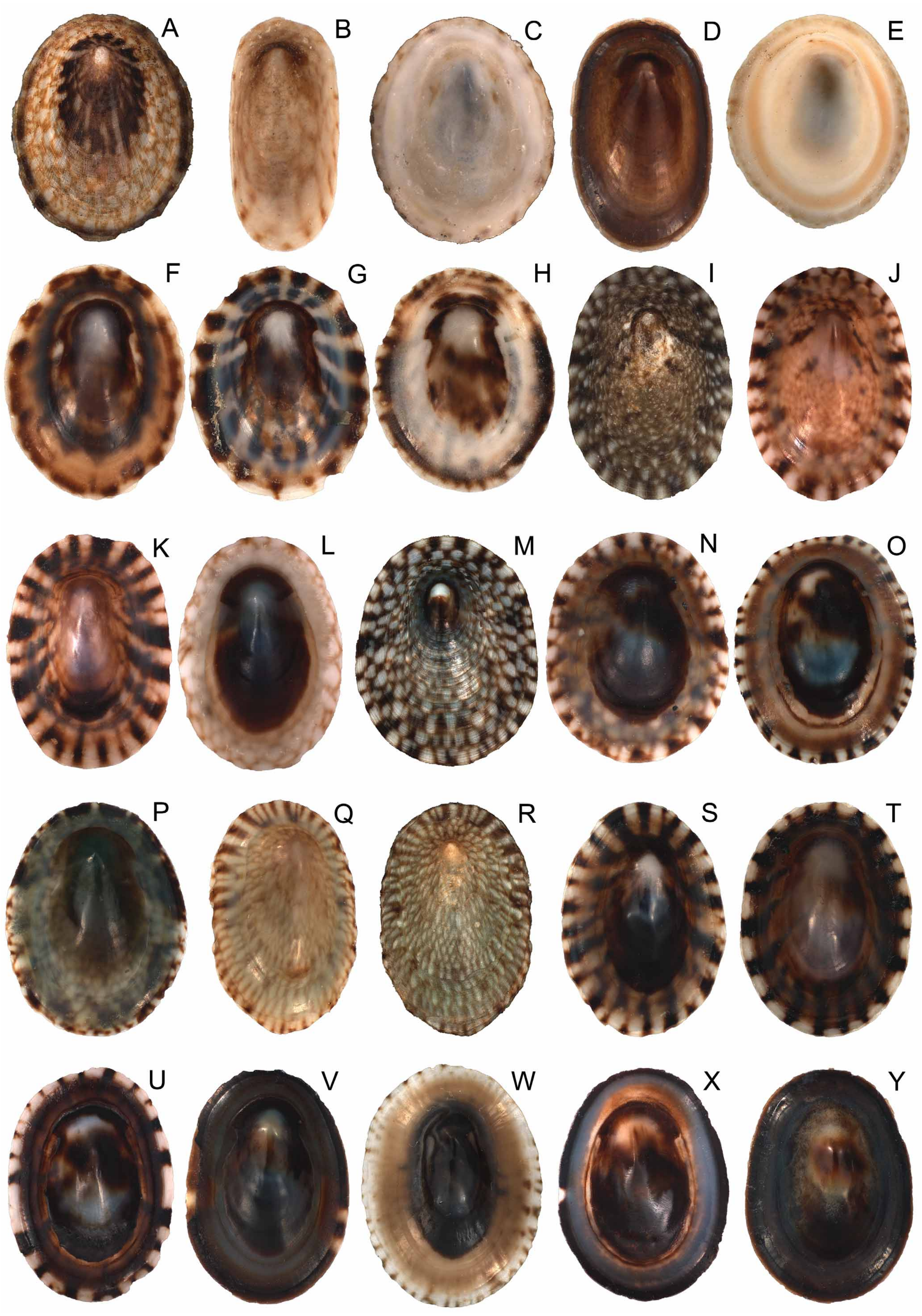
Remarks

The exterior is usually eroded, but the interior surface shows a variable pattern of divaricating and converging radial bands that transform to darker and broader maculations or short radial bands bordering the periphery. The degree of pigmentation of the spatula is variable, and may be dark brown and in stark contrast to the paler outer ground, or entirely absent. *Notoacmea potae* n. sp. frequently attains larger size than *N. scapha* and *N. rapida* n. sp. (length up to 11.6 mm, versus 9.10 and 8.00 mm respectively), which commonly occur with it on intertidal mudflats. Comparing specimens from the Heathcote Estuary, Christchurch (supported by sequences), the animal of *N. potae* n. sp. differs from that of *N. scapha* in that the dorsal surface of the mantle fringe is uniform dark green instead of white or brown at the edge bounded dorsally by a green band. This species was first noted as distinct by Nakano and Spencer (2007).

Etymology

Cap (Maori).

FIGURE 8. Shells of *Notoacmea* species (* = sequenced voucher material). **A–H**. *Notoacmea scapha* (Suter, 1907). A. Heathcote Estuary, Christchurch, M.274266* (6.20 × 4.95 mm). B. Whanganui Inlet, W of Collingwood, M.184198* (3.00 × 1.40 mm). C. Heathcote Estuary, lectotype of *Acmaea parviconoidea leucoma* Suter, 1907, NZGS TM 583 (6.50 × 5.32 mm). D. Cornwallis, Manukau Harbour, M.184202* (3.10 × 1.90 mm). E. Whanganui Inlet, W of Collingwood, M.184197* (9.10 × 7.80 mm). F. Harwood, Otago Harbour, M.184196* (5.70 × 4.40 mm). G. Vauxhall, Otago Harbour, M.184195* (6.25 ×4.80 mm). H. Raglan Harbour, M.184201* (6.35 × 5.15 mm). **I–Y**. *Notoacmea turbatrix* n. sp. I, J. Kaikoura, holotype, M.184224* (6.95 × 4.85 mm). K, Kaikoura, paratype, M.275226* (4.95 × 3.50 mm). L. Maketu, SE of Tauranga, M.184234* (5.30 × 3.70 mm). M, N. Motutara, W of Auckland, M.184239* (7.11 × 5.65 mm). O. Maunganui Bluff, NW of Dargaville, M.184243* (7.80 × 6.20 mm). P. Maunganui Bluff, M.184244* (7.19 ×5.58 mm). Q, R. Whale Bay, SW of Raglan, M.184236* (4.95 × 3.20 mm). S. Whale Bay, M.184235* (6.02 × 4.27 mm). T. Kaikoura, M.184227* (6.77 × 4.89 mm). U. Blowhole, Patura River mouth, W of Collingwood, M.184225* (7.45 × 5.20 mm). V, X. Oamaru, M.184228* (5.42 × 3.80 mm). W. Mahia, M.184231* (8.78 × 6.52 mm). Y. Castlepoint, M.184229* (5.60 × 4.03 mm).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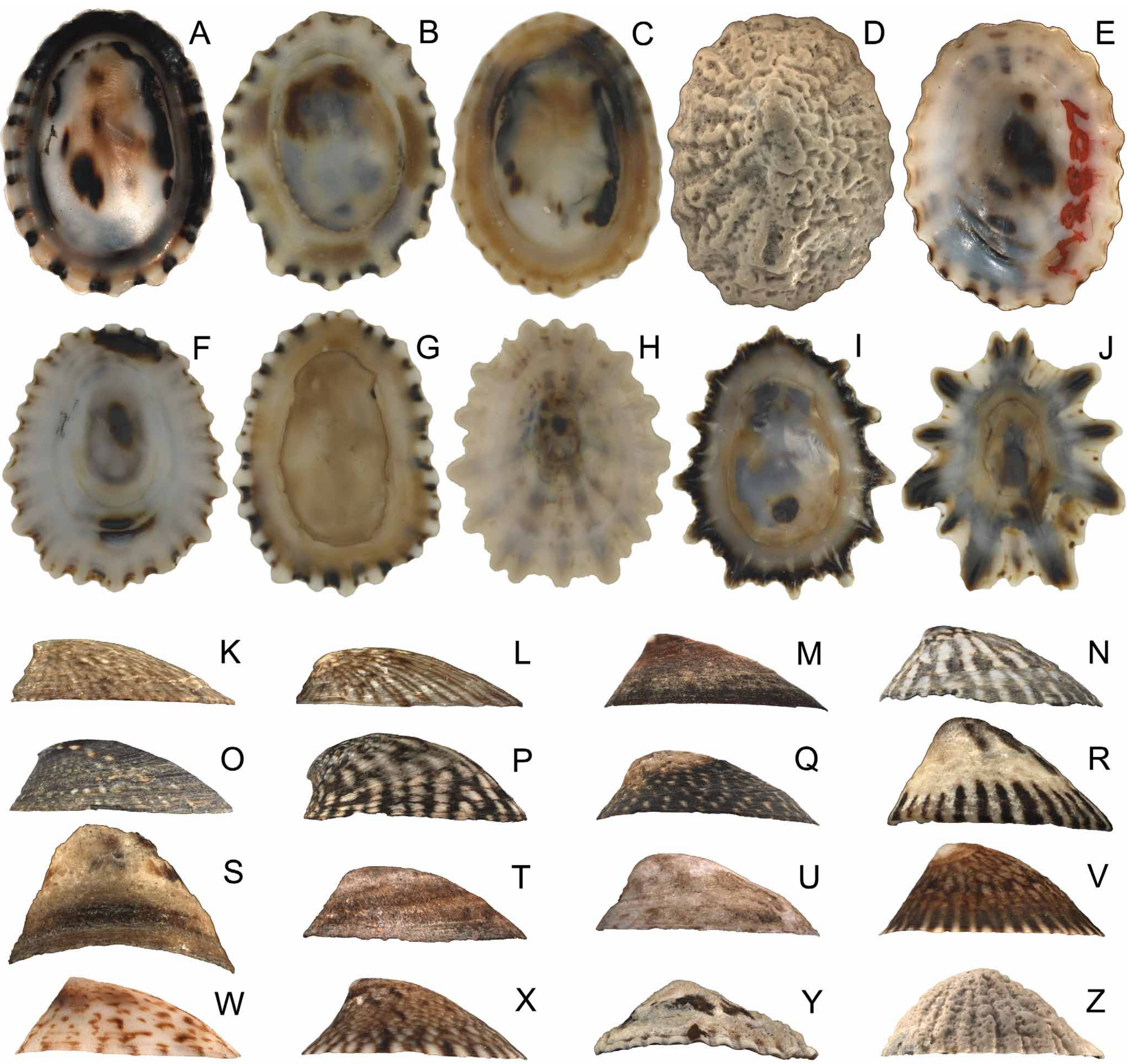

FIGURE 9. Shells of *Notoacmea* and *Patelloida* species (* = sequenced voucher material). **A, B, Y**. *Notoacmea scopulina* Oliver, 1926. A. Sponge Bay, Gisborne, M.184220* (11.4 × 8.80 mm). B, Y. Mahia, M.184219* (8.95 × 6.50 mm). **C–J, Z**. *Patelloida corticata* (Hutton, 1880). C. Shag Point, S of Oamaru, M.17414 (14.2 × 11.0 mm). D, E. Dunedin, syntype, CM M2807 (13.7 × 10.2 mm). F, Z. St Clair, Dunedin, M.184245* (15.5 × 12.7 mm). G. Ocean Beach, Whangarei, M.184275* (12.0 × 8.70 mm). H. Ocean Beach, M.184274* (16.0 × 13.4 mm). I. Castlepoint, M.184261* (18.2 × 14.5 mm). J. Mahia, M.184263* (13.0 × 11.2 mm). **K**. *Notoacmea daedala* (Suter, 1907), Auckland Harbour, lectotype, CM 2802 (7.05 × 2.05 mm). **L**. *Notoacmea elongata* (Quoy & Gaimard, 1834), lectotype, French Pass, Marlborough Sounds, MNHN (6.35 × 1.50 mm). **M**. *Notoacmea badia* Oliver, 1926, St Clair, Dunedin, M.174295* (7.20 × 2.40 mm). **N**. *Notoacmea cellanoides* Oliver, 1926, bay E of Taupiri Island, Cape Maria van Diemen, M.174303* (24.6 × 8.0 mm). **O**. *Notoacmea pileopsis* (Quoy & Gaimard, 1834), N of Cape Egmont lighthouse, M.184190* (28.0 ×9.0 mm). **P**. *Notoacmea sturnus* (Hombron & Jacquinot, 1841), Leask's Bay, Stewart Island, neotype, MNHN (20.0 × 7.7 mm). **Q**. *Notoacmea subantarctica* Oliver, 1926, Hanfield Inlet, Auckland Islands, M.8348 (13.5 × 4.4 mm). **R, S**. *Notoacmea parviconoidea* (Suter, 1907). R. Sumner, Christchurch, lectotype of *Acmaea parviconoidea*, CM2804 (5.85 × 3.80 mm). S. Titahi Bay, N of Wellington, lectotype of *Acmaea parviconoidea nigrostella* Suter, 1907, NZGS TM 572 (9.80 × 4.80 mm). **T, U.** *Notoacmea scapha* (Suter, 1907). T. Dunedin, lectotype, NZGS TM 585 (4.02 × 1.40 mm). U. Heathcote Estuary, Christchurch, lectotype of *Acmaea parviconoidea leucoma* Suter, 1907, NZGS TM 583 (6.50 × 2.35 mm). **V**. *Notoacmea potae* n. sp., Nelson Haven, Nelson, holotype, M.184210* (8.80 × 3.45 mm). **W**. *Notoacmea rapida* n. sp., Halls Beach, Northcote, Waitemata Harbour, holotype, M.184206* (4.42 × 1.50 mm). **X**. *Notoacmea turbatrix* n. sp., Kaikoura, holotype, M.184224* (6.95 × 2.40 mm).

Notoacmea rapida n. sp.

Figs 2F, 7T–X, 9W, 10C, D

?*Notoacmea helmsi* of authors in part.
Notoacmea sp. A Nakano & Spencer, 2007: 472, figs 4C, 5C.

Type material

Holotype NMNZ M.184206 (4.42 × 3.39 mm; Figs 7T, U, 9W, 10A, B) and paratype M.274539 (6.80 × 5.20 mm; Fig. 7W), Halls Beach, Waitemata Harbour, Auckland, New Zealand, H.G. Spencer & T. Nakano, 8 Sep. 2006.

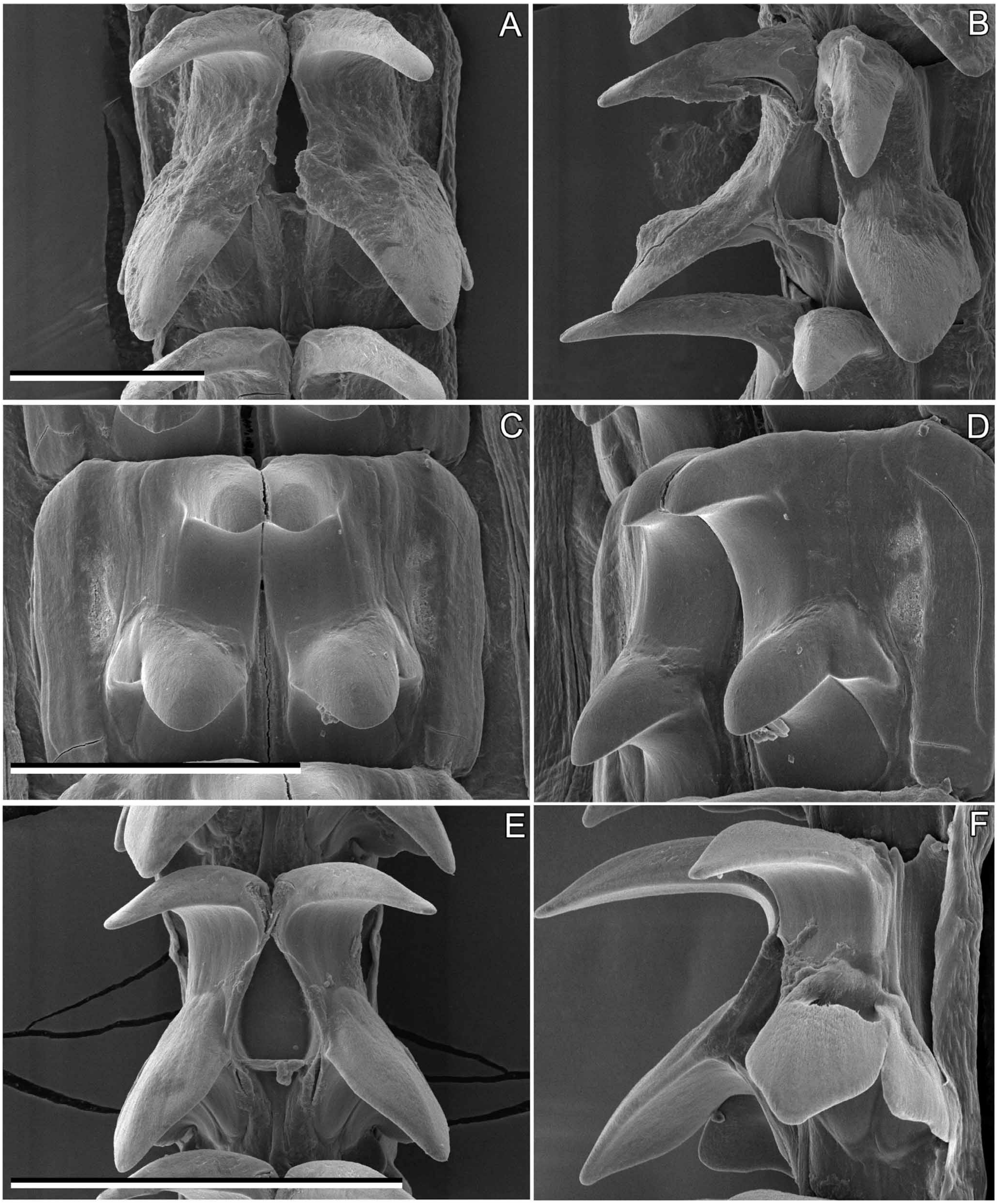

FIGURE 10. Radulae of new *Notoacmea* species. A, B. *Notoacmea potae* n. sp., Nelson Haven, Nelson, holotype, M.184210. C, D. *Notoacmea rapida* n. sp., Halls Beach, Northcote, Waitemata Harbour, holotype, M.184206. E, F. *Notoacmea turbatrix* n. sp. Kaikoura, holotype, M.184224. Scale bars A, E = 100 µm; C = 50 µm.

Material examined

Type material (see above); Table 1.

Description

Shell (type material) up to 6.50 mm long, apex at anterior sixth, height 35–41% of length, rather thin, margin very thin and fragile. Anterior slope more or less flat, posterior slope broadly convex, lateral slopes weakly convex. Exterior white with scattered, irregular, brown spots and streaks. Exterior with fine radial threads.

Animal. Inner half of dorsal surface of mantle fringe dark green, outer half brown or greenish white, a thin line of yellowish brown streaks bordering thin white outer margin. Radula: First lateral teeth short, broad with blunt cusps. Second lateral teeth trapezoid with rounded outer edge. Third lateral teeth reduced and rounded; separated from second lateral teeth except at bases.

Distribution

Whangarei Harbour, Waitemata Harbour and Napier, northeastern North Island, New Zealand (Fig. 2F).

Habitat

Intertidal mud flats, mainly on dead bivalve shells—*Austrovenus stutchburyi* (Gray, 1828), *Macomona liliana* (Iredale, 1915) and *Cyclomactra ovata* (Gray, 1843)—and usually on the inside of the valves and away from the light.

Etymology

Rapid (Latin). When the bivalve shells to which living animals were attached were turned over, this species moved quickly to avoid direct light, a behavior not seen in any other species of *Notoacmea* (Nakano and Spencer 2007).

Remarks

Notoacmea rapida n. sp. is typically whitish with a colour pattern of irregular brown spots, but in some individuals this pattern transforms to dark radial bands. The spatula may be brown and in contrast to the pale surrounding area, or differential pigmentation may be lacking, as in the type specimens. The shell of the largest specimen sequenced is 8 mm long (Napier; Fig. 7X). *Notoacmea rapida* n. sp. has previously been misidentified as part of the variation of *N. helmsi* (of authors, not E.A. Smith), but can be distinguished from all other species genetically and morphologically, as well as by its light-avoiding behavior.

Notoacmea scapha (Suter, 1907)
Figs 2G, 8A–H, 9T, U

Acmaea scapha Suter, 1907: 324, pl. 27, figs 34, 35.
Acmaea parviconoidea var. *leucoma* Suter, 1907: 322; Suter 1913: 70. New synonymy.
Notoacmea scapha.—Iredale 1915: 430; Nakano and Spencer 2007: 471, figs 4A, B, 5A, B.
Notoacmea helmsi var. *leucoma*.—Iredale 1915: 428, 430.
Notoacmea (*Parvacmea*) *helmsi*.—Oliver 1926: 576; Powell 1979: 48, fig. 4: 3, 4; Spencer *et al*. 2006. In part of E.A. Smith, 1894.
Notoacmea (*Parvacmea*) *scapha*.—Powell 1937: 67; Powell 1946: 68.
Notoacmea (*Parvacmea*) *helmsi scapha*.—Powell 1957: 86; Powell 1962: 78.
Notoacmea (*Parvacmea*) *helmsi* forma *scapha*.—Powell 1979: 48, fig. 4/5.

Type material: *Acmaea scapha*—lectotype (Boreham 1959: 23, Fig. 9T) NZGS TM 585, Dunedin, New Zealand.

Acmaea parviconoidea var. *leucoma*—lectotype (Boreham 1959: 23, Figs 8C, 9U) NZGS TM 583 and paralectotype TM 584, Heathcote Estuary, Christchurch, New Zealand.

Material examined

Type material (see above); Table 1.

Distribution

North and South Islands, New Zealand (Fig. 2G).

Habitat

Sheltered shores on *Zostera capricorni* leaves, living and dead shells and rocks.

Remarks

Our molecular analysis includes topotypes, which are perfectly accordant with the holotype in shell morphology. *Notoacmea scapha* was originally described as inhabiting the leaves of *Zostera*, but as Nakano and Spencer (2007) and our present trees show (Fig. 3), it is also found in sheltered inlets on living trochids (e.g., *Diloma subrostrata* (Gray, 1835)), and the outside of the venerid, *Austrovenus stuchburyi* (Gray, 1828), as well as the inside of dead bivalve shells such as *A. stutchburyi*, *Cyclomactra ovata* (Gray, 1843) and *Macomona liliana* (Iredale, 1915). The holotype is the small straight-sided, laterally compressed form, whereas those found on adjacent hard substrata on mudflats have larger and more typically patelliform shells. Most individuals previously identified as *N. helmsi* (e.g., by Morton and Miller 1968) are probably this species. The largest specimen identified by mantle pigmentation among other sequenced specimens is 9 mm long (Avon-Heathcote Estuary, M.274266).

The pigmentation of the dorsal surface of the mantle fringe is variable: occasional specimens are uniform whitish, but most are green or whitish over inner third, with a brownish intermediate area, and thin white margin.

Notoacmea scopulina Oliver, 1926
Fig. 2H, 9A, B, Y

Notoacmea (*Subacmea*) *scopulina* Oliver, 1926: 580, pl. 99, fig. 8; Powell 1937: 67, pl. 9, fig. 8; Powell 1946: 68, pl. 9, fig. 8; Powell 1957: 86, pl. 9, fig. 8; Powell 1962: 78, pl. 9, fig. 8; Powell 1976: 82, pl. 16, fig. 8; Powell 1979: 49, pl. 16, fig.11; Spencer *et al*. 2006.

Type material

Holotype NMNZ M.1563, Motutara, west of Auckland.

Material examined

Type material (see above); Table 1.

Distribution

North and South Islands, New Zealand (Fig. 2H).

Habitat

Notoacmea scopulina inhabits the high intertidal zone on highly exposed shores.

Remarks

We were unable to acquire topotypes for sequencing, and base our concept of the species on specimens that are perfectly accordant with the holotype in shell morphology.

One of the most striking results is that some individuals of *Patelloida corticata* have remarkably similar shells to *N. scopulina*. Moreover, although some animals of *P. corticata* are white, some are orange, almost identical to the colour of the animal of *N. scopulina*. We found both species at Sponge Bay, near Gisborne in the North Island. Our genetic data, however, indicates that the two species are distinct at the genus level (Fig. 3). Compared with *Patelloida corticata*, which it closely resembles in shell facies, including size (length up to 19.2 mm), *N. scopulina* may be distinguished by the more even developed radial ribs, especially posteriorly; the less acutely conical shape with apex closer to the anterior end; and the darker, generally more extensive pigmentation within and bordering the spatula, especially in adult shells

Notoacmea sturnus (Hombron & Jacquinot, 1841)
Figs 1, 6O–T, 9P

Patella sturnus Hombron & Jacquinot, 1841: 191.
Patelloides antarctica Hombron & Jacquinot, 1841: 192.
Patella cantharus Reeve, 1855, pl. 40, fig. 131.
Nacella cantharus.—Hutton 1873: 46.
Acmaea pileopsis.—Hutton 1880: 88; Suter 1907: 319; Suter 1909: 5; Suter 1913: 71; Odhner 1924: 10. In part of Quoy & Gaimard, 1834; in part = *N. subantarctica* Oliver, 1926.
Acmaea (*Collisella*) *pileopsis.*—Hutton 1884: 373. In part of Quoy & Gaimard, 1834; in part = *N. subantarctica* Oliver, 1926.
Helcioniscus radians.—Suter 1905: 347; Suter 1913: 81. In part not Gmelin, 1791.
Acmaea cantharus.—Suter 1904: 85; Suter 1907: 320; Suter 1909: 5; Suter 1913: 66, pl. 7, fig. 1; Odhner 1924: 10 (in part = *N. subantarctica*).
Acmaea septiformis.—Suter 1904: 85; Suter 1907: 318; Suter 1909: 5; Suter 1913: 72. Not Quoy & Gaimard, 1834; in part = *N. pileopsis* and *N. subantarctica*.
Notoacmea pileopsis.—Iredale 1915: 429. In part.
Notoacmea (*Notoacmea*) *pileopsis sturnus*.—Oliver 1926: 570; Powell 1937: 66; Powell 1946: 68; Powell 1957: 85; Powell 1962: 78.
Notoacmea pileopsis sturnus.—Powell 1955: 63.
Notoacmea (*Notoacmea*) *pileopsis sturnus*.—Powell 1976: 82; Powell 1979: 47, pl.16, figs 3, 4; Spencer *et al*. 2006. In part = *N. subantarctica*.

Type material

Patella sturnus—“Nouvelle-Zélande”. Original material no longer extant (V. Héros, 20 Jan. 2007): neotype (here selected, 20.0 × 14.3 mm; Figs 6R, S, 9P) MNHN 20780, Leask’s Bay, Stewart Island, New Zealand, M.A. Crozier, 2 Apr. 1965 (ex M.30982).

Patella antarctica: lectotype (here selected, 31.3 × 23.8 mm; Fig. 6Q) MNHN 20781 and 4 paralectotypes MNHN 4925, Auckland Islands**.**

Patella cantharus—lectotype (here selected, 15.5 × 11.7 mm; Fig. 6P) BMNH 19750615a and 2 paralectotypes BMNH 19750615b, c, “New Zealand; Earl” = southern South Island or Stewart Island.

Material examined

Type material (see above); Table 1.

Distribution

South Island, as far north as Banks Peninsula (43°35’S), and Stewart, Snares and Auckland Islands, New Zealand (Fig. 1).

Habitat

Notoacmea sturnus inhabits the high intertidal zone to splash zone on exposed shores.

Remarks

Notoacmea sturnus has been traditionally treated as a subspecies of *N. pileopsis* (Powell 1979; Spencer *et al*. 2006), including a ‘*subantarctica* form’ (see below), but our results show that they are morphologically and genetically distinct from each other (Figs. 3, 4). *Notoacmea sturnus* has a narrower outline than *N. pileopsis* and differs further from it and all other *Notoacmea* species in that the apex is situated more strongly anteriorly. It is most closely related to *N. pileopsis*, the COI distance between the two being ~4% (Table 2). *Notoacmea sturnus* (based on the distinctive shell morphology of several hundred specimens in 68 lots, NMNZ) replaces *N. pileopsis* on the east of the South Island south of Marlborough (Fig. 1) (i.e., the two species are allopatric) and is sympatric with *N. subantarctica* at the Auckland Islands. Like *N. pileopsis* and *N. cellanoides*, *N. sturnus* is notable among New Zealand *Notoacmea* species for the large size attained (shell length up to 30 mm).

Notoacmea subantarctica Oliver, 1926
Figs 1, 6U–Y, 9Q

Acmaea pileopsis.—Hutton 1880: 88; Suter 1907: 319; Suter 1913: 71; Odhner 1924: 10. In part of Quoy & Gaimard, 1834; in part = *N. sturnus* (Hombron & Jacquinot, 1841).
Acmaea septiformis.—Suter 1904: 85; Suter 1907: 318; Suter 1909: 5; Suter 1913: 72, pl. 7, fig. 5. Not Quoy & Gaimard; in part = *N. pileopsis* and *N. sturnus*.
Acmaea helmsi.—Odhner 1924: 10. Not E.A. Smith, 1894.
Acmaea cantharus.—Odhner 1924: 10. In part not Reeve, 1855.
Notoacmea (*Notoacmea*) *pileopsis subantarctica* Oliver, 1926: 571; Powell 1937: 66; Powell 1946: 68; Powell 1957: 85; Powell 1962: 78.
Notoacmea pileopsis subantarctica.—Powell 1955: 63.
Notoacmea (*Notoacmea*) *pileopsis sturnus*.—Powell 1976: 82; Powell 1979: 47; Spencer *et al*. 2006. In part.

Type material

Holotype CM M12834 (Fig. 6U), Campbell Island.

Material examined

Type material (see above); Table 1.

Distribution

Auckland and Campbell Islands, New Zealand (Fig. 1).

Habitat

Notoacmea subantarctica inhabits the high intertidal zone to splash zone on exposed shores.

Remarks

Our molecular analysis includes topotypes, which are perfectly accordant with the holotype in shell morphology. *Notoacmea subantarctica* has long been treated as either a subspecies or a synonym of *N. pileopsis*, having similar colour and colour pattern on the interior of the shell, but differs in attaining smaller size (length up to 20 mm, versus 32 mm) and in having a more finely spotted exterior colour pattern. The two species are strongly allopatric (Fig. 1). *Notoacmea subantarctica* is sympatric with *N. sturnus* at the Auckland Islands, differing in attaining smaller size (length up to 20 mm, versus 30 mm), in being more finely speckled, and in that the apex is set considerably further posteriorly. Our sequence data reveal that *N. subantarctica* is more closely related to *N. parviconoidea* than to *N. pileopsis*.

Notoacmea turbatrix n. sp.
Figs 2I, 8I–Y, 9X, 10E, F

Notoacmea sp. B Nakano & Spencer, 2007: figs 4D, 5D.

Type material

Holotype NMNZ M.184224 (6.95 × 4.85 mm; Figs 8I, J, 9X, 10E, F) and paratypes M.275226 (1) (4.95 × 3.50 mm; Fig. 8K), M.184227 (1); Kaikoura, on intertidal rocks, T. Nakano & J. Irwin, 8 Aug. 2006.

Material examined

Type material (see above); Table 1.

Description

Shell (type material) up to 6.95 mm long, apex at anterior sixth-eighth, height 35–46% of length, moderately thin, apertural margin thin and fragile. Anterior slope shallowly concave, posterior slope broadly convex, lateral slopes more or less flat. Externally white with dark brown radial bands, or with yellowish brown lines in diagonally reticulate pattern that transforms to radial bands at margin in adults. Exterior with fine radial threads.

Animal. Dorsal surface of mantle fringe green beside shell muscle, edge white. Ventral mantle surface and shell muscle whitish, head-foot cream.

Radula: First lateral teeth short, broad with blunt cusps. Second lateral teeth trapezoid with rounded outer edge. Third lateral teeth reduced and rounded; separated from second lateral teeth except at bases (Fig. 10E, F)

Distribution

North and South Islands, New Zealand (Fig. 2I).

Habitat

Notoacmea turbatrix n. sp. is found attached to smooth rocks on open coasts, the backs of the nacellid *Cellana denticulata* (Martyn, 1784), around the aperture of the turbinid *Lunella smaragdus* (Gmelin, 1791) and in tide pools on exposed shores.

Remarks

Compared with *N. parviconoidea*, which has similar shell colour and pattern and is about as variable, *N. turbatrix* n. sp. is immediately separable by the green rather than cream or reddish brown of the dorsal surface of the mantle fringe. Shells of *N. turbatrix* n. sp. are usually distinguishable from *N. parviconoidea* by the presence of a whitish or (rarely) greenish patch in the centre of the anterior end of the spatula, and by the lack of calligraphy-like markings on the interior that are commonly present in *N. parviconoidea*. Externally *N. turbatrix* n. sp. may have a well-developed brownish diagonal network pattern at early stages of growth (absent in *N. parviconoidea*). Where both species occur together, *N. turbatrix* n. sp. is more likely to be found in a sheltered position: a tide pool, as opposed to a vertical rock surface.

Etymology

trouble-maker (Latin). Alluding to the difficulties we experienced in recognizing this species.

Genus ***Patelloida*** Quoy & Gaimard, 1834

Patelloida Quoy & Gaimard, 1834: 349. Type species (by subsequent designation of Gray, 1847): *Patella rugosa* Quoy & Gaimard, 1834; Recent, Ambon, Indonesia.
Collisellina Dall, 1871: 259. Type species (by original designation): *Patella saccharina* Linnaeus, 1758; Recent, tropical Pacific.
Chiazacmea Oliver, 1926: 558. Type species (by original designation): *Patelloida flammea* of authors = *Acmaea crucis* Tenison Woods, 1876; Recent, Australia.

Remarks.

According to Lindberg and Vermeij (1985), *Patelloida* consists of at least two groups. One group includes species characterized by having low to medium profiles, strong radial ribs or many fine riblets, reduced third lateral teeth, and habitats including various substrata ranging from exposed rocky shores to sheltered mudflats. The other group, called the *P. profunda* group by Christiaens (1975) and Lindberg and Vermeij (1985), consists of species characterized by having moderate to high shell profiles, many riblets, and equal-sized lateral radular teeth, and is limited to the calcareous substrata in the high intertidal to supratidal zones. Recently, Nakano and Ozawa (2007) assigned the *P. profunda* group to their new genus *Eoacmaea*, since it is different from other species of *Patelloida* both morphologically and genetically.

Patelloida corticata (Hutton, 1880)
Fig. 2J, 9C–J, Z

Acmaea corticata Hutton, 1880: 89.
Acmaea (*Collisella*) *corticata*.—Hutton 1884: 372.
Acmaea pseudocorticata Iredale, 1908: 379.
Patelloida corticata corallina Oliver, 1926: 552; Powell 1937: 66, pl. 9, fig. 2; Powell 1946: 68, pl. 9, fig. 2; Powell 1957: 85, pl. 9, fig. 2; Powell 1962: 78, pl. 9, fig. 2.
Patelloida corticata pseudocorticata.—Oliver 1926: 554; Powell 1937: 66; Powell 1946: 68; Powell 1957: 85; Powell 1962: 78.

Patelloida corticata corticata.—Powell 1937: 66, pl. 9, fig. 3; Powell 1946: 68, pl. 9, fig. 3; Powell 1957: 68, pl. 9, fig. 3; Powell 1962: 78, pl. 9, fig. 3.

Patelloida corticata.—Powell 1976: 82, pl. 16, figs 2, 3; Powell 1979: 46, pl.16, figs 7–10; Spencer *et al*. 2006.

Type material

Acmaea corticata—syntypes CM M2807 (Fig. 9D, E), CM M2808 (2), Dunedin, New Zealand.

Acmaea pseudocorticata—type material (probably no longer extant), Lyttelton Harbour, New Zealand. Iredale (1908) stated "type to be presented to the Canterbury Museum, Christchurch", but this cannot be traced (Freeman *et al*. 1997; N. Hiller pers. comm. 2008) and indeed there is no evidence that type material of this or the other three taxa described in the same article was ever deposited there.

Patelloida corticata corallina—holotype NMNZ M.1566, Breaker Bay, Wellington, New Zealand.

Material examined

Type material (see above); Table 1.

Distribution

North and South Islands, New Zealand (Fig. 2J).

Habitat

Patelloida corticata lives in a wider range of intertidal zones ranging from low tide mark to high intertidal zone.

Remarks

Based on the extremely variable shell morphology, Oliver (1926) recognized three subspecies within *Patelloida corticata*: the nominate form with a high shell and numerous ribs, a larger depressed form with fewer ribs (*P. c. corallina*), and a smaller, elongate shell with few ribs, often found higher on the shore (*P. c. pseudocorticata*). Powell (1979), however, argued that this variation was found within populations of *P. corticata* and considered all forms conspecific; our genetic data supports this conclusion. Shells from the lower tidal zones are usually covered with the coralline alga *Melobesia*. The largest specimen included in our study has a shell length of 18.2 mm (Fig. 9I), but it grows considerably larger, the largest recorded specimen, from Kaikoura, having a length of 32 mm (B.F. Elliott collection, Kaikoura).

We collected an unusual form from Castlepoint at high tide level, with depressed shells that are larger than any others we found. At Ruapuke, we collected individuals with the usual white animals, but also some orange-bodied specimens. In spite of all this variation, the genetic data indicates that New Zealand has only a single species of *Patelloida*, *P. corticata*.

Discussion

Recently, Nakano and Spencer (2007) found both polyphenism and cryptic species within a species complex, subsumed under the name *N. helmsi*. In the present study, molecular phylogenetic analyses revealed further examples of both phenomena, polyphenism in *N. badia*, *N. parviconoidea* and *P. corticata*, and the cryptic species pair of *N. elongata* and *N. daedala*.

Shell morphology and colour variation may be caused by ecological factors. Using transplant experiments, Lindberg and Pearse (1990) showed that changes in the shell color of the limpets *Lottia asmi* (Middendorff, 1847) and *L. digitalis* (Rathke, 1833) were caused by differences in the food available (especially algae) in different habitats. Moreover, some of the differences mirror those of New Zealand taxa: *L. pelta* (Rathke, 1833) and *L. asmi*, which inhabit beds of *Mytilus* Linnaeus, 1758 (Bivalvia; Mytilidae) in the northeastern Pacific, have dark coloured shells (Lindberg 1981; Eikenberry and Wickizer 1964), as do the individuals of *N. parviconoidea* living amongst bivalves of the genera *Perna* Retzius, 1788 and *Mytilus* in New Zealand. In turn, *L. digitalis* individuals living in the colonies of the white goose-neck barnacles have a lighter coloured shells (Giesel 1970), a pattern that is also mirrored by *N. parviconoidea* inhabiting in the barnacle zone.

The convergence in shell morphology between *N. scopulina* and some individuals of *P. corticata* is especially surprising given the genetic distance between these taxa. Even more astounding is the polymorphism in the colour of the animal in the latter species: although most individuals are white, some are orange, very like *N. scopulina*. We are not aware of any other limpet species that exhibits this sort of polymorphism in animal colour.

Similar comments apply to the radulae. Although we have examined the radulae of a number of individuals (see Fig. 10), we do not have sufficient numbers to know if the differences we see among our samples provide any features that allow the separation of species. Indeed, given the plastic nature of the radula of *N. scapha* found by Nakano and Spencer (2007)—those attached to bivalve shells had rounded teeth, rather like those of the rock-dwelling *N. parviconoidea*, whereas those living on *Zostera* had straight cutting edges—we strongly suspect that the radula will not provide unambiguously diagnostic characters. Other lottiids, for instance, *Lottia fascicularis* (Menke, 1851), *Patelloida pygmaea* (Dunker, 1860) and *P. ryukyuensis* Nakano & Ozawa, 2005, are also known to exhibit radular variation within species (Simison and Lindberg 1999; Nakano and Ozawa 2005),

Another noteworthy result allows us to distinguish one cryptic species, *N. rapida* n. sp., from all others, and that is its rapid light-avoiding response. Again, so far as we are aware, this is a novel finding among limpet species. Nevertheless, several North American lottiids exhibit a more extreme, but possibly related, behavior, dubbed "bail-out," in which rotation of the substrate to which they are attached causes them to release their hold before rapidly re-attaching to another suitable surface (Wright and Shanks 1995, and references therein). We cannot rule out the possibility that *N. rapida* n. sp. may be responding to the movement of their substratum rather than avoiding light; nevertheless, we never observed bail-out in this (or any other) species.

One pair of cryptic species, *N. elongata* and *N. daedala*, shows a remarkable degree of similarity. We could find no conchological or ecological differences among them and they are sympatric to the degree of both being found under a single rock. In spite of this similarity, they are clearly genetically distinct and show no evidence of interbreeding.

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References

Abbott, R.T. (1974) *American seashells* [2nd edition]. Van Nostrand Reinhold, New York.

Anderson, T.J. & Adlard, R.D. (1994) Nucleotide sequence of a rDNA internal transcribed spacer supports synonymy of *Saccostrea commercialis* and *S. glomerata*. *Journal of Molluscan Studies* 60, 196–197.

Armbruster, G.F.J., van Moorsel, C.H.M. & Gittenberger, E. (2000) Conserved sequence patterns in the non-coding ribosomal ITS-1 of distantly related snail taxa. *Journal of Molluscan Studies* 66, 570–573.

Boreham, A.U.E. (1959) Biological type specimens in the New Zealand Geological Survey. 1. Recent Mollusca. *New Zealand Geological Survey Paleontological Bulletin* 30, 1–87.

Christiaens, J. (1975) Revision provisoire des Mollusques marine recents de la famille des Acmaeidae (second partie). *Informations de la Société Belge de Malacologie* 4: 91–116.

Donald, K.M., Kennedy, M. & Spencer, H.G. (2005) The phylogeny and taxonomy of austral monodontine topshells (Mollusca: Gastropoda: Trochidae), inferred from DNA sequences. *Molecular Phylogenetics and Evolution* 37, 474–483.

Eikenberry, A.B. & Wickizer, D.E. (1964) Studies on the commensal limpets *Acmaea asmi* in relation to its host *Tegula funebralis* (Mollusca: Gastropoda). *Veliger* 6 (Supplement), 66–77.

Farris, J.S., Källersjö, M., Kluge, A.G. & Bult, C. (1995) Constructing a significance test for incongruence. *Systematic Biology* 44, 570–572.

Felsenstein, J. (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39, 783–791.

Felsenstein, J. (1988) Phylogenies from molecular sequences: inference and reliability. *Annual Review of Genetics* 22, 521–565.

Giesel, J.T. (1970) On the maintenance of a shell pattern and behavior polymorphism in *Acmaea digitalis*, a limpet. *Evolution* 24, 98–119.

Goldstien, S.J., Gemmell, N.J. & Schiel, D.R. (2006) Molecular phylogenetics and biogeography of the nacellid limpets of New Zealand (Mollusca: Patellogastropoda). *Molecular Phylogenetics and Evolution* 38, 261–265.

Gray, J.E. (1843) Catalogue of the species of Mollusca and their shells, which have hitherto been recorded as found at New Zealand, with the description of some lately discovered species. Appendix 4 in: Dieffenbach, E., *Travels in New Zealand; with contributions to the geography, geology, botany, and natural history of that country.* 2. Murray, London, 228–265.

Habe, T. & Kosuge, S. (1967) *Common shells of Japan in color.* Hoikusha, Osaka.

Habe, T. & Okutani, T. (1975) *Mollusca I, chiefly from Japan.* Gakken, Tokyo.

Hombron, J.B. & Jacquinot, C.H. (1841) Suite de la description de quelques mollusques, provenant de la campagne de l'Astrolabe et de la Zélée. *Annales des Sciences Naturelles* (2), Zoologie 16: 190–192.

Hombron, J.B. & Jacquinot, C.H. (1854) Description des mollusques coquilles et zoophytes. In: Rousseau, L. (Ed.), *Voyage au Pole Sud et dans l'Océanie sur les corvettes l'Astrolabe et la Zélée; execute par ordre du Roi pendant les anées 1837–1838–1839–1840, sous le commandement de M.J. Dumont-Durville, capitaine de vaisseu, commandant de la Zélée*. Zoologie 5. Gide and Baudry, Paris. 132 pp.

Huelsenbeck, J.P. & Ronquist, F. (2001) MrBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17, 754–755.

Hutton, F.W. (1873) *Catalogue of the marine Mollusca of New Zealand, with diagnoses of the species.* Didsbury, Government Printer, Wellington.

Hutton, F. W. (1878) Révision des coquilles de la Novelle-Zélande et des îles Chatham. *Journal de Conchyliologie* 26, 5–57.

Hutton, F.W. (1880) *Manual of the New Zealand Mollusca. A systematic and descriptive catalogue of the marine and land shells, and of the soft mollusks and polyzoa of New Zealand and the adjacent islands.* Colonial Museum and Geological Survey Department. Hughes, Government Printer, Wellington.

Hutton, F.W. (1883) Additions to the molluscan fauna of New Zealand. *Transactions and Proceedings of the New Zealand Institute* 15, 131–133.

Hutton, F.W. (1884) Revision of the Recent rhipidoglossate and docoglossate Mollusca of New Zealand. *Proceedings of the Linnean Society of New South Wales* 9, 354–378.

Iredale, T. (1908) Notes on some New Zealand Mollusca. *Transactions and Proceedings of the New Zealand Institute* 40, 373–387.

Iredale, T. (1915) A commentary on Suter's Manual of the New Zealand Mollusca. *Transactions of the New Zealand Institute* 47, 417–497.

Keen, A.M. (1971) *Sea shells of tropical America* (2nd. edn). Stanford University Press, California.

Kira, T. (1961) On three new species of *Notoacmea*. *Venus* 21, 292–295.

Kirkendale, L.A. & Meyer, C.P. (2004) Phylogeography of the *Patelloida profunda* group (Gastropoda: Lottiidae): diversification in a dispersal-driven marine system. *Molecular Ecology* 13, 2749–2762.

Koufopanou, V., Reid, D.G., Ridgway, S.A. & Thomas, R.H. (1999) A molecular phylogeny of the patellid limpets (Gastropoda: Patellidae) and its implications for the origins of their antitropical distribution. *Molecular Phylogenetics and Evolution* 11, 138–156.

Lindberg, D.R. (1981) *Acmaeidae: Gastropoda, Mollusca.* Boxwood Press, Pacific Grove, California.

Lindberg, D.R. (1986) Name changes in the Acmaeidae. *Veliger* 29, 142–148.

Lindberg, D.R. & Pearse, J.S. (1990) Experimental manipulation of shell color and morphology of the limpets *Lottia asmi* (Middendorff) and *Lottia digitalis* (Rathke) (Mollusca, Patellogastropoda). *Journal of Experimental Marine Biology and Ecology* 140, 173–185.

Lindberg, D. R. & Vermeij, G. J. 1985. *Patelloida chamorrorum* spec. nov.: A new member of the Tethyan *Patelloida profunda* group (Gastropoda: Acmaeidae). *Veliger* 27: 411–417.

Maddison, D.R. & Maddison, W.P. (2002) *MacClade 4: Analysis of phylogeny and character evolution, version 4.03.* Sinauer Associates, Sunderland, Massachusetts.

Morton, J.E. & Miller, M. (1968) *The New Zealand sea shore*. Collins, Auckland.

Nakano, T. & Ozawa, T. (2004) Phylogeny and historical biogeography of limpets of the order Patellogastropoda based on mitochondrial DNA sequences. *Journal of Molluscan Studies* 70, 31–41.

Nakano, T. & Ozawa, T. (2005) Systematic revision of *Patelloida pygmaea* (Dunker, 1860) (Gastropoda: Lottiidae), with a description of a new species. *Journal of Molluscan Studies* 71, 357–370.

Nakano, T. & Ozawa, T. (2007) Worldwide phylogeography of limpets of the order Patellogastropoda: molecular, morphological and paleontological evidence. *Journal of Molluscan Studies* 73, 79–99.

Nakano, T. & Spencer, H.G. (2007) Simultaneous polyphenism and cryptic species in an intertidal limpet from New Zealand. *Molecular Phylogenetics and Evolution* 45, 470–479.

Odhner, N.H. (1924) New Zealand Mollusca. Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening; Kjobenhavn* 77, 1–90.

Oliver, W.R.B. (1926) Australasian Patelloididae. *Transactions of the New Zealand Institute* 56, 547–582.

Ponder, W.F. & Creese, R.G. (1980) A revision of the Australian species of *Notoacmea*, *Collisella* and *Patelloida* (Mollusca: Gastropoda: Acmaeidae). *Journal of Malacological Society of Australia* 4, 167–208.

Posada, D. & Crandall, K.A. (1998) MODELTEST: testing the model of DNA substitution. *Bioinformatics* 14, 817–818.

Powell, A.W.B. (1937) *The shellfish of New Zealand: an illustrated handbook*. Unity Press, Auckland.

Powell, A.W.B. (1946) *The shellfish of New Zealand: an illustrated handbook* [edition 2]. Whitcombe and Tombs, Christchurch.

Powell, A.W.B. (1955) Mollusca of the southern islands of New Zealand. *Cape Expedition Series Bulletin* 15. *Department of Scientific and Industrial Research*, Wellington. 1–152.

Powell, A.W.B. (1957) *Shells of New Zealand: an illustrated handbook* [edition 3]. Whitcombe and Tombs, Auckland,

Powell, A.W.B. (1962) *Shells of New Zealand: an illustrated handbook* [fourth edition]. Whitcombe and Tombs, Christchurch.

Powell, A.W.B. (1973) The patellid limpets of the world (Patellidae). *Indo-Pacific Mollusca* 3, 75–206.

Powell, A.W.B. (1976) *Shells of New Zealand: an illustrated handbook* [fifth, revised edition]. Whitcoulls, Christchurch.

Powell, A.W.B. (1979) *New Zealand Mollusca: marine, land and freshwater shells*. Collins Auckland.

Quoy, J.C.R. & Gaimard, P. (1834) Mollusques 3. In: Voyage de découverts de l'Astrolabe, exécuté par ordre du Roi pendant les années 1826–1827–1828–1829, sous le commandement de M.J. Dumont d'Urville. Zoologie. Tastu, Paris. 1–366.

Reeve, L. (1854–55) *Conchologia iconica; or, illustrations of the shells of molluscous animals*.8. Monograph of the genus *Patella*. Reeve, London.

Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19, 1572–1574.

Sasaki, T. & Okutani, T. (1993) New genus *Nipponacmea* (Gastropoda: Lottiidae): A revision of Japanese limpets hitherto allocated in *Notoacmea*. *Venus* 52, 1–40.

Sasaki, T. (1999) The present state and problems of the taxonomy of Japanese Patellogastropoda limpets. Part 2: Lottiidae. *Chiribotan* 29, 37–46.

Simison, W.B. & Lindberg, D.R. (1999) Morphological and molecular resolution of a putative cryptic species complex: a case study of *Notoacmea fascicularis* (Menke, 1851) (Gastropoda: Patellogastropoda). *Journal of Molluscan Studies* 65, 99–109.

Simison, W.B. & Lindberg, D.R. (2003) On the identity of *Lottia strigatella* (Carpenter, 1864) (Patellogastropoda: Lottiidae). *Veliger* 46, 1–19.

Smith, E.A. (1894) On some new species of shells from New Zealand and Australia, and remarks upon some Atlantic forms occurring in deep water off Sydney. *Proceedings of the Malacological Society of London* 1, 57–99.

Spencer, H.G., Willan, R.C., Marshall, B.A. & Murray, T.J. (2006) *Checklist of the Recent Mollusca described from the New Zealand Exclusive Economic Zone*. http://www.molluscs.otago.ac.nz/index.html [accessed May 2008]

Suter, H. (1904) Mollusca. In: Hutton, F.W. (Ed.), *Index faunae Novae Zealandiae*. Dulau, London, 57–95.

Suter, H. (1905) Revision of the New Zealand Patellidae, with descriptions of a new species and subspecies. *Proceedings of the Malacological Society of London* 5, 346–355.

Suter, H. (1907) Acmaeidae of New Zealand. *Proceedings of the Malacological Society of London* 7, 324–326.

Suter, H. (1909) The Mollusca of the subantarctic islands of New Zealand. In: Chilton, C. (Ed.), *The subantarctic islands of New Zealand*. 1. Philosophical Institute of Canterbury, Christchurch: 1–57

Suter, H. (1913) *Manual of the New Zealand Mollusca. With an atlas of quarto plates* (1915). Government Printer, Wellington.

Swofford, D.L. (2002) *PAUP*: Phylogenetic Analysis Using Parsimony (* and other Methods), Version 4.* Sinauer Associates, Sunderland, Massachusetts.

Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F. & Higgins, D.G. (1997) The Clustal X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* 24, 4876–4882.

Williams, S.T. & Reid, D.G. (2004) Speciation and diversity on tropical rocky shores: a global phylogeny of snails of the genus *Echinolittorina*. *Evolution* 58, 2227–2251.

Williams, S.T., Reid, D.G. & Littlewood, D.T.J. (2003) A molecular phylogeny of the Littorinidae (Gastropoda: Littorinidae): unequal evolutionary rates, morphological parallelism and biogeography of the Southern Ocean. *Molecular Phylogenetics and Evolution* 28, 60–86.

Wright, W.G. & Shanks, A.L. (1995) Interspecific association between bail-out behavior and habitat is geographically and phylogenetically widespread. *Journal of Experimental and Marine Biology and Ecology* 188, 133–143.