

***Powelliphanta augusta*, a new species of land snail, with a description of its former habitat, Stockton coal plateau, New Zealand**

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Abstract A recently discovered and threatened large land snail, *Powelliphanta augusta* n. sp. is described from Mt Augustus on the western scarp of the Stockton Plateau, North Westland. On shell characters it is readily distinguishable from all other *Powelliphanta*, with narrow red spiral lines underlying irregular and variable dark reddish-brown axial bands, a small adult size and sculptured dorsal surface. Differences in the shell morphology of *P. augusta*, its closest phylogenetic relative *P. lignaria*, and its closest geographic neighbour *P. patrickensis*, were investigated using principal components analysis. *P. lignaria* is much larger than either *P. augusta* or *P. patrickensis*, and there are significant differences in shell shape between the three taxa. Earlier mitochondrial DNA sequencing data, which supported specific status of *P. augusta*, is discussed. The snail's only habitat on the Mt Augustus ridgeline is described, but most has now been removed by coal mining. Snails salvaged before the destruction of their habitat have been taken into captivity or released in the wild outside their natural range.

Keywords coal mining; habitat loss; Mollusca; new species; Pulmonata; taxonomy

INTRODUCTION

Powelliphanta O'Connor, 1945 is a genus of large, predatory land snails endemic to New Zealand. The shells of many taxa are strongly patterned and brightly coloured, and have been used as the primary tool in identification. Most taxa were described on the basis of shell morphology in the 1930s and 1940s (Powell 1930, 1932, 1936, 1938, 1946), producing a taxonomy of 10 species and 27 subspecies. Later, Climo (1978) proposed an alternative classification reducing the number of species to two with four subspecies, but this was considered contentious (Parkinson 1979; Powell 1979) and failed to gain wide acceptance. More recently, molecular studies (Walker 2003; Trewick 2008) provided substantial support for the original morphologically-based classification (Powell 1979).

Almost all taxa of *Powelliphanta* occupy small ranges. This restricted distribution pattern has made *Powelliphanta* particularly vulnerable to habitat loss and degradation, and these snails are afforded high conservation status (Walker 2003). The recent discovery of an unknown *Powelliphanta* in a small part of a large open-cast coal mine at Stockton led to intense interest in its taxonomic status and long-term prospects.

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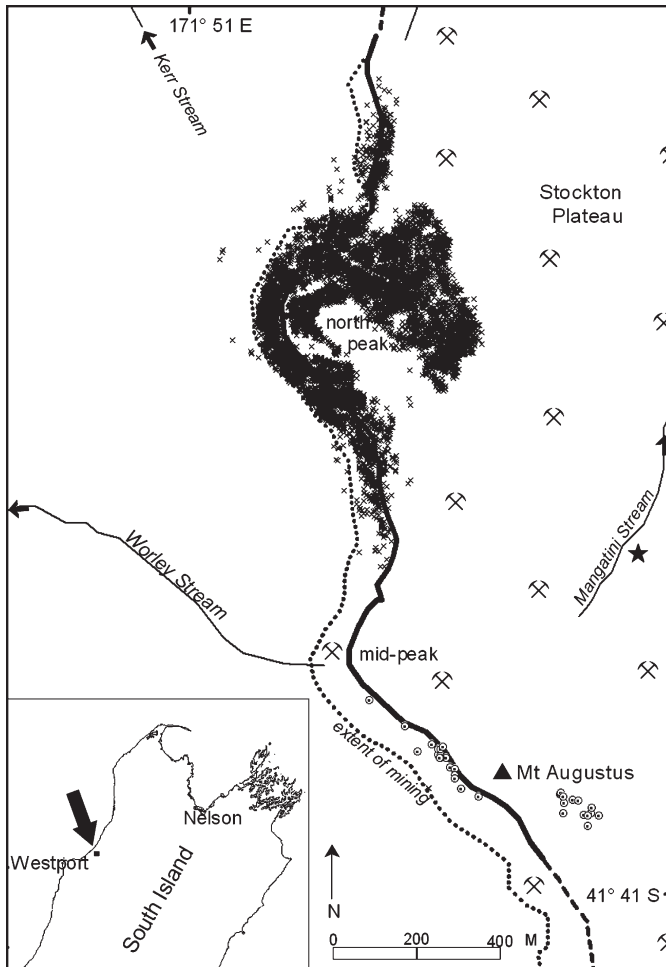


Fig. 1 Distribution of live *Powelliphanta augusta* n. sp. snails in the period 2004–07. Crosses indicate where snails of the northern morph were seen (and 6113 collected) and solid circles nested within an open circle where 26 snails of the southern morph were seen and collected. A black star indicates the site where six shells were collected by the Botanical Society in 1996. The western escarpment of the Stockton Plateau where high cliffs form the Augustus massif is shown by a solid black line, with dashed lines indicating the ridgeline north and south of the massif. The sharp edges of the snail's distribution east of the ridgeline are not natural boundaries but rather indicate the presence of bulldozed roads and mine pits. By late 2007 coal mining had removed all the snails and snail habitat east of the dotted line.

In April 1996 members of the Nelson Botanical Society collected six *Powelliphanta* shells on the north-eastern slopes of Mt Augustus, the southernmost of three high points which collectively form the Augustus massif, on the western scarp of the Stockton Plateau, north of Westport, South Island, New Zealand (Fig. 1). The Stockton and adjacent Denniston coal plateaux are an elevated and exposed former peneplain where very acid and infertile soil parent materials (Brunner coal measures), montane to subalpine altitude (400–1106 m above sea level (a.s.l.)), poor drainage, low sunshine hours, high wind exposure, and a very high rainfall have produced dramatic and unique landscapes and biota (Overmars et al. 1998). It is a somewhat unlikely habitat for large land snails which normally need alkaline, well-drained soils supporting abundant earthworms as their primary prey, and high levels of available calcium for shell and egg formation. However, one species was already well known from the plateau, *Powelliphanta patrickensis* (Powell, 1949), and initially the shells found on Mt Augustus were assumed to be this species. In apparent response to the harsh conditions, *P. patrickensis* is relatively small, has a thin and fragile shell, and is patchily and sparsely though widely distributed on the plateau. The Mt Augustus shells were also small, but their shape and colour patterning were very different from the glossy *P. patrickensis*. The shells of the Mt Augustus snails appeared most similar to those of *P. lignaria* (Hutton, 1880), a large,

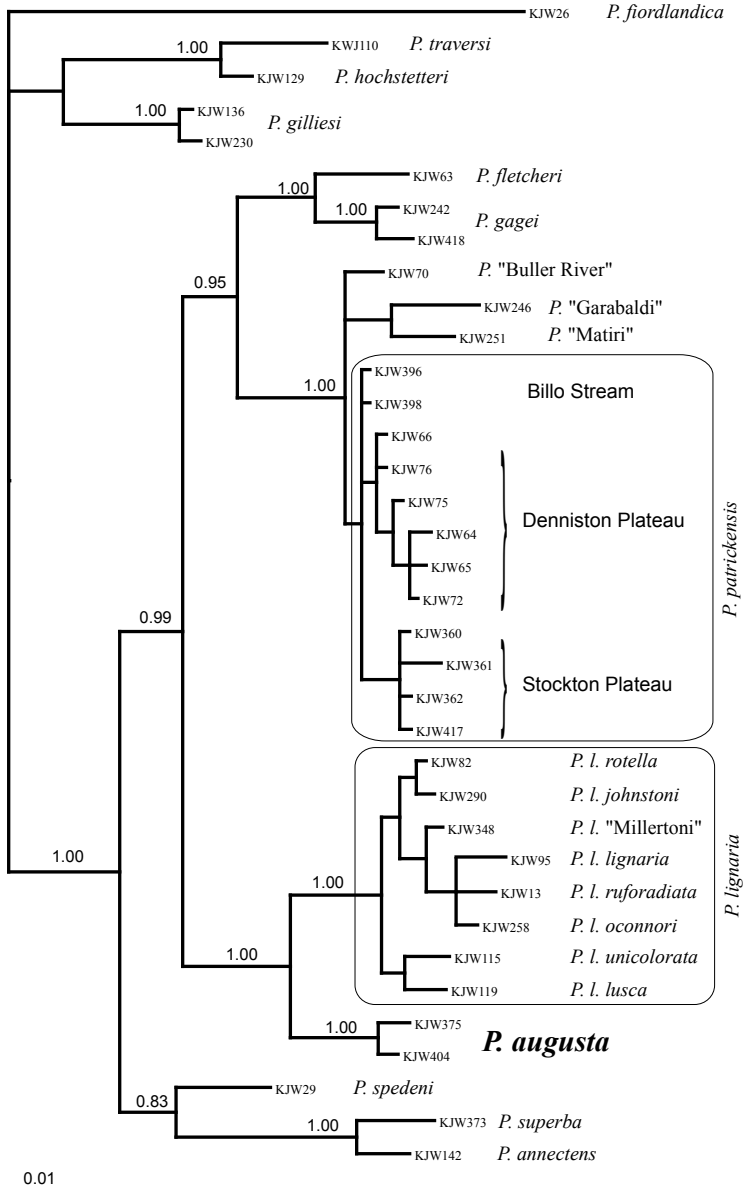


Fig. 2 Evolutionary hypothesis from a Bayesian analysis of 36 mtDNA COI sequences up to 800 bp long from *Powelliphanta* snails. Numbers at nodes are Bayesian credibility values, with maximum support indicated by highest value (1.0). Reproduced with minor changes from Trewick et al. (2008).

thick-shelled lowland species with seven described subspecies found just north of Stockton Plateau, but there were sufficient differences to conclude that while *P. lignaria* and the Mt Augustus snails probably shared a common ancestry, the latter was a distinct taxon.

By the time the Mt Augustus shells were critically examined in late 2003, the site they had been collected from had been destroyed by coal mining, but in March 2004 KJW found a surviving population on the north peak of the Augustus massif. The shells of the north peak

snails differed slightly in colour and banding from the original six, but were still recognisably members of the same taxon. Subsequent further searches found that the extant population was restricted to about 8.5 ha in the immediate vicinity of the Augustus ridgeline between 900–1011 m. Most surviving snails were on the north peak, but a small number referable to the southern morph collected by the Botanical Society were still present on the northwestern and southeastern flanks of Mt Augustus (Fig. 1).

In 2005 the taxonomic status of the snails on Mt Augustus and their phylogenetic relationship with other *Powelliphanta* was assessed using COI mitochondrial DNA sequence data (Trewick 2005). This study found the Mt Augustus snails to be a distinctive evolutionary lineage, and concluded on genetic and other evidence that they comprised a specialised local endemic species with a phylogenetic sister-taxon relationship to *P. lignaria* (Trewick 2005; Trewick et al. 2008; Fig. 2). It found two haplotypes, differing by 0.5%, which were distributed along the same spatial lines as the shell differences already noted, with all individuals from the ridge south of Mt Augustus (= “southern-morph”) having one haplotype, and those from the north peak having the other.

In 2006 and 2007, subsequent to the discovery of the snail population on Mt Augustus and its confirmation as a distinct taxon, all remaining snail habitat above the escarpment on the Augustus massif was destroyed by coal mining, leaving only a sliver of snail habitat on the stump of the north peak. Before mining began, the area was searched for live snails, 6139 of which were taken into captivity, and during this process many empty shells were also found and collected. This provided a ready source of tissue biopsies for genetic analysis and shells for morphological analysis, but of course also left the new species without its habitat.

The purpose of this paper is to describe the Mt Augustus snail as *P. augusta* n. sp., to quantify the shell characteristics which distinguish it from its closest relatives and neighbours, and to characterise the environment the snails formerly occupied.

MATERIALS AND METHODS

Powell’s nomenclature, with additions and revisions as proposed by Walker (2003) on the basis of allozyme analysis and wider field studies, is adopted here.

Materials examined

Between 1980 and 1990 the extensive collections of *Powelliphanta* shells held at the National Museum of New Zealand Te Papa Tongarewa (NMNZ) were examined by KJW. Much of the material held at NMNZ had been collected at or near type localities, but shell examination was not restricted to type material. Between 1987 and 1994 KJW visited all sites where *Powelliphanta* were at that time known or thought to occur and collected shells and examined live snails as part of a study into the taxonomy of the genus. Shells collected at that time formed the basis of a large collection presently held at the Department of Conservation, Nelson (DoCNn). Since then the collection has been expanded to include shells collected in the period 1995–2007 from newly discovered snail populations, and from more intensive sampling within the range of well-known taxa (K. Walker unpubl. data). The type specimens of most *Powelliphanta*, held at the Auckland Institute and Museum (AI&M), were examined by KJW in 2000 to confirm that identifications afforded by the extensive NMNZ and DoCNn collections were consistent with typological material.

KJW examined 8057 *Powelliphanta* shells (including those from c. 1000 freshly-dead “mature” animals) received by DoCNn in 2006/07 as a result of the searches for live snails on Mt Augustus that preceded mining activities. In addition, about 100 live snails collected from all parts of the snail population on the north peak of the Augustus massif (New Zealand Map Series 260, map L29, between grid co-ordinates 147easting–476northing and 146–480;

L29/145–478 to 148–478) and 24 live snails from the southern ridgeline near Mt Augustus (L29/147–473 and L29/149–472) were examined while they were in captivity during parts of 2005–07. The six shells collected by the Nelson Botanical Society east of Mt Augustus (L29/150–475) in 1996, presently in DoCNn, were also examined.

The anatomy of six specimens of *P. augusta* from the north peak of the Augustus massif (L29/146–480) was examined by GMB. A further eight snails representing a range of *Powelliphanta* taxa were also examined anatomically by GMB for comparative purposes. These were: *P. superba superba* (Powell, 1930) and *P. hochstetteri anatokiensis* (Powell, 1938), both from the Haupiri Range, western Golden Bay, M26/367–837 (one specimen each); *P. gilliesi aurea* (Powell, 1946) from the type locality at Mangarakau, 200 m a.s.l. c. M25/658–630, collector FM Climo 1967 (one specimen); *P. patrickensis*, mid Waimangaroa Valley L29/145–395 (one specimen); *P. l. lignaria*, Gentle Annie Point, L28/222–663 (one specimen); *P. l. johnstoni* (Powell, 1946) behind Ngakawau, L28/167–543 (three specimens).

Morphometric analyses of shell morphology

The shells of 90 large adult snails were measured: 30 *P. augusta* from the north peak of the Augustus massif, 30 *P. patrickensis* from sites across the Denniston and Stockton Plateau (Mt Rochfort, mid Waimangaroa Valley, Happy Valley and the western escarpment north of Mt Frederick), and 30 *P. l. johnstoni* from the mid-reaches of Charming Creek in Mokihinui Forest at L28/202–558. *P. l. johnstoni* was selected to represent *P. lignaria* as its shell morphology was the most similar of all the *P. lignaria* subspecies to that of *P. augusta*, and its range was the closest.

Shells for measurement were selected on the basis of size and intactness. Shell growth in *Powelliphanta* continues throughout life. This indeterminate growth makes it difficult to separate size and shape variation attributable to ontogeny from that attributable to variation among individuals, and thus complicates efforts to distinguish taxa on the basis of morphometrics. Nonetheless, growth in *Powelliphanta* does slow greatly in “old age”, and we know from breeding studies the size at which each taxon becomes reproductive (K. Walker unpubl. data). Further, in old age the last portion of the body whorl descends more relative to the preceding whorl (i.e., the point of insertion of the upper aperture rim on the body whorl descends from the horizontal plane), so that we can be certain in those individuals that growth has all but ceased. In some species, including *P. augusta*, the descent from the horizontal plane is very pronounced, while in other species, such as *P. patrickensis*, it is very limited. To increase the likelihood that shell characteristics of adults of a similar age were compared, only shells which had reached the standard adult 4.5–5.0 whorls, were amongst the largest, and/or had the greatest last-whorl-descent within each collection, were selected for measurement.

Twelve point to point measures were taken from each shell using digital display callipers. The measurements (Fig. 3) were chosen because they encompassed the obvious sources of phenotypic variation amongst *Powelliphanta*, and they included the standard biometric variables of many molluscan studies (Gould & Woodruff 1986).

Multivariate analysis was used to determine whether *P. augusta* could be consistently distinguished from its closest phylogenetic and spatial neighbours on quantifiable shell shape characters, in addition to its unique shell banding and colour pattern. Relationships between individuals were examined with principle components analysis (PCA) of the log-transformed variables. The log transformation was performed to minimise deviations from normality and distortion effects caused by allometric relationships of the raw variables, and to find shape components that were independent of size effects. After preliminary PCA analysis indicated substantial amounts of variation still related to size, a new set of variables was created that expressed each measure as proportions of maximum diameter (Table 2), to identify similarities

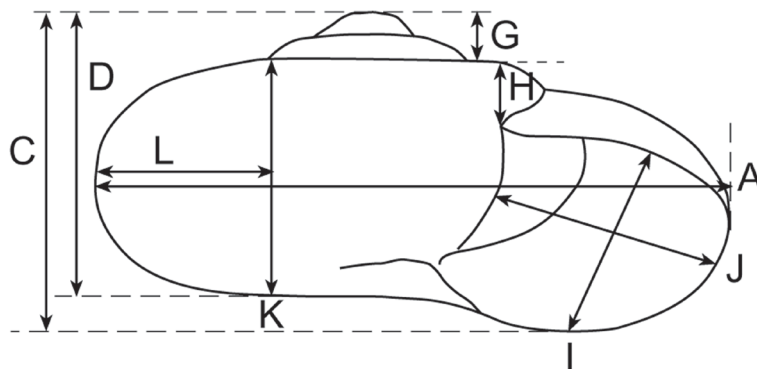


Fig. 3 Dimensions of *Powelliphanta* shells used for morphometric analyses. **A**, Maximum diameter; **C**, total height of shell with last whorl; **D**, total height of shell without last whorl; **G**, spire height, from the last whorl to the apex, measured above the aperture; **H**, descent in aperture incision: the distance from the top of the aperture to the top of the previous whorl; **I**, height of the aperture at its widest point; **J**, width of the aperture, from midway up to its widest point; **K**, height of the last whorl opposite the aperture; **L**, width of the last whorl opposite the aperture. Not visible in this view are **B**, minimum diameter; **E**, umbilicus depth; and **F**, umbilicus width.

and differences between the taxa that related to shape alone and not to size. Comparisons of these new variables between the taxa were made using the Tukey test (Zar 1996).

RESULTS

The banding pattern, colour and size displayed in *P. augusta* shells forms a combination unique to that species. *P. augusta* is always distinguishable from its near geographic neighbour *P. patrickensis* by the consistent presence of narrow red spiral lines on the former, underlying any axial banding (Fig. 4). While *P. patrickensis* occasionally has sculpturing on the dorsal surface that might be mistaken for spiral lines, it never has spiral lines. Several subspecies of *P. lignaria* have red spiral lines, but they are always distinguishable from those on *P. augusta* by their variable width, colour and much greater prominence (*P. l. johnstoni* (Fig. 4) and *P. l. rotella* (Powell, 1938)), or by the additional presence of dominant, strong and very regular axial bands (*P. l. oconnori* (Powell, 1938)); always on much larger and heavier shells.

PCA found that while there was some overlap in shape of *P. augusta* and *P. patrickensis*, shape on its own was also diagnostic (Fig. 5). The shell shape principal component 1, which accounted for 72% of the total variance, was primarily a reflection of descent in the last whorl, and to a lesser extent umbilicus depth and width; these were both expressions of differences in the extent of the descent in the last whorl. The second principal component incorporated 16.7% of the remaining variation, and was largely an expression of descent in the last whorl, with spire height and aperture height of secondary importance.

Shell minimum and maximum diameter, and height, were all significantly greater in *P. l. johnstoni* than in *P. augusta* or *P. patrickensis* (Table 1). Once size differences had been removed and only ratios used, *P. augusta* still had a significantly greater descent in the last whorl, wider aperture, wider and shallower umbilicus and proportionally lower spire than its closest phylogenetic relative *P. l. johnstoni*. It also had a significantly greater descent in the last whorl, wider umbilicus, narrower aperture and proportionally smaller-diameter whorl profile than the similarly-sized but genetically distant *P. patrickensis* (Table 2, Fig. 2).

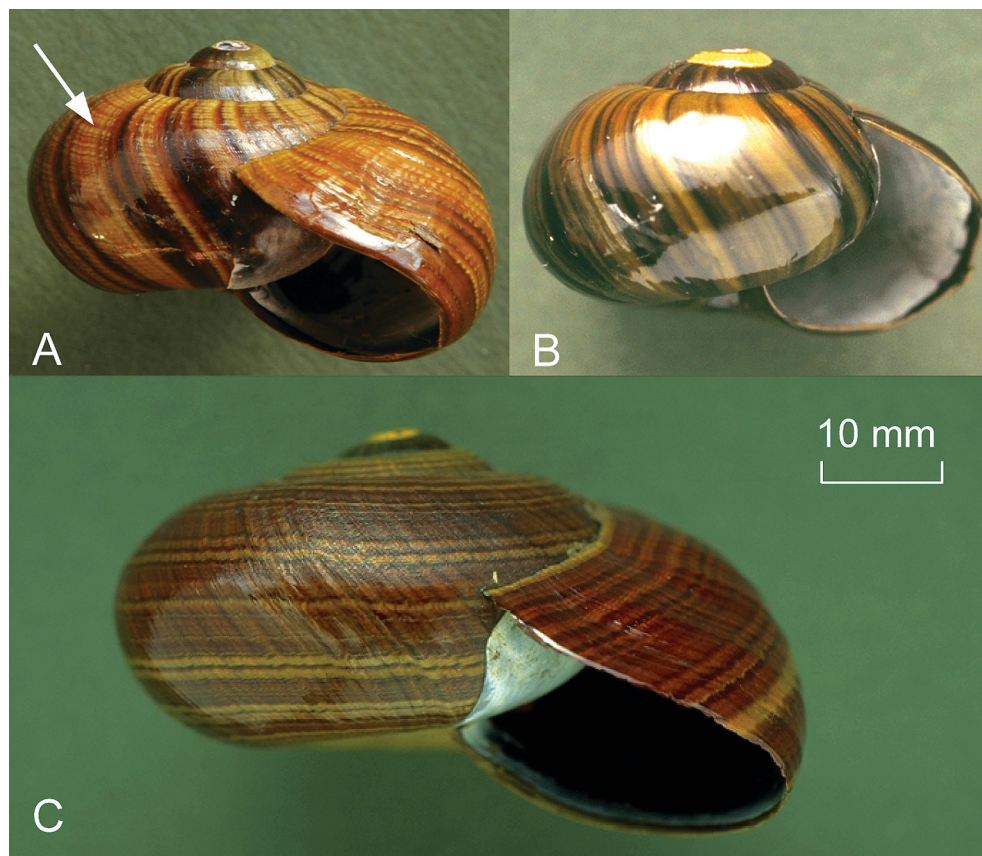


Fig. 4 Banding pattern differences between **A**, *Powelliphanta augusta* n. sp.; **B**, *Powelliphanta patrickensis*; **C**, *Powelliphanta lignaria johnstoni*. Arrow on *P. augusta* shell indicates the diagnostic narrow red spiral lines which underlie more conspicuous dark radial bands. Spiral lines are absent in the similarly-sized *P. patrickensis*, and are present but much more dominant and abundant in *P. l. johnstoni*. All *P. lignaria* snails, including the illustrated *P. l. johnstoni*, have much larger and heavier shells than *P. augusta*.

While this morphometric analysis shows the taxa can be distinguished by shell shape measurement, they are easy to separate without resorting to measurement.

SYSTEMATICS

Family Rhytididae Pilsbry, 1893

Genus *Powelliphanta* O'Connor, 1945

Powelliphanta O'Connor, 1945: 55 (erected as a subgenus of *Paryphanta* Albers, 1850).

TYPE SPECIES: *Helix hochstetteri* Pfeiffer, 1862 by original designation.

DIAGNOSIS: Land snails, with a shell capable of fully housing the retracted animal. Shells large, moderately to strongly depressed, tightly coiled, with whorl periphery well rounded and wide umbilicus; aperture ovate, the opening without teeth, the margin simple. Shell with reduced calcareous content, but with thick periostracum, usually brightly coloured, often with either spiral or radial lines or zones of alternating and contrasting yellow, brown, red and black hue,

Table 1 Morphometric shell variation in *Powelliphanta* (all measures in mm).

	<i>P. augusta</i>				<i>P. lignaria johnstoni</i>				<i>P. patrickensis</i>				
	NMNZ 277582	Mean	Min.	Max.	SD	Mean	Min.	Max.	SD	Mean	Min.	Max.	SD
Maximum diameter	37.97	37.9	34.0	44.3	2.8	52.3	47.5	55.8	2	36.4	32.5	43.6	2.2
Minimum diameter	31.84	31.0	27.6	36.1	2.2	42.9	38.6	46.0	1.6	29.1	27.0	36.9	1.8
Height + last whorl	25.08	22.9	20.5	27.8	2.0	30.4	25.8	33.6	1.9	21.0	18.1	26.1	1.6
Height – last whorl	18.84	17.7	15.8	20.1	1.0	23.9	21.9	25.5	0.9	17.6	16.1	20.7	0.9
Umbilicus depth	5.8	4.7	3.7	6.5	0.7	7.3	5.5	9.0	0.9	4.4	3.3	5.9	0.7
Umbilicus width	7.69	7.6	6.0	9.9	1.2	9.8	6.5	12.1	1.1	5.8	4.6	7.8	0.7
Spire height	2.96	2.6	2.0	3.0	0.3	3.9	3.1	5.0	0.5	2.3	1.6	3.1	0.3
Aperture drop	9.32	7.3	2.7	11.9	2.3	7.6	3.6	12.2	2.0	4.1	2.1	9.4	1.4
Aperture height	15.04	15.5	12.7	18.4	1.3	21.5	18.4	25.0	1.4	15.6	12.2	19.9	1.9
Aperture width	16.33	16.8	8.2	22.4	2.6	21.4	18.6	23.8	1.3	15.9	13.0	19.1	1.6
Last whorl width	15.48	14.7	12.8	17.2	1.0	19.5	16.9	21.0	0.8	14.8	13.7	17.7	0.8
Last whorl depth	9.75	8.7	6.6	11.2	1.2	11.7	9.7	12.8	0.7	8.5	6.5	9.9	0.8

Table 2 Tukey multiple comparisons of differences in morphometric measures between *Powelliphanta lignaria johnstoni* and *P. augusta*, *P. patrickensis* and *P. augusta*, and *P. patrickensis* and *P. l. johnstoni*.

	<i>P. l. johnstoni</i> – <i>P. augusta</i>		<i>P. patrickensis</i> – <i>P. augusta</i>		<i>P. patrickensis</i> – <i>P. l. johnstoni</i>	
	Difference (mm)	P	Difference (mm)	P	Difference (mm)	P
Maximum diameter (MD)	14.39	<0.001	-1.51	0.037	-15.90	<0.001
Minimum diameter	11.90	<0.001	-1.86	0.001	-13.76	<0.001
Total height incl. last whorl	7.50	<0.001	-1.96	<0.001	-9.46	<0.001
Aperture drop/MD	-0.05	<0.001	-0.08	<0.001	-0.03	0.005
Aperture width/MD	-0.04	0.001	-0.01	0.801	0.03	0.009
Umbilicus depth/MD	0.02	<0.001	-0.00	0.736	-0.02	<0.001
Umbilicus width/MD	-0.01	0.039	-0.04	<0.001	-0.03	<0.001
Spire height/MD	0.00	0.260	-0.01	0.019	-0.01	<0.001
Aperture height/MD	0.00	1.000	0.02	0.196	0.02	0.196
Height without last whorl/height with LW	0.01	0.617	0.07	<0.001	0.06	<0.001
Last whorl width/MD	0.23	0.026	0.22	0.011	0.24	0.017
Last whorl depth/MD	-0.02	0.009	0.02	0.002	0.04	<0.001

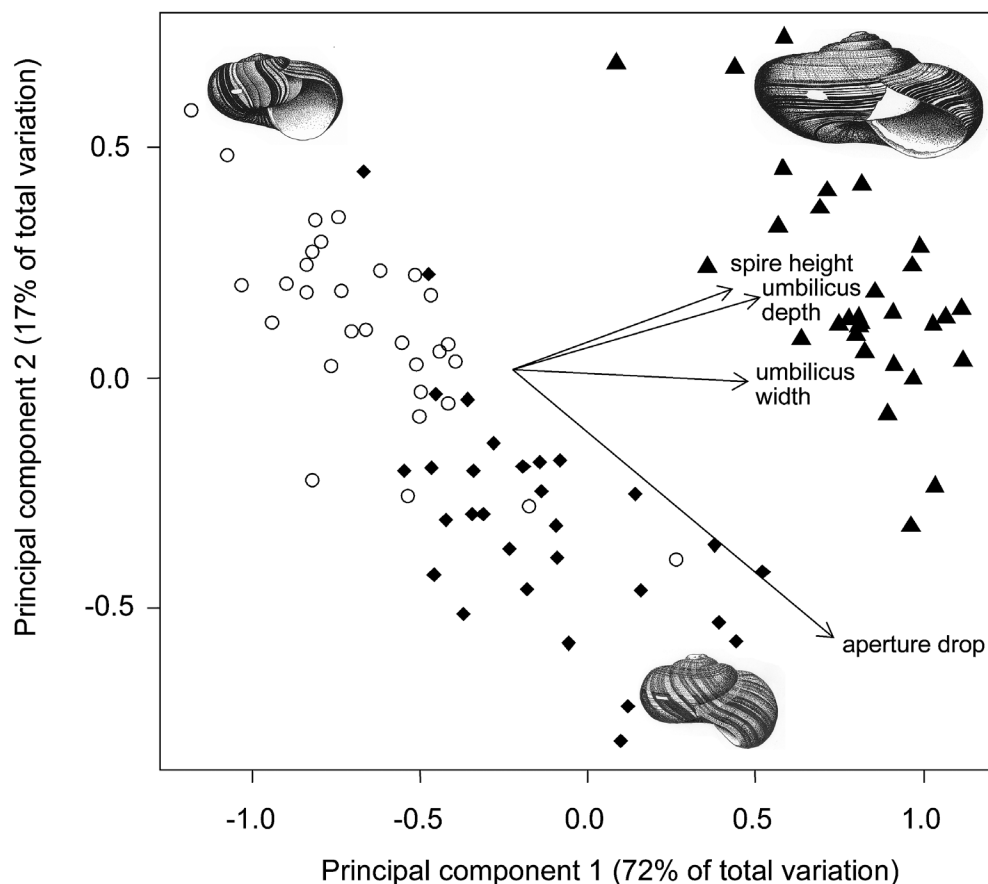


Fig. 5 Plot of the first two principal components of the log-transformed shell measures of *Powelliphanta augusta* n. sp. (black diamonds), its phylogenetically closest related lineage *Powelliphanta lignaria johnstoni* (black triangles) and its spatially and ecologically closest neighbour, *Powelliphanta patrickensis* (open circles).

ventral surface always glossy and dorsal surface sometimes matt due to sculpture of spirally arranged short wrinkles and crescent-shaped malleations. Genitalia characterised with long, thin penis, dark grey to black due to pigmentation of internal epithelium and connective tissue; with the retractor muscle attached apically, and with the vas deferens bound to the side of the organ by fibrous connective tissue to open more or less distant from the penial apex. Bursa copulatrix a large ovate sac, on a short stout duct. No epiphallus, penial sheath or accessory glands on the genitalia. Secondary ureter enclosed. Carnivorous, with enlarged pharynx accommodating a radula with V-shaped rows of large, sharply-pointed aculeate teeth, protrusible for impalement and capture of earthworms and slugs; radula with or (rarely) without a rachidian tooth, and with 50–70 lateral-marginal teeth. Jaw absent.

North, South, Stephens, D'Urville, Arapawa, Maud, Secretary and Resolution Islands, New Zealand.

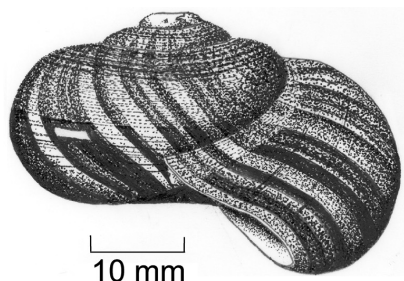
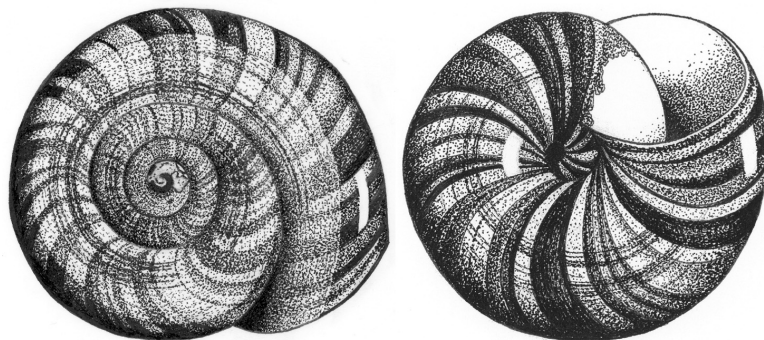


Fig. 6 *Powelliphanta augusta* n. sp. holotype (NMNZ M.277582), actual size 38 mm diameter \times 25 mm height. Illustration: Cathy Jones.



Powelliphanta augusta n. sp.

(Fig. 6, 7; Table 1)

Powelliphanta “Mt Augustus” Hitchmough et al. (2007, p. 35).

Powelliphanta “Augustus” Trewick et al. (2008).

HOLOTYPE: NMNZ M.277582, shell (Fig. 6) collected on 12 March 2007: type locality; snail-search Area 8c, NNE of north peak of Mt Augustus massif, 955 m elevation, Stockton Plateau, north Westland, New Zealand, L29/E 2414704, N 5947941, in shrubland of low mountain beech (*Nothofagus solandri* var. *cliffortioides*) and manuka (*Leptospermum scoparium*).

PARATYPES: 22 in total, all from north peak of the Augustus massif: NMNZ M.277583 (four shells) and AI&M AK73318 (two shells) from L29/2414630–5947675 to 2414650–5947570 in snail-search Areas 3a, 10d and 10c under litter in low mountain beech and leatherwood (*Olearia colensoi*) scrub, and under prostrate manuka and wire rush (*Empodisma minus*) on western escarpment, 950 m elevation; NMNZ M.277584 (four shells) and AI&M AK73319 (two shells) from L29/2414580–5947760 in snail-search Areas 5a, 5b, 6d and 6c under flax (*Phormium cookianum*) and low manuka and wire rush on flat ridge top with scattered small tarns just east of western escarpment, 980 m elevation; NMNZ M.277585 (four shells, three dissected reproductive tracts and one adult body) and AI&M AK73320 (two shells) from L29/2414610–5947940 to 2414800–5947800 in snail-search Areas 4 and 8 under low manuka on gentle slopes east of the ridgeline, 945–955 m elevation.

Fig. 7 *Powelliphanta augusta* n. sp. shells and live animal. **A**, Some of the first recorded shells (36–38 mm diameter) found, collected by Botanical Society in 1996 from the north-east flanks of Mt Augustus showing the characteristics of the “southern” morph of the species. **B**, Profile and dorsal view of an old adult (37 mm diameter) “southern” morph snail found alive on the southeastern flanks of Mt Augustus (Mining Block A11b). **C**, Large (43 mm diameter) old adult “southern” morph snail collected from the ridgeline just west of Mt Augustus (Mining Block A12) and now held in captivity. Note erosion pits on the shell apex, the rapidly descending last whorl, and the fleshy pink colour of the foot between widely-spaced reticulated dark pigmentation. **D**, “Northern” morph snail shells from all parts of the north peak of the Mt Augustus ridgeline (Mining Blocks A10 and A14). Note the stronger axial banding and overall redder shell colour of the “northern” morph (largest shell 38 mm diameter).



DIAGNOSIS: *Powelliphanta augusta* can be distinguished from all other *Powelliphanta* by the presence of underlying narrow red spiral lines over the entire shell (most clearly seen on the shell's dorsal surface) on a small shell (adult size ≤ 44 mm) which in old age has a rapidly descending last whorl.

The diagnostic red spiral lines on *P. augusta* shells have some similarity to those on *P. l. johnstoni*, *P. l. rotella* and *P. l. oconnori*. However, the spiral lines on *P. augusta* are weaker, narrower and more regular in width than that on *P. l. johnstoni* and *P. l. rotella*, and there are conspicuous axial bands on *P. augusta* which are entirely absent in *P. l. johnstoni* (Fig. 4) and *P. l. rotella*. The spiral lines on *P. augusta* shells are more pronounced and redder than those on the strongly-axially banded *P. l. oconnori*. The shells of all *P. lignaria* subspecies are significantly larger and heavier than those of *P. augusta*.

Powelliphanta patrickensis is similar in size to *P. augusta*, but it lacks the diagnostic red spiral lines of *P. augusta*, has a more glossy shell (normally glossy on the dorsal as well as the ventral surface), and a more globose and lower-spired shell.

DESCRIPTION: Shell medium to small for genus (maximum diameter 44 mm), subdiscoidal, with elevated but rounded spire, without the spire nearly rectangular in lateral profile, in mature adults a corkscrew-appearance with pronounced descent of the last whorl from the horizontal plane, about four to five whorls including protoconch of about one whorl, rapidly expanding, slightly inflated, bluntly-shouldered. Final suture impressed; keeled ridge above suture in last whorl. Umbilicus comparatively wide, about 0.2 of maximum diameter, but shallow, revealing only the previous whorl. Shell only weakly calcareous, thin, but with strong, flexible periostracum. From protoconch to periphery, shell microscopically sculptured with close spiral striae, giving the upper surface a matt appearance. Ventral surface glossy and smooth. Aperture elongated oval, with smooth thin edge; parietal callus smooth when viewed macroscopically and pale greyish-white.

Shell ground colour old gold (Ridgeway 1912, pl. 16), with narrow reddish-brown spiral lines always present over the whole shell, faint and sparse below the periphery, but much more conspicuous on dorsal surface. Spiral lines overlain by broad, irregular, mahogany-red (Ridgeway 1912, pl. 2) axial streaks, occasionally so comprehensive above the periphery as to appear a diffuse wash over the entire dorsal surface. Below the periphery, the axial streaks are more dominant and are alternately warm brown shades (mars brown pl. 15, chestnut pl. 2; Ridgeway 1912) and old gold (Fig. 7).

Considerable variability in shell colour and banding and in overall size between individuals (Fig. 7D). Notably smaller and darker shells on snails just north of the north peak of the Augustus massif, with the mahogany red axial streaks tending to be replaced by alternate black, chestnut, antique brown (Ridgeway 1912, pl. 3) and old gold axial bands. Snails just south-west of the north peak are larger and lighter coloured than those further north. Snails on Mt Augustus itself ("southern" morph) have only sparse mars brown axial bands, narrow reddish-brown spiral lines, and occasionally a small circular zone of plain yellow around the umbilicus, free of spiral lines (Fig. 7A–C).

ANIMAL: Foot fleshy-pink to light grey (Ridgeway 1912, pallid purplish gray pl. 53) with dark slate grey (Ridgeway 1912, pl. 53) pigmentation forming regular but widely spaced reticulation (Fig. 7C). Mantle usually pale and mucus clear, but particularly in juveniles the mantle and mucus are sometimes a deep inky blue colour. Short wide tail protruding only a little behind the shell when the animal is active.

REMARKS: Dentition and reproductive anatomy have not previously been used to separate species within *Powelliphanta*, and these characters also proved taxonomically uninformative in separating *P. augusta* from its closest relative, *P. lignaria* (Appendix A).

Powell described (1930, 1932, 1946) and illustrated (1930) the radula of various *Powelliphanta* based on light microscopy. While no information was presented on variation among individuals, Powell's descriptions indicate taxon differences to be subtle and to involve primarily the relative size of the rachidian tooth and numbers of the transverse rows. In this study we found the radula of the very large snails *P. h. anatokiensis* and *P. s. superba* could only be distinguished from that of the smaller snails *P. augustus*, *P. patrickensis*, *P. gilliesi*, and *P. lignaria* by the number of teeth in the transverse rows, which is consistent with scaling of the width of the radula with animal size.

The anatomy of the type species for the genus, *P. h. hochstetteri* (Pfeiffer 1862) is known from the published works of Godwin-Austen (1893), Collinge (1901), Beutler (1901), Powell (1930, 1979), and Schileyko (2000). Our dissection of the subspecies, *P. h. anatokiensis* (not illustrated) generally confirmed these earlier descriptions of the type species. Our dissections of a limited number of individuals from several other species of *Powelliphanta* (not illustrated) found that, in addition to variation among species in size of the genitalia that scale with animal size, there were a few further differences. *P. h. anatokiensis* and *P. s. superba* could be distinguished anatomically from *P. l. lignaria* by possession of a longer vagina, and a longer penis in which the proximal region is lined with scale-like, uniformed-size and distally-oriented papillae, as opposed to upright papillae decreasing in size toward the junction of proximal and distal penis sections. *P. h. anatokiensis* was distinguishable from both *P. s. superba* and *P. l. lignaria* in that the length of the proximal caecum above the entry to the vas deferens was considerably longer. *P. patrickensis* and *P. g. aurea* were very similar in genitalia to *P. l. lignaria*, differing primarily in a slightly longer vagina and slightly shorter penis (relative to the female genitalia) and more strongly developed vas deferens in its proximal sections in the former, and the vas deferens opening closer to the penial apex in the latter. Vaginal length, penis length and degree of dilation of the vas deferens in *P. augusta* varied slightly to that of *P. lignaria*, but these genital differences on their own would not be sufficient to differentiate the taxa.

If these subtle differences in reproductive anatomy are due to more than stage of maturity/activity and preservation artifacts (this is likely, but confirmation requires a much larger sample of dissected animals), then the existing *Powelliphanta* taxonomy based on shell morphology (Powell 1979; Walker 2003) and molecular genetics (Walker 2003; Trewick et al. 2008) is generally mirrored by reproductive anatomy (this study). Using genitalia the species *P. hochstetteri*, *P. superba* and *P. lignaria* were distinguishable, and the close relationship of *P. lignaria* and *P. augusta* was supported. On anatomical grounds the closest relative of *P. augusta* was *P. l. lignaria*, but they were not identical. In contrast, the subspecies of *P. lignaria* appeared to have identical genitalia (with *P. l. johnstoni* indistinguishable from *P. l. lignaria* in this study).

The differences in reproductive anatomy appear less marked than those in shell, animal external morphology, allozymes and mtDNA. Minimal differences were found between the genitalia of *P. g. aurea* and *P. lignaria*, *P. augusta* and *P. patrickensis*, or between *P. s. superba* and *P. h. anatokiensis*, yet these taxa have discrete and distinctive shell morphologies, and the latter pair occur in sympatry with no evidence of interbreeding. They also differ substantially genetically: between *P. g. aurea* and *P. lignaria* there are fixed-differences at six allozyme loci, and mtDNA sequences differ by 11.8%; between *P. augusta* and *P. patrickensis* mean mtDNA sequence divergence is 7.7%; between *P. s. superba* and *P. h. anatokiensis* there are fixed-differences at seven allozyme loci, and mtDNA sequences differ by 9.2% divergence (K. Walker unpubl. data; Trewick et al. 2008).

Given the level of genetic and conchological differentiation, the absence of substantial genital differentiation within *Powelliphanta* perhaps indicates uncoupling of, or different

rates of evolution in these characters, as has been noted in other molluscan studies (Chiba 1999; Alonso et al. 2006; Giokas et al. 2006). It has been hypothesised (Giokas et al. 2006; Thomaz et al. 1996) that both the hermaphrodite reproductive system of many land snails and the spatial structure of their populations (small, isolated, sedentary, “stepping stones”) means there may be little pressure to develop strong sexual isolating mechanisms. In *Powelliphanta*, genital morphology appears to be conserved, and is therefore not informative about reproductive isolation.

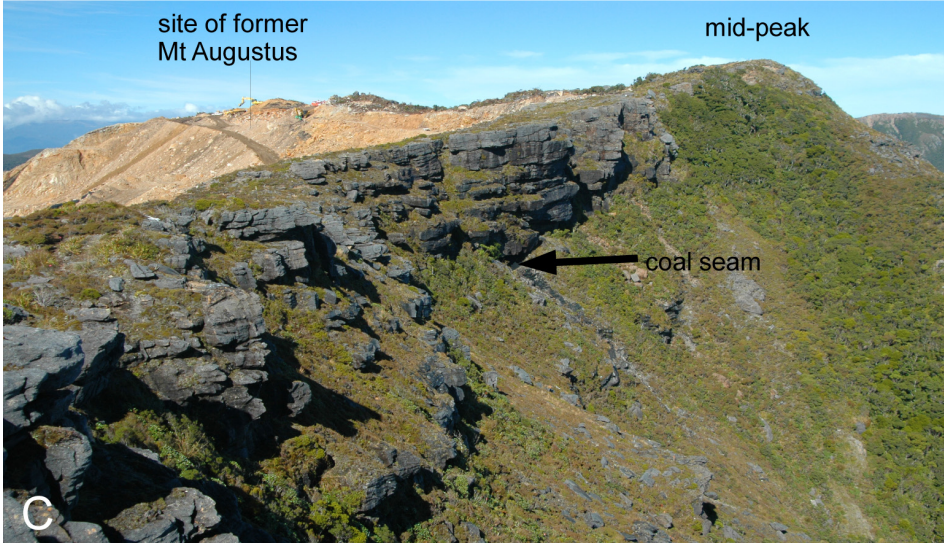
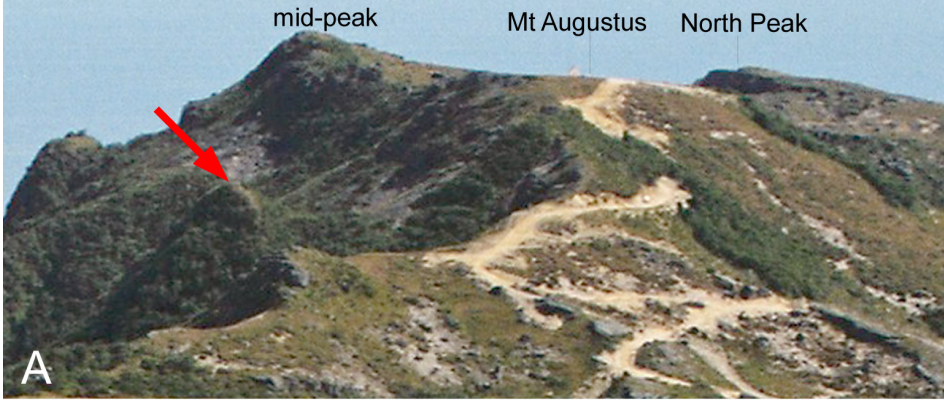
ETYMOLOGY: The species epithet *augusta* is a reference to the Mt Augustus massif, the site this species was apparently naturally confined to. The feminine form, *augusta* was selected for use in conjunction with the feminine genus name *Powelliphanta*. From the Latin adjective *augustus* or French *auguste* meaning “consecrated, venerable”, “Augustus” has come to mean “inspiring reverence and admiration, eminent, dignified” (Brown 1993), which seems apt as a memorial for both the mountain and the snail, since the mountain and snail habitat have now been destroyed by mining.

DISTRIBUTION: Whilst most of the land *P. augusta* formerly occupied has now gone, its distribution was studied in some detail just after the taxon was recognised (2004–05) but before the remaining ridgeline was removed by mining in 2006–07. *P. augusta* was most common at high altitude (940–980 m a.s.l.) on the north peak of the Augustus massif. It also occurred at the same altitudes at the south end of the massif on the ridge just north-west of Mt Augustus, and on the slopes south-east of it. The summit of Mt Augustus and all the northeastern faces had been destroyed by 2004, but as there were snails on its remaining flanks, they probably also formerly occurred on the summit itself at 1011 m.

The three high peaks which together formed the Augustus massif lay on the western escarpment of the Stockton Plateau, and towered on cliffs above the headwaters of Worley Stream and Kerr Stream (Fig. 1, 8). Except for a narrow ridgeline about 10–15 m wide and the north peak, all the land east of the ridge had been mined before the snail surveys began, so it is unclear to what extent the snail populations on Mt Augustus and on the north peak were formerly connected. There was an apparent gap in distribution at and just north of mid-peak (L29/2414620–5947470 to 2414630–5947330), and snails were sparse on the ridgeline either side of this gap. However, the shells found in 1996 by the Botanical Society came from about this latitude but on the eastern side of the ridge, so the two populations may have been continuous on the eastern side but not the west.

On the long ridgeline which forms the western escarpment, snails occurred only on the highest protruding rocky portion here described as the Augustus massif. Snails were absent north of L29/2414685–5948150 and south of about L29/2414885–5947120 where the altitude dropped and the nature of the landform and vegetation changed. To the west, snail densities dropped off sharply with decreasing altitude, with snails absent below about 900 m. To the east, at north peak, snails were still present in high numbers up to the point where the unmodified land met

Fig. 8 Location of *Powelliphanta augusta* n. sp. habitat. **A**, The south-end of the Augustus massif in 1994 when damage to Mt Augustus had just begun (photo: Lloyd Homer, GNS Science). **B**, The south end of the Augustus massif in 2007 when much of the massif had been removed to access the coal seam visible in the right middle distance (photo: Pete Lusk). The amount of snail habitat removed can be seen by lining up the distinctive knob (arrowed) in both (A) and (B). The fence line in the middle distance indicates what the final height of the ridge will be once habitat-stripping is completed. **C**, The western escarpment of the Augustus massif in 2006, looking south-east from north peak to the stump of Mt Augustus. Snails lived in the runnels of vegetation down and just below the cliffs. The entire escarpment is being removed to access the, just visible, seam of coal. ➤





the mined land, at about 940 m. Old pre-mining photos show a topography and vegetation on the rest of the eastern side of the massif similar to snail habitat at north peak. It therefore seems probable that the eastern side of the ridgeline formerly provided much of the species' habitat, particularly as the comparatively gentle slopes meant much more land lay above 900 m than on the steep western slopes.

Since the Augustus massif was mined, the species' natural range has shrunk to a sliver of land (c. 1 ha) below the western escarpment under north peak. Salvaged snails have been artificially transferred to three other sites: to the ridgeline 500–1000 m north of the Augustus massif between L29/2414615–5948190 and 2414580–5948840; to the summit of Mt Rochfort at K29/053–357; and to a small basin just south-west of Mt Rochfort at K29/045–355, about 16 km from the Augustus massif.

HABITAT: Preferred habitat of *P. augusta* was moist soil under dense knee-high vegetation which maintained high levels of ground humidity and supplied comparatively abundant litter material, on and above the outcrops of sandstone forming the Augustus massif. The snails lived only on the highest peaks in an altitudinally demarcated cool microclimate with persistent cloud, and frequent rain and fog.

Powelliphanta augusta lived under the litter in all parts of a mosaic of vegetation types just at and above the tree line, though snail density was very patchy. Field workers searching and retrieving snails before the ridgeline was destroyed reported that plant diversity was a good indication of snail density, with more snails found in complex than in simple vegetation communities. They appeared to prefer the ecotones between subalpine forest and shrubland and between shrubland and low rush-tussockland more than large expanses of either community on its own (Fig. 9). The dominant species of the shrubland were manuka, leatherwood, tussock (*Chionochloa flavescens*, *C. rubra*), mountain flax, *Astelia fragrans*, *Dracophyllum uniflorum*, *Pseudopanax lineare* and *Gahnia procera*. The rush-tussockland largely comprised wire rush, *Chionochloa juncea*, *Celmisia dubia* and manuka, either prostrate or emergent. The forest comprised variable amounts of low stunted mountain beech, pink pine (*Halocarpus biformis*), southern rata (*Metrosideros umbellata*), *Dracophyllum longifolium*, and leatherwood. Plant species diversity over the whole snail colony was significantly higher ($P \leq 0.001$) than on nearby land without snails just north of the Augustus massif, with a mean 28 species (SD = 5.611) per 100 m² plot within the snail colony compared to 18 (SD = 5.059) species per plot just outside it (Bartlett 2006; Walker 2006).

The substrate in the snail colony was hard gritty quartz-rich sandstone with a mean soil pH of 4.3 (SD = 0.199), mean C/N ratio of 27.1, and mean levels of exchangeable calcium of 2.0 me/100 g (SD = 3.264), magnesium 2.7 me/100 g (SD = 2.658) and potassium 0.5 me/100 g (SD = 0.351) (Bartlett 2006; Gruner & Bartlett unpubl. data). While the soils in *P. augusta* habitat were thus acidic, they were significantly more alkaline ($P = 0.021$) and had a lower C/N ratio ($P \leq 0.001$) than the soils outside the snail's range just north of the Augustus massif, where mean pH is 4.1 (SD = 0.145) and mean C/N is 43.3 (SD = 4.892). Just beyond the

◀ **Fig. 9** Habitat types of *Powelliphanta augusta* n. sp. on north peak in 2004–05. **A**, Flax, manuka and inaka shrubland on the edge of low mountain beech and southern rata forest on the northeastern slopes, with overburden piles in the Stockton open cast coal mine in the middle distance and the Glasgow Range on the far horizon. **B**, Rush-tussockland with flax, inaka and scattered emergent manuka amidst small tarns on the summit. **C**, Shrubby ecotone between the mountain beech and rata forest and clearings of wire-rush and tussock on the northern slopes. **D**, Mixed shrubland on the western slopes. The tall forest on the steep land just below the snail colony (right of picture) does not support snails. Westport is just visible at the left-hand end of the coastal flats below.

snail's range exchangeable calcium was lower, but not significantly so (1.8 me/100 g; SD = 1.420, $P = 0.788$), whilst magnesium and potassium levels were similar inside and just outside the snails' range (Bartlett 2006; Gruner & Bartlett unpubl. data).

Long-term mean rainfall recorded at Downertown on the Stockton Plateau, 1.5 km east of the Mt Augustus snail colony is 6.116 m per year with little seasonality (Anderson 2006). As there are strong rainfall gradients (6 mm per m a.s.l.) in this region (Anderson 2006), it is estimated rainfall in the snail colony, 100–200 m above the Downertown Station, was 6.716–7.316 m per year. Even within the snail colony a strong rainfall gradient existed, with about a metre more rain per annum on the top of north peak where most snails lived than just below the western escarpment where snail habitation ceased (Walker 2006). The steep rainfall gradient occurred as the predominant, moisture-laden westerly winds coming off the Tasman Sea were forced up and over the Augustus massif. These physical conditions also caused regular and persistent cloud formation over the Augustus massif, even in otherwise dry sunny weather when lower parts of the ridgeline north and south of the massif were still clear.

The mean daily air temperature at 900 m just below the main snail colony was about 3°C in the winter months (Jun–Aug) and 11–13°C in summer (Jan–Mar). Temperatures would have been 1°C colder at 1000 m at the top of the snail colony, so most of the snails lived in slightly colder temperatures than those at 900 m at the ambient weather station shown in Table 3. For about 3 months of the year, exposed parts of the ground were frequently frozen with frost or, less commonly, snow.

LIFE HISTORY: *Powelliphanta augusta* is evidently normally an out-crossing hermaphrodite, but individuals kept separately in captivity have laid eggs from either stored sperm or self-fertilisation. The fertility of these eggs is as yet unknown. In captivity, breeding *P. augusta* laid on average 2–3 hard-shelled eggs in spring, mostly between late September and October, though some eggs were laid throughout the spring and summer from August to March. Five eggs laid in late October/early December 2005 by snails which had mated shortly after being taken into captivity hatched in December 2006 and January 2007 (i.e., after 12–15 months incubation). Mean size of eggs laid in the wild on north peak was $8.02 (6.99–8.58) \times 6.76 (5.50–7.48)$ mm ($n = 40$) (Department of Conservation unpubl. data). Snails were sexually mature at about 36 mm shell diameter, but productivity seemed to decline in older animals, with more snails in the 36–39 mm shell-size range laying eggs than those over 40 mm. Growth rates and longevity in the wild are unknown, but as *P. augusta* eggs in captivity took about 12–15 months to hatch, compared to 2–6 months for lowland species of *Powelliphanta* in captivity (KJW pers. obs.), *P. augusta* snails may grow more slowly and live longer than their lowland relatives.

Table 3 Air temperature, humidity and rainfall recorded under the western escarpment at the bottom of the snail colony on north peak during the 6 months from July 2006 to February 2007 before the Augustus massif was removed.

Month (2006/07)	No. of days	Rainfall (mm)	Mean monthly humidity (%)	Monthly extremes in temp. (C°)	Mean daily min. air temp. (C°)	Mean daily max. air temp. (C°)	Mean daily air temp. (C°)
Jul 06	23	76.2	80	–1.4–12.1	2.0	5.7	3.8
Aug	31	137.2	90	–2.7–8.5	1.6	5.3	3.2
Sep	30	230.4	93	–0.3–11.3	3.9	7.6	5.7
Oct	31	256.2	90	–2.1–12.9	3.3	7.9	5.5
Nov	30	445.8	95	–0.7–13.1	4.1	9.1	6.6
Dec	31	205.4	89	1.4–14	4.9	10.0	7.2
Jan 07	31	372.2	94	5.4–17.7	9.0	12.7	10.8
Feb	24	165.0	87	7.9–20.5	10.8	15.3	12.8

Prey items seen being eaten in the wild were unidentified species of native earthworm. In captivity snails grew on a diet of exotic earthworms, particularly the pasture worms *Lumbricus rubellus* and *Aporrectodea caliginosa* and the compost worm *Eisenia andrei*. In the wild snails were most active in late spring (Oct–Nov); during winter months (Jun–Aug) when the ground was frozen, snails apparently retreated up to 5 cm underground and buried themselves in litter and soil in crevices formed by large rocks, or in the bases of *Gahnia* or tussocks, and moved very little. Surface activity was greatest on comparatively warm wet nights after a dry spell.

Invariably by the time adults were “middle-aged”, the periostracum had worn from the apex of their shell, and the conchin was pitted (Fig. 7C). In “old age” the erosion was sometimes so extensive that small holes formed right through the shell. While these pits and holes are probably a consequence of reduced shell density from the low-calcium environment the snails were living in, such erosion was almost never found in *Powelliphanta patrickensis*, which similarly has a thin fragile shell and lives in equally or even lower calcium-environments on the Stockton–Denniston coal plateau.

Powelliphanta augusta on the Augustus massif were preyed on by the native weka (*Galirallus australis*), and also by introduced possums (*Trichosurus vulpecula*), ship rats (*Rattus rattus*) and song-thrushes (*Turdus philomelos clarkei*). However, rates of predation were comparatively low: in a sample of 883 fresh shells collected in 2006 from north peak, 72% were intact and these snails probably died of natural causes. Of the rest, 7% had been killed by weka, 10% had been crushed, presumably by people during the preliminary mining activities, and only 11% had been preyed on by exotic pests (5% by possums, 3% by thrushes and 3% by rats).

DISCUSSION

This study found that, using easily visible characters, the large land snail here described as *Powelliphanta augusta* is distinct from all other *Powelliphanta*, with a unique combination of shell-banding pattern, colour, size and shape. A more detailed comparison of shell shape in *P. augusta* and its closest phylogenetic neighbour (*P. lignaria*) and geographic neighbour (*P. patrickensis*) found simple measures of shape alone were sufficient to separate most individuals from these adjacent species.

Shell form can be influenced by environmental selection or by the vagaries of population establishment and genetic drift (Goodfriend 1986; Thomaz et al. 1996; Davison 2002) so caution is required in erecting new snail taxa on the basis of shell morphology alone. An independent, but complementary study using COI mtDNA sequence data supports recognition of *P. augusta* as a monophyletic lineage (Trewick et al. 2008). That study found *P. augusta* differed from *P. lignaria* (its closest extant relative) by an average genetic distance of 3.6%. This is consistent with, though towards the low end of, the range of species-level differences observed in molluscs, and indicates a comparatively recent separation. If an accelerated sequence evolution rate of 5% per million years is applied (fast rates of mtDNA evolution have been inferred in some pulmonates; Chiba 1999), *P. augusta* may have diverged from *P. lignaria* about 700 000 years ago. More conventional calibration rates of change for molluscan COI (ranging from 0.7–2.4% per million years; Hellberg & Vacquier 1999; Marko 2002), imply divergence occurred about 1.5 million years ago, but also within the Pleistocene. The restricted distribution to a single mountain range suggests that *P. augusta* evolved in this region: regional speciation with subsequent local persistence seems to be typical for this genus. The phylogenetic sister relationship of *P. augusta* with *P. lignaria*, rather than with *P. patrickensis*, the closest neighbour geographically and ecologically, suggests independent occupation of the Denniston–Stockton Plateau by *P. augusta* and *P. patrickensis*.

With both shell characters and DNA sequences indicating *P. augusta* is more closely related to *P. lignaria* than to other *Powelliphanta*, why should this taxon not be regarded as a highly distinctive subspecies of *P. lignaria* rather than as a distinct species? Firstly, the level of sequence divergence between these two taxa is, at 3.6%, within the range of genetic distances between other pairs of well-differentiated land snail species. The genetic distance between long-established *Powelliphanta* species ranges from 1.9% between *P. hochstetteri* and *P. traversi* to 13.7% between *P. lignaria* and *P. traversi* (Trewick et al. 2008); the New Zealand rhytidid species *Amborhytida forsythia* and *A. duplicata* differ by 4.6% (Spencer et al. 2006); and species in the Hawaiian subfamily Achatinellinae have a mean divergence among all species of 5.9%, ranging from 0.9% between *Partulina semicarinata* and *Partulina variabilis* to 9.7% between *Achatinella lila* and *Partulina redfieldi* (Holland & Hadfield 2004). The Hawaiian land snail *Succinea quadrata* differs from *Succinea konaensis* by only 2.5% (Rundell et al. 2004), and Douris et al. (1998) studying Cretan land snail radiations also report quite low interspecific differences (e.g., 3.9–4.5% and 2.1–5.1%) for some *Albinaria* species.

Secondly, the differences in shell morphology between *P. augusta* and *P. lignaria* are far more marked than are any of the differences between the existing well-supported subspecies within *P. lignaria*. (Within *P. lignaria* the described subspecies have easily recognisable constant shell morphology within their respective distributional areas, and differ in environmental preferences.) Whilst a reduction in shell size and thickness in *P. augusta* could reasonably be assumed to be a response to the low pH/low Ca environment of the Stockton coal plateau, other *P. lignaria* subspecies confined to similarly acidic and mineral-depleted environments (i.e., *P. l. rotella* and *P. l. johnstoni* in wire-rush and yellow-silver pine pakihi bogs) have retained their large and heavy shells. This evidence suggests that *P. augusta* is not simply an extreme ecological variant within the *P. lignaria* lineage.

Powelliphanta augusta seems nonetheless to be a specialist of an unusual niche. It survived within an inhospitably acidic and infertile environment by exploitation of the one part which was slightly but significantly more fertile, less acidic, wetter, and with more continuous and extensive pockets of deeper-soil than the surrounding landscape. Probably as a consequence of these characteristics, the flora of the snail habitat was also significantly more diverse than that on land without snails nearby. With so much of the Stockton Plateau including Mt Augustus mined before the snails were discovered, and with the loss of most of the rest of the snail's habitat only a couple of years after this, knowledge of this species' environment, gleaned in the brief interlude between discovery and demise, is irreplaceable. For this reason, and because some of the snails but not their habitat were retained, this environment has been described here at length.

In the absence of other habitat of the same character and quality but lacking competing *P. patrickensis* populations, the best chance for survival of this species in the wild probably lies in the sliver of habitat left under the western escarpment on completion of coal mining. This is low quality habitat on the margins of the former north peak snail colony, and is fragmented by the intrusion of barren unsuitable habitat. Further, it may become drier with the removal of the Augustus massif above it as the landform itself appeared in large part responsible for the creation of the local cloud cover which formerly characterised it.

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provided the drawings of *P. patrickensis*, *P. lignaria* and *P. augusta*. Graeme Elliott helped with the principal components analysis, and with Rod Hitchmough and Ingrid Gruner provided useful comments which helped improve the manuscript. Constructive comments by M. G. Hadfield and an anonymous reviewer greatly improved the final paper. We thank all these people, particularly Ingrid Gruner whose contributions to knowledge of *P. augusta* have been substantial.

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Appendix A Anatomy of *Powelliphanta augusta* n. sp.

REPRODUCTIVE SYSTEM: (Fig. 10, 11) Ototestis consisting of 3 clusters of claviform lobes, embedded on dorsocolumellar side of the digestive gland. Hermaphrodite duct rather long, for the greater part highly convoluted and modestly distended, but narrowing to its entry to carrefour which has a vesicular seminalis as short bulbous-headed diverticulum. Albumen gland linguiform, varying considerably in size with phase in reproductive activity. Male and female pallial gonoducts fused and thus of spermooviduct condition, rather long, slender; female part with weak transversal folds; prostatic part a ribbon of acini along entire length. Free oviduct rather short. Bursa copulatrix duct short, stout; bursa copulatrix reservoir an oval sac, bound to the spermooviduct by fine connective tissue that extends to the vicinity of the pericardium. Vagina moderately long, with numerous muscle strands connecting the organ with the body wall. Vas deferens proximally convoluted and modestly distended, narrowing distally to run around oviduct-penial junction and extending along penis, bound to side of the latter by fibrous connective tissue, to open below penial apex. In life, the phallus lies across the pharynx, the right tentacular retractor muscle crossing over it at the distal end. Phallus rather long, dark grey to black due to coloration of the luminal epithelium and the underlying connective tissues; proximal part slightly bulbous, internally with the epithelium thrown into numerous, upright conical to scale-like papillae that decrease in size towards distal penis; these papillae are enlarged around the perimeter of a furrow leading a short distance from the opening of the vas deferens towards the penial apex; distal penis more or less cylindrical, with the internal epithelium produced as longitudinal folds which are initially weakly papillate and reticulated, but become more or less smooth towards genital opening. Atrium very short, essentially a shallow vesicle via which the male and female open more or less separately to the body exterior. Genital opening on the right side mid way between the pneumostome and the base of the right ocular peduncle.

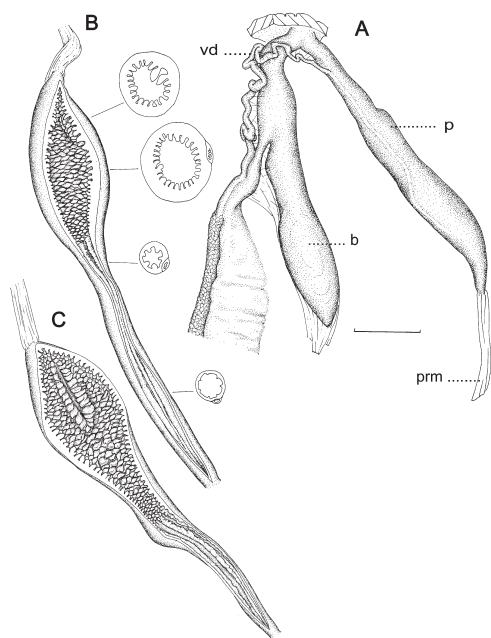


Fig. 10 Genitalia of *Powelliphanta augusta* n. sp. **A**, General view (paratype NMNZ.M.277585). Note that the numerous muscle strands that bind the vagina to the right body wall in life are not illustrated. Scale line 5 mm. **B, C**, (paratype NMNZ.M.277585). Penis, opened longitudinally to show internal structure. Note the papillae lining the proximal penis, which are elaborated around the furrow running from the opening of the vas deferens towards the penial apex. b, bursa copulatrix; p, penis; prm, penial retractor muscle; vd, vas deferens.

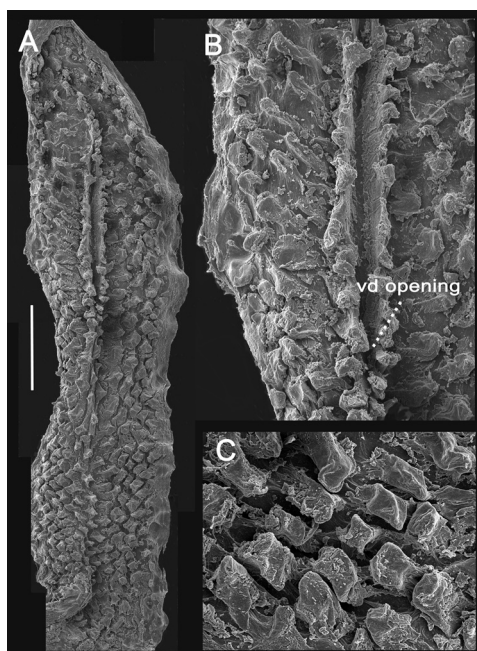


Fig. 11 Scanning electron micrographs of the papillae lining the proximal penis in *Powelliphanta augusta* n. sp., topotype. **A**, Overview of apical region of the penis, with surface covered in papillae and elaborated around the furrow running from the opening of the vas deferens towards the penial apex. Scale line 1 mm. **B, C**, Close-up views of the furrow and papillae from the general penial wall. vd, vas deferens.

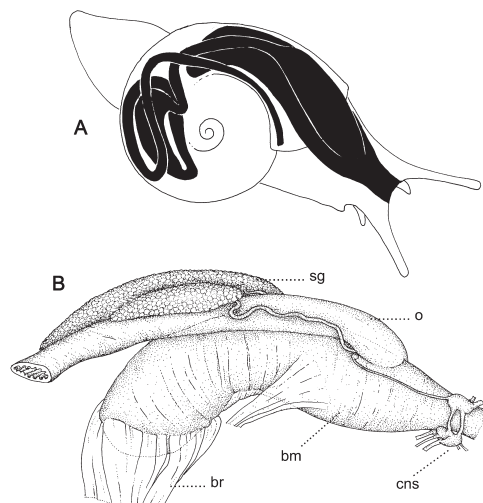


Fig. 12 Digestive tract of *Powelliphanta augusta* n. sp. topotype. **A**, Layout of digestive tract (schematic). **B**, Right lateral view of the pharynx and associated oesophagus and salivary glands. bm, buccal mass; br, buccal retractor; cns, central nervous system; o, oesophagus; sg, salivary gland.

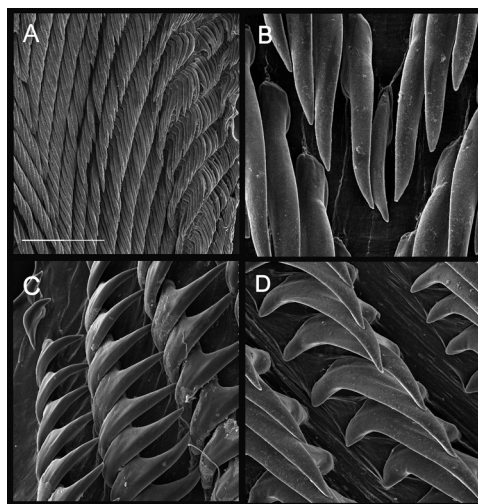


Fig. 13 Scanning electron micrographs of the radular dentition of *Powelliphanta augusta* n. sp. topotype. **A**, Overview of the radular dentition, showing V-shaped rows of teeth. Scale line 500 µm. **B–D**, Detail of central tooth and adjacent lateral teeth, marginal teeth, lateral teeth, respectively.

Penial retractor muscle long, arising from diaphragm at posterior of pallial cavity. No spermatophore produced. Seminal material, comprising a multi-layered ovoid mass, evidently deposited directly into bursa copulatrix during mating.

DIGESTIVE TRACT: (Fig. 12) Pharynx enlarged, long, cylindrical, occupying almost all the cephalic space, with massive retractor muscles attached to posterior, and weaker retractors attached mid laterally; radular sac weakly protruding from posterior of pharynx. Oesophagus slender, long, arising from the dorso-anterior aspect of the pharynx, abruptly giving rise to a dilated stomach. Intestine extending in a short anteriorly-directed loop to abut the kidney, then producing a short posteriorly-directed loop before running forwards to anus in mantle collar. Salivary glands flanking the oesophagus, unequal in size with the right gland small.

RADULA: (Fig. 13) with V-shaped transverse rows of unicuspid, sharply-pointed, aculeate teeth, each row with formula $59-60 + 1 + 59-60$. The rachidian tooth is about half the size of the lateral teeth. There is no clear differentiation between lateral and marginals, just a simple gradation from elongate lanceolate form to small, more or less triangular form. The teeth increase in size from the centre to a maximum at about tooth 50, then decrease gradually towards the radular margin.

PALLIAL COMPLEX: Pulmonary cavity deep, extending to about 0.5 of the body whorl; venation of the roof modestly developed. Kidney triangular, extending to about 0.25-0.3 of pulmonary cavity, with pericardium extending along the greater part of its left wall. Ureter sigmoid, closed to the excretory orifice adjacent to the pneumostome, rather broad in its primary arm along the anterior face of the kidney, more slender in its secondary part along the rectum.

FREE MUSCLE SYSTEM: Columellar muscle extending forwards as a broad fan, attaching to pedal and lateral body walls, and near its origin giving rise to paired tentacular retractors, each of which divides anteriorly into branches to ocular peduncle, inferior tentacle, and cephalic body wall. Right ocular retractor passing across phallus. Buccal retractors originating from columellar stem adjacent to and immediately in front of tentacular muscles, extending anteriorly as a broad ribbon to attachment to posterior and posterior-lateral aspects of the pharynx.