KOKOPAPA, A NEW GENUS OF LAND SNAILS (PULMONATA: PUNCTIDAE). WITH DESCRIPTION OF SIX NEW SPECIES AND DISCUSSION OF SOUTH ISLAND, NEW ZEALAND BIOGEOGRAPHY

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ABSTRACT - *Kokopapa* n. gen. and six member species are described from New Zealand. With the exception of one widespread species, all occur on the west coast of the South Island from Oparara, Karamea to Stewart Island. The species and their distributions are discussed in paleogeographical and biogeographical context. The distributions of two *Kokopapa* species with distinct triangular periostracal spikes are transcurrently displaced along the Alpine Fault which had its inception ca. 23 million years ago. Faults, that were inherited from Late Cretaceous-Paleocene and Eocene extensional tectonics and that are undergoing compressional inversion since the change in the Pacific-Australia plate motions between 25-20 Ma (inception of the Alpine Fault), are also associated with the distributions of other Kokopapa species. These correlations suggest that the ancestors of these species persisted through the Cenozoic despite claims for New Zealand being completely submerged at this time. Detailed geological mapping also provides evidence for persistent terrestrial conditions through the Cenozoic and it is argued here that due to the mobile geological nature of the New Zealand terrain, small refugia existed throughout this time that supported ancestral land snail populations, including *Kokopapa* species.

KEYWORDS - Mollusca, new species, taxonomy, ecology, heterochtony, paleogeography, biogeography, disjunction, endemism.

INTRODUCTION

New Zealand is a centre of diversity for punctid land snails. Spencer *et al.* (2009) list 90 described and 259 undescribed punctid species. Many have restricted distribution ranges and are recorded in the Department of Conservation inventory of threatened species as species of conservation concern (Hitchmough *et al*, 2007). This paper addresses the lack of formal taxonomic treatments of New Zealand land snails by introducing a new genus and six new species of minute punctid snails. The teleoconch ontogeny and distributions of species of *Kokopapa* n. gen. present an interesting case of heterochrony and South Island biogeography.

In recent years biogeography has experienced a revival in New Zealand and the debate about the Oligocene drowning of the New Zealand microcontinent has even spilled over into newspapers with letters to editors and discussions on public radio. The prevalent view on New Zealand biogeography is that many organisms became extinct over vast tracks of land due to the effects of marine transgressions during Cenozoic time and Pleistocene glaciations, and that New Zealand's present fauna and flora is the result of widespread dispersal from elsewhere (predominantly Australia). This view does not take into account geological evidence for terrestrial landscapes during the Oligocene and the possibility that even small and ephemeral (in geological time) islands could have provided refugia from which subsequent remergent land was repopulated. Evidence from detailed geological mapping on the west coast of the South Island, an area that was widely inundated by the sea in the Oligocene, and species distributions of minute punctid snails are presented here to demonstrate an alternative understanding of New Zealand Cenozoic biogeography.

MATERIALS AND METHODS

Snail shells were illustrated with the aid of a drawing tube attached to a "Wild M7A" stereomicroscope. Shell dimensions were measured using a microscope eyepiece graticule. Some specimens were mounted and then carbon and gold/palladium coated for scanning electron microscopy and others were photographed in colour using automontage software. For dissection, specimens were submerged in 70 percent ethanol. Dissecting tools were made of ends of 3 mm square plastic strips that served as handles with 0.11 mm entomological pins melted into one end. The anatomical illustrations were drawn free hand. The examined material is held in the collections of Museum of New Zealand Te Papa Tongarewa (NMNZ). Charopidae and Punctidae species numbers refer to species vouchers in the collections of Museum of New Zealand Te Papa Tongarewa. Localities mentioned in the text are mapped in Fig. 9.

TAXONOMY

Superfamily PUNCTOIDEA Morse, 1864

Family PUNCTIDAE Morse, 1864
Genus *Kokopapa* new genus

Type species: *Kokopapa unispathulata* n. sp.; Recent, New Zealand.

DIAGNOSIS. Minute, narrowly umbilicate shells of pyramidal to domed architecture. Shells coloured light gold to green-bronze; flat base highly glossy with a metallic silvery shine (especially in fresh shells). Periphery adorned with two rows of spathulate or spike shaped processes. Umbilicus partially covered by a columellar reflection of the lip, which is otherwise simple. Suture slightly impressed. Aperture trapezoidal, without barriers. Protoconch of convex to broadly convex shape sculptured throughout with fine, twisted spiral cords knotted around low axial wrinkles, forming segments on axial folds. Teleoconch whorls convex in profile, variably flattened between two rows of peripheral processes from species to species. Periphery of last whorl strongly angular. Primary axials calcareous with elaborate periostracal spike- or spoon-shaped blades. Micro-sculpture consisting of fine, entirely periostracal, secondary axials and fine calcareous spiral corrugations, best visible on shell base.

Anatomy. Only known for *Kokopapa unispathulata* n. sp. (see below).

REMARKS. Further analyses of inter-generic relationships are required to determine the taxonomic position of *Kokopapa* n. gen. in a punctid family context. The shells of *Kokopapa* species are domed to pyramidal like many laomine species but unicolouredness is characteristic of punctine species. *Laoma ciliata* Suter, 1894 is the only unicoloured laomine species with multi-lamellate periostracal blades but also has apertural teeth that are lacking in *Kokopapa* species. Multi-lamellate blades are also found in the punctine species *Obanella spectabilis* (Powell, 1928) and some undescribed relatives, but the shape of the periostracal blades have a broader base and are more rounded. At the current level of analysis, all we can say is that *Kokopapa* species have a combination of laomine and punctine characteristics. Another feature that the genus *Kokopapa* shares with punctine genera is the North and South Island distribution of *K. unispathulata* n. sp. whereas most laomine species occur either north or south of Cook Strait. The reproductive anatomy of *Kokopapa unispathulata* n. sp. is similar in complexity to laomine anatomies while punctine terminal genitalia are structurally simpler.

Kokopapa unispathulata n. sp., *K. bispathulata* n. sp., *K. milleneri* n. sp., *K. mokihinui* n. sp., *K. rapahoe* n. sp. and *K. mataura* n. sp. are ground-dwellers and are found in slimy, wet places near seepages, under rocks and logs, nikau palm (Rhopalostylis) and treefern fronds, wet and muddy places on the forest floor and in cavities. The snails are often camouflaged because dirt sticks to the periostracal processes. They can be found amongst flax (*Phormium*), in coastal shrub/bush remnants, mixed broadleaf forest and beech (*Nothofagus*) forest. The altitudinal range of the genus extends from sea level to the montane zone.

ETYMOLOGY. Maori, *koko* (shovel, scoop, spoon) and *papa* (shell of mollusc), with reference to the distinctive shell ornamentation.

Kokopapa unispathulata new species
Figs 1A, 2, 3A-B, 4, Plate 1E-H

Punctidae sp. 50 (NMNZ M.14135) Spencer *et al.*, 2009.

DESCRIPTION. Shell up to 3.1 mm wide, 2.9 mm high, narrowly umbilicate, domed. Protoconch of 1.5-1.75 whorls, up to 710 µm in diameter, broadly convex, sculptured with 30-35 spiral cords. Teleoconch of up to 4.75 whorls with approximately 22-32 primary axial folds on the second postnuclear whorl. All whorls ornamented with 2 rows of peripheral processes, one supramedian the other peripheral. At first both processes start as weakly tapering spikes made of adaperturally in-rolled, narrow blades, then adapical processes become spathulate by progressive out-folding of distal part whereas peripheral processes remain spike-shaped.

Anatomy. Reproductive structures relatively compact (Fig. 4). Oviduct similar in diameter but slightly longer than spermathecal base, both broadly round. Apical part of spermatheca large and elongate-ovate. Hermaphroditic duct short, broad and kinked. Gonads relatively large, bilobed; each lobe consisting of several elongate acini. Albumen gland roundly ovate, alveoli small; round talon on stalk buried in albumen gland. Prostatic gland compact with large folds; uterus surface smooth. Vagina relatively long, cylindrical. Vas deferens loops around penis retractor muscle near its attachment point at apex of phallus close to vas deferens entrance. Vas deferens enters phallus lumen as a short free hanging papilla with divided fringe. Apical part of phallus more expanded than basal part, which slowly tapers towards atrium. Phallus interior with three slim,

longitudinal pilasters in lower part of lumen; two of them merge below another oval pilaster, which is divided into 4, partially free hanging folds that taper into thinner strands towards apex taking up half of the apical lumen space. Third longitudinal pilaster connects to second apical pilaster shaped like an oval doughnut with a median longitudinal pilaster. Kidney (Fig. 4B) bilobed, pericardial lobe longer than rectal one. Secondary ureter opens just below pneumostome (missing in this dissection), mantle gland present.

TYPE MATERIAL. Holotype NMNZ M.14135: Hapuku, Kaikoura, P31/708763, W.L. Wallace, 1910, ex Oliver Collection (2.7 mm wide, 2.4 mm high, 5.5 whorls); 6 paratypes from same locality, NMNZ M.129976.

OTHER MATERIAL EXAMINED. 554 lots (NMNZ).

DISTRIBUTION. North, South, Stewart Islands (Figs 1, 2).

REMARKS. *K. unispathulata* n. sp. is the most widespread species (Fig. 1). The shells are more beehive-shaped than the shells of *K. rapahoe* n. sp. and *K. matarua* n. sp., which are more pyramidal in shape. *Kokopapa unispathulata* n. sp. shells are taller but similar in shell diameter to *K. milleneri* n. sp. and *K. mokihinui* n. sp. *K. bispathulata* n. sp. shells are larger and flatter than *Kokopapa unispathulata* n. sp. shells. The distance between the two sets of peripheral processes is larger in *K. unispathulata* n. sp. than in the other species and the stalk of the spathulate processes is also longer than in the other species (Fig. 1, Plate 1).

ETYMOLOGY. Latin *unus*, meaning one, single, alone; Latin *spatha*, meaning paddle for stirring or mixing, spoon.

Kokopapa bispathulata new species
Figs 1C, 2, 5, Plate 1A-B

Punctidae sp. 52 (NMNZ M.78614) Spencer *et al.*, 2009.
Laoma regularis: Suter, 1913, p. 756; Suter, 1915, plate 30, fig. 3; Powell, 1979, p. 329, plate 59, fig. 22 (Not *Helix regularis* Pfeiffer, 1855).

DESCRIPTION. Shell up to 3.65 mm wide, 2.8 mm high, narrowly umbilicate, pyramidal. Protoconch of 1.5-1.75 whorls, convex, up to 750 µm in diameter, sculptured with 20-25 spiral, twisted cords. Teleoconch of up to 5 whorls, with up to 39 primary axial folds on 2nd postnuclear whorl. All whorls with 2 rows of peripheral blades; at first both processes similar, weakly tapering spikes, then spikes become stalked spathulae by progressive out-folding of distal part of blade.

Anatomy of the animal is unknown.

TYPE MATERIAL. Holotype NMNZ M.78614: Barrytown-Croesus Track, Westland, K31/722833, G. Mason, 19.5.1983, under ponga log (3.25 mm wide, 2.05 mm high, 5.5 whorls); 1 paratype NMNZ M.86315: Pororari River, Punakaiki, A.C. O'Connor, -/1/1949.

OTHER MATERIAL EXAMINED. 33 lots (NMNZ).

DISTRIBUTION. South Island, Westland: Honeycomb Hill Cave System at Oparara, Fox River Cave and surroundings, Punakaiki, Pororari, Barrytown, (Figs 1, 2).

REMARKS. *K. bispathulata* n. sp. is the only species where both sets of processes change synchronically from the juvenile spike-like into the adult spathulate form. The spathulate processes of *K. bispathulata* n. sp. are on shorter stalks (Plate 1B) in comparison to those of *K. milleneri* n. sp. and *K. unispathulata* n. sp. The short spathulate processes of *K. rapahoe* n. sp. are broader than those of *K. bispathulata* n. sp.

Suter (1913, 1915) and Powell (1979) refer to specimens of *K. bispathulata* n. sp. as *Laoma regularis* (Pfeiffer, 1855) but Climo (1979) showed, that *Helix regularis* Pfeiffer is in fact a species of the helicarionid genus *Coneuplecta* Moellendorff, 1893. Suter (1915) and Powell (1979) illustrate and describe a shell with two rows of spathulate processes like *K. bispathulata* n. sp. but the shell drawings resemble that of *K. rapahoe* n. sp.

ETYMOLOGY. From Latin bi-, referring to two sets of spathulate processes.

Kokopapa matarua new species
Figs 1F, Plates 1C-D, 2

Punctidae sp. 54 (NMNZ M.37831) Spencer *et al.*, 2009.

DESCRIPTION. Shell up to 3.25 mm wide, 2.95 mm high, narrowly umbilicate, pyramidal. Protoconch of 1.5 to 1.75 whorls, up to 710 µm in diameter with 18-22 spirals. Teleoconch of up to 4.75 whorls; all whorls with 2 rows of triangular processes, one supraperipheral and one peripheral. Supraperipheral process always 3 or 4 times smaller than peripheral one. Second postnuclear whorl sculptured with up to 44 primary axials.

Anatomy of the animal is unknown.

TYPE MATERIAL. Holotype NMNZ M.86307: Stewart Island, southern end of Sealer's Bay, Codfish Island, D48/015690, F.M. Climo, 16.11.1973. (2.7 mm wide, 2.6 mm high, 6 whorls); 5 paratypes from same locality, NMNZ M.37831.

OTHER MATERIAL EXAMINED. 9 lots (NMNZ).

DISTRIBUTION. South Island: Fiordland, Southland; Codfish Island (Stewart Island; Fig. 1).

REMARKS. The two sets of processes of *K. matarua* n. sp. and *K. mokihinui* n. sp. are both triangular and keep this shape throughout shell growth. In both species the adapical processes are always smaller than the abapical ones. *K. matarua* n. sp. is of intermediate height and diameter with respect to the other five species.

ETYMOLOGY. Double pointed (Maori).

Kokopapa mokihinui new species
Figs 1D, 2, Plate 2

Punctidae sp. 55 (NMNZ M.79947) Spencer *et al.*, 2009.
Punctidae sp. 233 (NMNZ M.77777) Spencer *et al.*, 2009; Hitchmough *et al.*, 2007.

DESCRIPTION. Shell up to 2.55 mm wide, 2.3 mm high, narrowly umbilicate, pyramidal. Protoconch of 1.5 to 1.75 whorls, up to 710 µm in diameter with ca. 20 spiral cords. Up to four teleoconch whorls, all whorls with two rows of triangular, peripheral blades, supraperipheral blades smaller than peripheral ones. Up to 41 primary axials on 2nd postnuclear whorl.

Anatomy of the animal is unknown.

TYPE MATERIAL. Holotype NMNZ M. 77777: Corbyvale, 6.1 km from Karamea Bluff, L28/327703, D.J. Roscoe, 28.12.1980 (2.45 mm wide, 1.95 mm high, 5.25 whorls). 11 paratypes from same locality, NMNZ M.115017.

OTHER MATERIAL EXAMINED. 2 lots (NMNZ).

DISTRIBUTION. South Island: Karamea, northern Westland (Figs 1 & 2).

REMARKS. *K. mokihinui* n. sp. and *K. matarua* n. sp. share the same type of periostracal processes, but *K mokihinui* n. sp. shells are smaller and flatter (Fig. 1D & F).

ETYMOLOGY. Mokihinui is the Maori name of a river near the type locality.

Kokopapa rapahoe new species
Figs 1E, 2, Plate 2

Punctidae sp. 252 (NMNZ M.96782) Spencer *et al.*, 2009; Hitchmough *et al.*, 2007.

DESCRIPTION. Shell up to 3.95 mm wide, 3.45 mm high, narrowly umbilicate, pyramidal. Protoconch of 1.5 to 1.75 whorls, up to 700 µm wide ornamented with ca. 20 spiral cords. Up to 6.25 teleoconch whorls,

supraperipheral and peripheral processes close together. Supraperipheral spike smaller than peripheral spathula. Up to 30 primary axials on 2nd postnuclear whorl.

Anatomy of the animal is unknown.

TYPE MATERIAL. Holotype NMNZ M.98776: Ace Motel, Greymouth, J31/638604, P. Mayhill, -.1.1988 (4.85 mm wide, 3.45 mm high, 6.75 whorls). 1 paratype from the same locality, NMNZ M.129977.

OTHER MATERIAL EXAMINED. 8 lots (NMNZ).

DISTRIBUTION. South Island: Westland, near Greymouth (Figs 1 & 2).

REMARKS. This is the largest *Kokopapa* species at maturity. The stalk of the spathulate processes is broader (similar to *K. milleneri* n. sp.) and much shorter than the periostracal stalk of *K. unispathulata* n. sp. or *K. bispathulata* n. sp.

ETYMOLOGY. Rapahoe is the Maori name of a small township near Greymouth, the type locality.

Kokopapa milleneri new species
Figs 1B, 2, 3C-F

Punctidae sp. 53 (NMNZ M.79720) Spencer *et al.*, 2009.

DESCRIPTION. Shell up to 2.8 mm wide, 2.45 mm high, narrowly umbilicate, pyramidal. Protoconch of 1.5 to 1.75 volutions, up to 620 µm in diameter, sculptured by ca. 25 very fine spiral cords. Ca. 4.5 teleoconch whorls, up to 40 primary axials on 2nd postnuclear whorl. Supraperipheral and peripheral processes close to each other, supraperipheral spoon-shaped, peripheral spike-shaped, peripheral blade smaller than supraperipheral.

Anatomy of the animal is unknown.

TYPE MATERIAL. Holotype NMNZ M. 79720: Swanburn Creek, Heaphy Track, SW Nelson, L26/347147, B.F. Hazelwood, 21.4.1984 (2.65 mm wide, 2.35 mm high, 6 whorls). **Paratypes** NMNZ M.86318: Swanburn Creek, Heaphy Track, SW Nelson, B.F. Hazelwood, 21.4.1984.

OTHER MATERIAL EXAMINED. 19 lots (NMNZ).

DISTRIBUTION. South Island: NW Nelson to Oparara, Karamea (Figs 1 & 2).

REMARKS. The two sets of the periostracal processes of *K. milleneri* n. sp. and *K. rapahoe* n. sp. shells are different in form, one set spike-like, one set spathulate. The spathulate processes are supraperipheral in the former species and subperipheral in the latter. Shell diameter and height as well as protoconch diameter are smallest in *K. milleneri* n. sp. Shells of *K. unispathulata* n. sp. are of similar shell diameter but the shells are taller.

ETYMOLOGY. Named in honour of our former colleague and paleo-ornithologist Dr P.R. Millener who has provided NMNZ with many specimens from various cave sites around Oparara, Karamea.

DISCUSSION

Taxonomy

The axial periostracal teleoconch blades of *Kokopapa* species differ in shape and size, and during shell growth they change from being in-rolled in the juvenile to fully unfolded processes in the adults of *Kokopapa bispathulata* (Figs. 1- 3, 5; Plate 2), while only one set of the periostracal processes change to the adult form in *Kokopapa unispathulata*, *K. milleneri* and *K. rapahoe*. The other two species develop the stalk but not the oval-shaped tip. Altogether there are four different sets of teleoconch periostracal processes (Figs 1 & 2):

i) spathulate adapical process and spike-like abapical process (*K. unispathulata* n. sp., *K. milleneri* n. sp.);
ii) smaller, triangular adapical process and larger, triangular abapical process (*K. matarua* n. sp., *K. mokihinui* n. sp.);
iii) spathulate adapical and abapical process (*K. bispathulata* n. sp.);
iv) spike-shaped adapical process and spathulate abapical blade (*K. rapahoe* n. sp.).

Another combination - larger, adapical triangular process and smaller, abapical triangular blade - is not developed in *Kokopapa* species but is found in *Laoma ciliata*, which occurs in the North Island.

Changes in the onset and the duration of developmental stages lead to differences in shape and size of characters and are associated with the concept of heterochrony. In terms of onset and offset of the developmental stage involved with forming the periostracal teleoconch processes, the smaller triangular processes in *Kokopapa mokihinui* and *Kokopapa matarua* are neotenic or progenetic, i.e., the juvenile state is retained in the adult. Obviously there are on and off switches in gene expressions involved and also different combinations of them in the two bands of teleoconch processes. However, the morphology of the ancestors is not known and heterochronic terms are difficult to apply under these circumstances.

Analysis of *Kokopapa* distributions provides a biogeographic source of evidence for timing the divergence of species and therefore the geological and geomorphic setting for the common ancestor.

Biogeography

The only widespread species, *K. unispathulata*, occurs in the North and South Islands of New Zealand, whereas all the other species are restricted to the west coast of the South Island and Stewart Island. Most species occur in close vicinity of each other in northern Westland, which is also a centre of taxonomic diversity for other rhytidid, punctid and charopid genera (see discussion). Like *Kokopapa* n. gen., many New Zealand land snail genera consist of a widespread species or cryptic species complexes and several other more localized and geographically largely non-overlapping peripheral species.

The distributions of *Kokopapa matarua* and *K. mokihinui* (Fig. 1) provide a classic example of the Alpine Fault disjunction (Figs. 6-8) described by Henderson (1985), and subsequently supported by Heads (1990, 1998), Heads & Craw (2004), Fenwick & Marshall (2006), Gibbs (2006) and authors cited in these publications. When reconstructions of New Zealand prior to transcurrent movement on the Alpine Fault are considered, ancestral populations of the now disjunct populations of *K. mokihinui* and *K. matarua* would have been much closer together when Nelson and Fiordland were adjacent to each other in the early Miocene about 20 Ma (Fig. 6). Most of the transcurrent movement occurred in the late Miocene (King, 1999). This tectonic correlation provides a minimum age for the peripheral and supraperipheral periostracal spikes being already present in the ancestral populations before they were geographically isolated.

The same North West Nelson-Fiordland disjunction is also found for the large, carnivous rhytidid snails *Powelliphanta annectens* (Powell, 1930), *P. superba* (Powell, 1930) and *P. spedeni* (Powell, 1930) and also pairs of small charopid snails (Fig. 8). *P. annectens.* and *P. superba* (NW Nelson–Karamea) are most closely related to *P. spedeni lateumbilicata* in Fiordland (Walker, 2003, Appendix 2; Trewick *et al*., 2008). Many other plants and animals also have disjunct Nelson-Fiordland/Stewart Island distributions (Heads, 1998) and even broader disjunctions spanning the distance from Northland to Nelson and/or Fiordland occur in the punctine genus *Taguahelix* Powell, 1955 (Climo, 1992).

Two *Kokopapa* species have their distribution limits at Karamea: *Kokopapa milleneri* n. sp. occurs in NW Nelson and reaches its southern limit at Oparara, Karamea, where *K. bispathulata* n. sp. has its northern limit (Fig. 2, open squares and diagonal crosses respectively). Other NW Nelson endemic gastropod species that reach their southern limit at Karamea are *Phacussa oconnori* (Powell, 1941), *Thalassohelix prousei* Powell, 1952 (also Kaikoura), *Flammulina* aff. *lateaperta* n. sp., and Punctidae sp. 3. Charopidae sp. 87 is endemic to Kohaihai just north of Oparara and Charopidae sp. 195 is only found at Kohaihai, Oparara and Mokihinui (Mahlfeld, 2005). Punctidae sp. 181 is most diverse at Oparara, where four colour forms occur (Craw *et al.*, 1999, Fig. 7-3d). *Powelliphanta superba*-group and *Powelliphanta annectens* snails only occur north of Karamea. An early Miocene paleogeographic reconstruction (Fig. 6) shows emergent land, Karamea Peninsula, that largely coincides with the distributions of the endemic species mentioned above. The distribution of *Kokopapa bispathulata* is disjunct across the Paparoa basin occurring at the northern and southern ends.

As shown in Fig. 7, the distributions of localized *Kokopapa* species are delimited in the west by the Cape Foulwind Fault and in the east by the Paparoa Tectonic Zone (16) and Glasgow (8) Faults and further north the Kohaihai and Wakamarama Faults (Fig. 7): *Kokopapa rapahoe* is only found near Greymouth on the western side of the Rapahoe Range, west of the Paparoa Fault (16); *K. milleneri* is only found west of the Wakamarama and Kohaihai Faults; *K. mokihinui* is only found at the north and west of the Glasgow Fault and *K. bispathulata* is only found west of the Kohaihai, Glasgow and Paparoa Faults. The species distributions

follow these geological breaks that have been dynamic for a long time (all major faults on the west coast of the South Island are reverse faults (Neef, 1981) of Late Cretaceous to Eocene age that have moved in the opposite direction since the start of the compressional tectonic style 25-20 Ma ago, i.e., former extensional basins of Late Cretaceous to mid Cenozoic age evolved into the present day ranges through eversion of the old landscape). The Oligocene is generally considered to be a period of passive subsidence with little tectonic activity but there is much evidence for faulting, folding and volcanism across the region and elsewhere in the South Island (Lever, 2001; 2007).

Geology

During the early Cenozoic the western side of the lower Paparoa Tectonic Zone was tilting down while the eastern side was up-faulting. In contrast, the northern part, west of the fault, was up-faulting and the eastern side was down-faulting until the movement was reversed in the later Cenozoic. The hinge of this scissor movement, first described by Laird (1967), is somewhere near Punakaiki in the middle of the fault zone, where only the widespread *Kokopapa unispathulata* (Figs 2, 7 & 9) now occurs, while *Kokopapa bispathulata* and the other *Kokopapa* species are found north and south of this hinge area. Early Cenozoic transgressional seas advanced on the western coast from the south inundating most of the land area except for the Karamea Peninsula (Fig. 6), which was later covered by the Oligocene-early Miocene platform facies (Nile Group). These platform facies, which covered large areas of the basinal margins on the west coast, consists mainly of shallow-water bioclastic limestone, while much greater sediment deposition occurred in small, deep basins separated by faults from shallow seas and land such as islands as described by Neef (1981): “during the Oligocene (Whaingaroan and Duntroonian) the area west of the Gunner Anticline, north of Kohaihai Bluff, formed a shallow sea, whereas in the east, in the Oparara valley, there was probably land”. In addition, “during the Waitakian the area now covered by the Oparara valley was a widespread wave-cut platform lacking much sand and beach gravel, but islands formed by Karamea Granite were present nearby” (p. 206). Paleogeographic maps of Fiordland by Turnbull and Uruski (1993) show emergent land throughout the Cenozoic transgressions, providing refugia for ancestral populations of *Kokopapa matarua*.

Numerous local formations have been recognized because of the considerable vertical and lateral variation in faunal composition and the amount of interbedded terrigenous material (Nathan *et.al*., 1986). For example, the Stony Creek limestone formation described by Neef (1981) contains limy arkose (coarse sandstone) overlying the basal sandy limestone near Blacktopp Creek, ca. 15 km southeast of Karamea, which indicates erosion of Karamea Granite nearby. This formation was deposited very slowly during the Duntroonian and Waitakian (late Oligocene/early Miocene; Neef, 1981, p. 183). Lower Miocene Scorpion Creek Sandstone is also exposed in the northern Oparara Valley, , the upper Fenian, Scorpion and Quoich Creeks, and Postal River (eastern tributaries of Oparara River), where fossil wood fragments have been found in the sandstone (Fig. 2; Neef, 1981, p. 188).

The Oligocene Nile Group (Westland) and Takaka Limestone (NW Nelson) both make up the platform facies and include a variety of different depositional settings that large scale paleogeographical reconstructions of New Zealand cannot show in detail. Islands may have been short-lived as far as geological time is concerned but their presence nevertheless provided refugia for ancestral populations during the Oligocene. Further geological evidence for Oligocene islands has been found offshore from Karamea where Cahill (1992) reports limestone aprons around granite bumps found by seismic mapping. Some show distinct peneplanated Oligocene surfaces.

Granitic massflow breccia and breccia-conglomerates of early to mid-Oligocene age between the mouths of the Mokihinui and Little Wanganui Rivers (Fig. 2) are derived from the western uplifted side of the basin at the northern end of the Paparoa trough, immediately west (i.e. seaward) of the present coastline (German, 1976, Lever, 2001). *Kokopapa mokihinui* has been collected only from Glasseye Creek, Corbyvale and near Lake Hanlan (Fig. 2, open circles), west of the Radiant Range between the mouths of the Little Wanganui and Mokihinui Rivers. Other local endemics in this area are Charopidae sp. 101 (a new species of *Ptychodon* Ancey, 1888), and ten different races and hybrids of *Powelliphanta* O’Connor 1945 that occur approximately 15 km north and south of the Mokihinui River and up the river valley. The endemics of these three genera also have close taxonomic links with Fiordland species, and this relationship is indicative of a pre-late Miocene shared ancestry predating the Alpine Fault disjunction.

In general, spatial factors such as underlying geological history and persistence of regional species pools have been found to best explain species distributions and assemblages: Solem *et al*. (1981) and Solem and Climo (1985, p. 25) discuss the lack of specific functional correlations between habitat, shell architecture and

sculpture. The majority of species analysed in their study of land snail communities of forest remnants SW of Auckland were collected from several different microhabitats (Solem *et al*., 1981).

In another more recent study, additive partitioning of standardized search effort samples of New Zealand land snails from a substantial range of habitats showed that 18 percent of total species richness was explained by the conditions of the sample plot, 18 percent by environmental factors and 65 percent by bioregion components that were defined by spatial intersections of geological attributes such as terranes, displacement along the Alpine Fault, Oligocene and Pliocene marine transgressions, Pliocene to Recent volcanism, Pleistocene to Present alluvial deposition and late Pliocene and Pleistocene glaciations (Barker, 2005, p. 83).

CONCLUSION

The high number of endemics found in Westland-Karamea, Alpine Fault disjunctions of species pairs, geographical species limits replicated in other land snail distributions as well as other organisms, and the north-south trending distributions delimited by faults, all suggest that ongoing tectonic movement guaranteed the continuity of habitats and lineages by maintaining a mosaic landscape. This provides many micro refugia, contrary to the widespread view that that organisms became extinct over vast tracks of land through the effects of marine transgressions and glaciations (authors cited in Gibbs, 2006; Campbell and Hutchings, 2007). Comprehensive phylogeographical analyses of the New Zealand land snails are unavailable at present. But unpublished molecular phylogenetic data for athoracophorid slugs supports the view that the New Zealand land snails have evolved in isolation since the Mesozoic (Barker, 2005, cf. Climo, 1975).

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REFERENCES

Barker, G.M. 2005. The character of the New Zealand land snail fauna and communities: some evolutionary and ecological perspectives. In *Pattern and process in land mollusc diversity* (ed. by R.A.D. Cameron, J.C. Nekola, B.M. Prokryszko & F.E. Wells), pp. 53-102. Records of the Western Australian Museum, Supplement No. 68.

Cahill, J.P. 1992. Distribution of Oligocene limestone from seismic mapping offshore, Karamea Basin, North Westland or limestone aprons-granite bumps offshore Karamea. *New Zealand Geological Survey Record*, 44, 1-8.

Campbell, H. & Hutching, G. 2007. *In search of ancient New Zealand*, Penguin, Auckland and GNS Science, Lower Hutt, 239 pp.

Climo, F.M. 1975. The land snail fauna. In *Biogeography and ecology in New Zealand* (ed. by G. Kuschel), pp. 459-492. W. Junk, The Hague.

Climo, F.M. 1978. Classification of New Zealand Arionacea (Mollusca: Pulmonata). A review of the New Zealand charopine snails with lamellate apertures. *National Museum of New Zealand Records*, 1, 177-201.

Climo, F.M. 1979. The systematic status of some land snails mistakenly assigned to the New Zealand fauna. *New Zealand Journal of Zoology*, 6, 407-410.

Climo, F.M. 1988. Punctid snails. A path to panbiogeography. *Revista di Biologia*, 81, 533-551.

Climo, F.M. 1990. The panbiogeography of New Zealand as illuminated by the genus *Fectola* Iredale, 1915 and subfamily Rotadiscinae Pilsbry, 1927 (Mollusca: Pulmonata: Punctoidea: Charopidae). *New Zealand Journal of Zoology*, 16, 587-649.

Climo, F.M. 1992. Some Tasman punctid land snail (Pulmonata: Punctidae) margins and centres–a collage. *Cookia*, 6, 17-36.

Craw, R.C., Grehan, J.R. & Heads, M.J. 1999. *Panbiogeography. Tracking the history of life*. Oxford University Press, New York and Oxford, 229 p.

Dell, R.K. 1955. The land mollusca of Fiordland, South-West Otago. *Transactions of the Royal Society of New Zealand*, 82, 1135-1148.
Fenwick, M.C. & Marshall, B.A. 2006. A new species of *Echyridella* from New Zealand, and recognition of *Echyridella lucasi* (Suter, 1905) (Mollusca: Bivalvia: Hyriidae). *Molluscan Research*, 26, 69-76.
Gardner, N.W. 1968. Four new species of land snails from New Zealand. *Transactions of the Royal Society of New Zealand, Zoology*, 10, 159-162.
German, R.C. 1976. *Stratigraphy and sedimentology of the Nile Group (Oligocene) southwest Nelson*. Unpublished MSc thesis, University of Canterbury, Christchurch, New Zealand.
Gibbs, G.W. 2006. *Ghosts of Gondwana: the history of life in New Zealand*. Craig Potton Publishing, Nelson, 232 p.
Gray, J.E. 1850. Description of a new genus and several new species of terrestrial, fluviatile and marine molluscous animals inhabiting New Zealand. *Proceedings of the Zoological Society of London*, 1849, 164-169.
Grindley, G.W. 1974. New Zealand. In *Mesozoic-Cenozoic orogenic belts* (ed. by Spencer), pp. 387-416. Scottish Academic Press for the Geological Society, London.
Heads, M. 1990. Integrating earth and life sciences in New Zealand natural history: the parallel arcs model. *New Zealand Journal of Zoology*, 16, 549-585.
Heads, M. 1998. Biogeographic disjunction along the Alpine Fault, New Zealand. *Biological Journal of the Linnean Society*, 63, 161-176.
Heads, M. & Craw, R.C. 2004. The Alpine Fault biogeographic hypothesis revisited. *Cladistics*, 20, 184–190.
Henderson, I.M. 1985. *Systematic studies of New Zealand Trichoptera and critical analysis of systematic methods*. Unpublished PhD thesis, Victoria University, Wellington, 340 p.
Hutton, F.W. 1883. Additions to the molluscan fauna of New Zealand. *Transactions and Proceedings of the Royal Society of New Zealand*, 15, 131-141.
Hutton, F.W. 1888. Description of a new land shell, from the Province of Nelson. *Transactions and Proceedings of the New Zealand Institute*, 20 May 1888, 43-44.
Iredale, T. 1913. The land Mollusca of the Kermadec Islands. *Proceedings of the Malacological Society of London*, 10, 364-388, pl. 18.
Iredale, T. 1937. A basic list of the land Mollusca of Australia. *Australian Zoologist*, 8, 287-333.
Iredale, T. 1941. Guide to the land shells of New South Wales. Part II. *Australian Naturalist*, April, 262-269.
Kershaw R.C. & Smith, B.J. 1986. Description of two punctid snail genera from Tasmania (Mollusca : Pulmonata). *Victorian Naturalist*, 103, 16-18.
King, P. R., Naish, T. R., Browne, G. H., Field, B. D. & Edbrooke, S. W. (1999) Cretaceous to Recent sedimentary patterns in New Zealand. *Institute of Geological and Nuclear Sciences folio series 1*.
Laird, M.G. 1967. The Paparoa Tectonic Zone. *New Zealand Journal of Geology and Geophysics*, 11, 435-454.
Lever, H. 2001. An Eocene to early Oligocene unconformity-bounded sequence in the Punakaiki-Westport area, West Coast, South Island, New Zealand. *New Zealand Journal of Geology & Geophysics*, 44, 355-363.
Lever, H. 2007. Review of unconformities in the late Eocene to early Miocene successionsof the South Island, New Zealand: ages, correlations, and causes. *New Zealand Journal of Geology & Geophysics*, 50, 245-261.
Mahlfeld, K. 2005. *Biogeography and systematics of Cavellia Iredale, 1915*. Unpublished PhD thesis, Victoria University, Wellington, New Zealand.
Moellendorff, O.F. von 1893. Materialien zur Fauna der Philippinen. XI. Die Insel Leyte. *Berichte der Senckenbergischen Naturforschenden Gesellschaft in Frankfurt am Main*, 24, 51-154.
Morse, E.S. 1864. Observations on the terrestrial Pulmonifera of Maine, including a catalogue of all the species of terrestrial and fluviatile Mollusca known to inhabit the State. *Journal of the Portland Society of Natural History*, 1, 1-63, 10 pls.
Nathan, S., Anderson, H.J., Cook, R.A., Herzer, R.H., Hoskins, R.H., Raine, J.I. & Smale, D. 1986. Cretaceous and Cenozoic sedimentary basins of the West Coast region, South

Island, New Zealand. *New Zealand Geological Survey Basin Studies*, 1.
O'Connor, A.C. 1945. Notes on the eggs of New Zealand Paryphantidae, with the description of a new subgenus. *Transactions of the Royal Society of New Zealand*, 75, 62-64.
Pfeiffer, L. 1855. Descriptions of forty-two new species of *Helix*, from the collection of H. Cuming, Esq. *Proceedings of the Zoological Society of London*, 22, 49-57.
Pfeiffer, L. 1866. Beschreibung neuer Landschnecken. *Malakozoologische Blätter*, 13, 76-91.
Powell, A.W.B. 1928. Descriptions of five new land-shells from New Zealand. *Transactions and Proceedings of the New Zealand Institute*, 59, 365-367.
Powell, A.W.B. 1930. The Paryphantidae of New Zealand: their hypothetical ancestry, with descriptions of new species and a new genus. *Records of the Auckland Institute and Museum*, 1, 17-56.
Powell, A.W.B. 1941. Seven new species of New Zealand land mollusca. *Records of the Auckland Institute and Museum*, 2, 260-264.
Powell, A.W.B. 1948. Land mollusca of the Three Kings Islands. *Records of the Auckland Institute and Museum*, 3, 273-290.
Powell, A.W.B. 1949. The Paryphantidae of New Zealand. No. VI. Distribution, hybrids and new species of Paryphanta, Rhytida and Schizoglossa. *Records of the Auckland Institute and Museum*, 3, 347-367.
Powell, A.W.B. 1952. Four new species of New Zealand land snails and the systematic position of *Gerontia cordelia* Hutton. *Records of the Auckland Institute and Museum*, 4, 163-168.
Powell, A.W.B. 1955. Mollusca from the southern islands of New Zealand. *Cape Expedition Series Bulletin 15*, Department of Scientific and Industrial Research, Wellington, 1-152 pp.
Powell, A.W.B. 1979. *New Zealand Mollusca. Marine, Land and Freshwater Shells*. Collins, Auckland, 500 pp.
Solem, A. 1983. Endodontoid land snails from Pacific Islands (Mollusca: Pulmonata: Sigmurethra). Part II. Families Punctidae and Charopidae, Zoogeography. Field Museum of Natural History, Chicago, Illinois, 336 p.
Solem, A., Climo, F.M. & Roscoe, D.J. 1981. Sympatric species diversity of New Zealand land snails. *New Zealand Journal of Zoology*, 8, 453-485.
Solem, A. & Climo, F.M. 1985. Structure and habitat correlations of sympatric New Zealand land snail species. *Malacologia*, 26, 1-30.
Spencer, H.G., Marshall, B.A. & Willan, R.C. 2009. Recent Mollusca. In *The New Zealand inventory of biodiversity: a species 2000 symposium review* (ed. by D.P. Gordon). Canterbury Press, Christchurch, New Zealand.
Suter, H. 1892. On the dentition of some New Zealand land and fresh-water Mollusca, with descriptions of new species. *Transactions and Proceedings of the New Zealand Institute*, 24, 286-303.
Suter, H. 1894. Further contributions to the knowledge of the molluscan fauna of New Zealand, with descriptions of eight new species. *Transactions and Proceedings of the New Zealand Institute*, 26, 121-138.
Suter, H. 1913. *Manual of the New Zealand Mollusca*. John Mackay, Government Printer, Wellington, 1120 p.
Suter, H. 1915. *Manual of New Zealand Mollusca: atlas of plates*. John Mackay, Government Printer, Wellington, 72 plates.
Trewick, S.A., Walker, K.J. & Jordan, C.J. 2008. Taxonomic and conservation status of a newly discovered giant landsnail from Mount Augustus, New Zealand. Conservation Genetics, 9, 1563-1575.
Turnbull, I.M. & Uruski, C.I. 1993. Cretaceous and Cenozoic sedimentary basins of western Southland, South Island, New Zealand. *Institute of Geological and Nuclear Science Monograph*, 1.
Walker, K.J. 2003. Recovery plans for *Powelliphanta* land snails. *Threatened Species Recovery Plan 49*. Department of Conservation, Wellington, x, 208 p., 64 plates.

Figure captions

Fig. 1. Distribution of taxa. With the exception of A, all whole shell drawings are holotypes.

A, *Kokopapa unispathulata* n. sp., Halfmoon Bay (NMNZ M.86281), filled circles; B, *K. milleneri* n. sp., Swanburn (NMNZ M.79720) - shell detail from Anaweka River (NMNZ M.81081), filled squares; C, *K. bispathulata* n. sp., Barrytown - Croesus Track (NMNZ M.78614), open squares; D, *K. mokihinui* n. sp., Corbyvale (NMNZ M.77777), black circles with white centre; E, *K. rapahoe* n. sp., Greymouth (NMNZ M.98776), square with dot; F, *K. matarua* n. sp., Codfish Island (NMNZ M.86307), open circles.

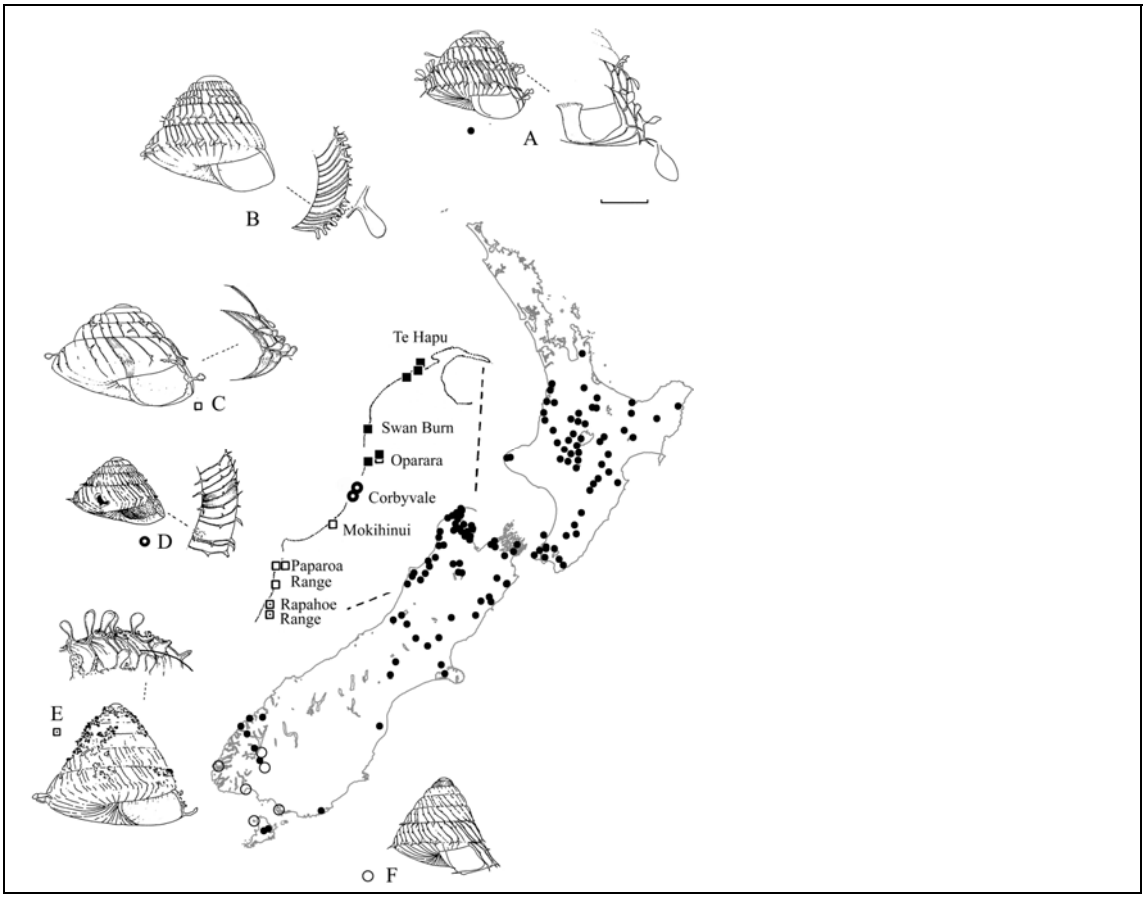

Fig. 2. Detail of *Kokopapa* species distributions on the west coast of the South Island: spike-shaped periostracal processes on first teleoconch whorls changing during teleoconch ontogeny to adapical spathulate and abapical spike-shaped processes on later teleoconch whorls - *Kokopapa milleneri* n. sp. (open squares) and *K. unispathulata* n. sp. (+); adapical and abapical spike-shaped periostracal processes on teleoconch whorls – *K. mokihinui* n. sp. (open circle); spike-shaped periostracal processes on first teleoconch whorls changing into adapical and abapical spathulate processes on later teleoconch whorls – *K. bispathulata* n. sp. (diagonal crosses); spike-shaped periostracal processes on first teleoconch whorls changing into abapical spathulate and adapical spike-shaped processes – *K. rapahoe* n. sp. (filled circle). While the juvenile sculpture changes synchronically to adult sculpture in both rows of processes in *K. bispathulata*, it is heterochronic in *K. unispathulata*, *K. milleneri* and *K. rapahoe*. The development of the shell sculpture of *K. unispathulata*, *K. milleneri* and *K. rapahoe* resembles transcurrent fault geology with sculptural processes being displaced transcurrently in both peripheral bands.

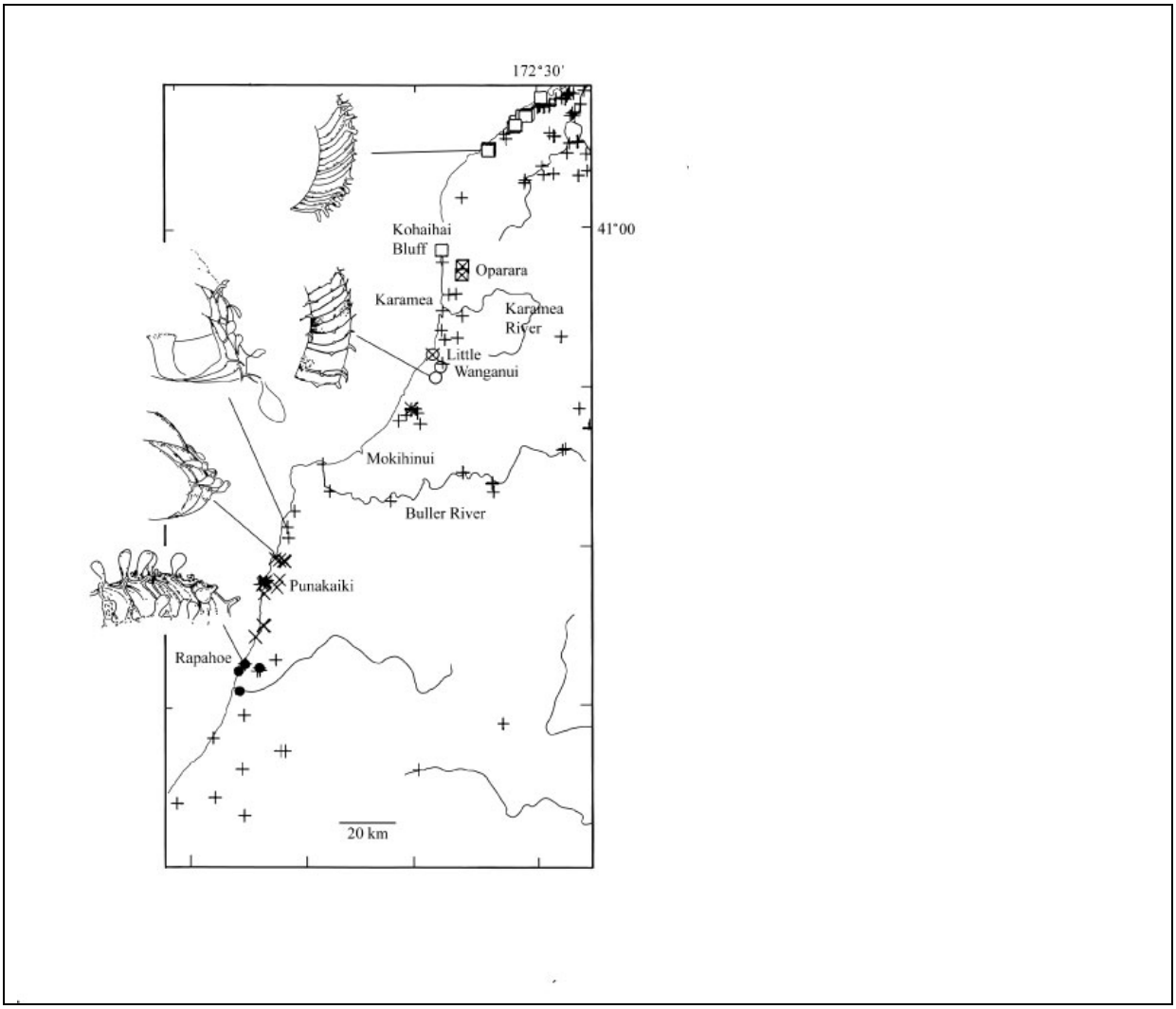

Fig. 3. A-B, *Kokopapa unispathulata* n. sp., Halfmoon Bay, Stewart Island (NMNZ M.86281) at 3 & 4 whorls, respectively (adult shell see Fig. 1A); C, *K. milleneri* n. sp., Te Hapu (NMNZ M.80992); D, same, with periostracum absent, Honeycomb Hill, Oparara (NMNZ M.77892); E-F, same, holotype, Swanburn (NMNZ M.79720). Scale lines 1 mm.

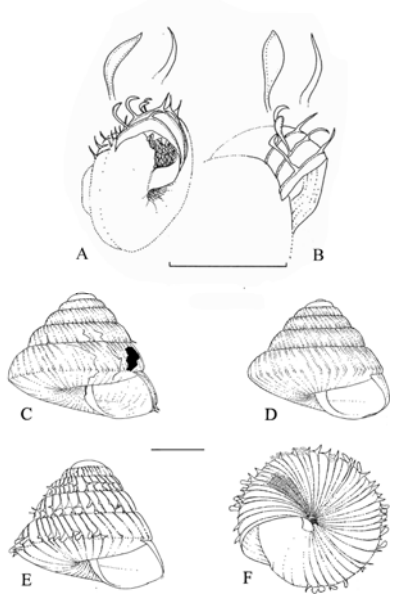

Fig. 4. *Kokopapa unispathulata* n. sp., Puponga Point, NW Nelson, F.M. Climo, 3.1.1967. A, reproductive system; B, mantle collar and pallial cavity; scale lines 1 mm; abbreviations: a, anus; ag, albumen gland; g, gonad (ovotestis); hd, hermaphroditic duct; hg, hindgut; k, kidney; mc, mantle collar; mg, mantle gland; ov, oviduct; p, phallus; pg, prostatic gland; pr, phallus retractor muscle; s, spermatheca and duct; t, talon (buried in folds of ag); ur, ureter; ut, uterus; v, vagina; vd, vas deferens.

Fig. 5. A-C, holotype, *Kokopapa bispathulata* n. sp., Barrytown – Croesus Track (NMNZ M.78614). D, same species, with periostracum absent, from Honeycomb Hill Cave (NMNZ M.77331). Scale line 1 mm.

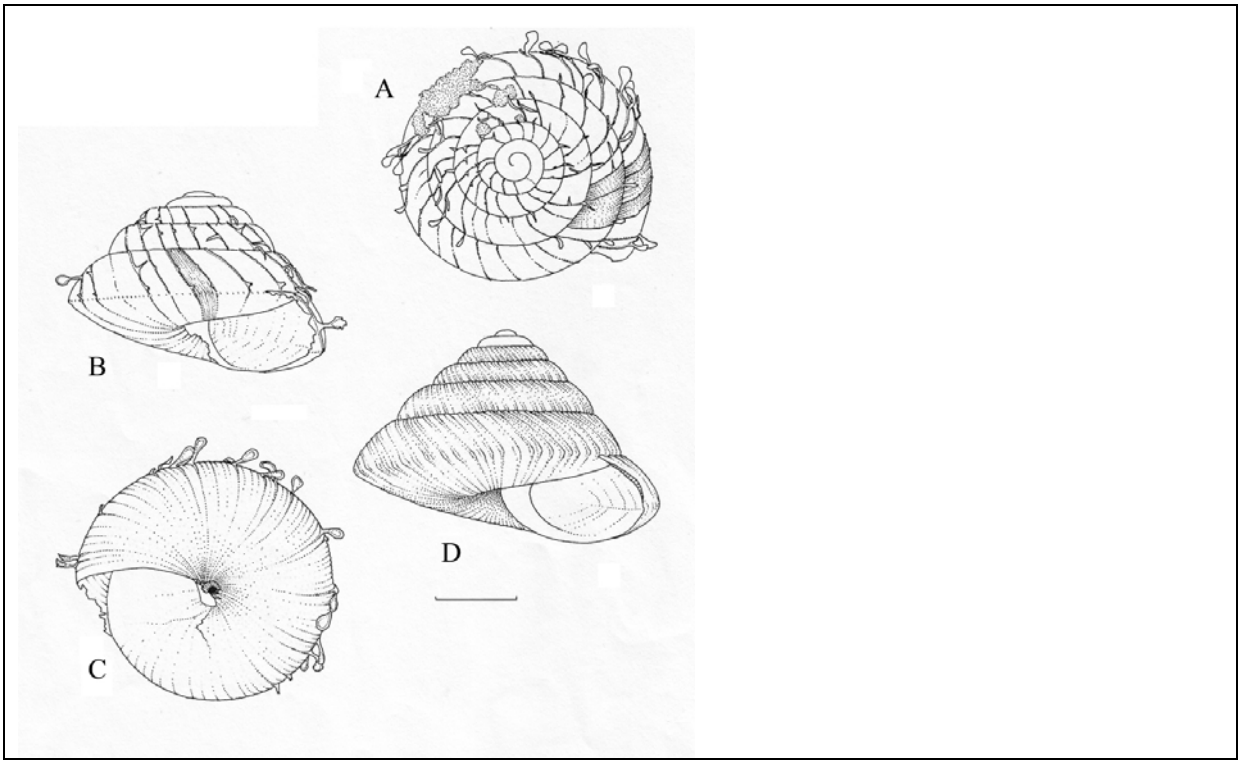

Fig. 6. Early Miocene paleogeographic reconstruction of New Zealand (modified from King *et al*., 1999). ECB, East Coast Basin; GSB, Great South Basin; TB, Taranaki Basin; N, Nelson; F, Fiordland; AF, Alpine Fault; KP, Karamea Peninsula; V, volcano.

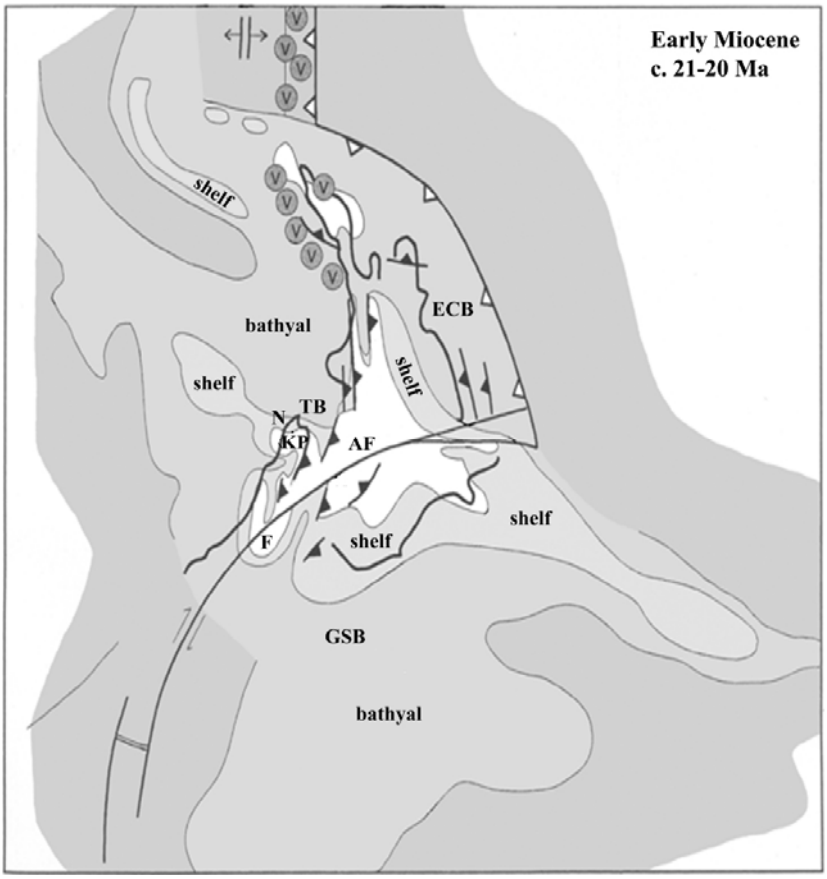

Fig. 7. Map of northwestern South Island showing pre-Cambrian to lower Cretaceous rocks (blank), Cenozoic faults, upper Cretaceous-lower Cenozoic transgressive sequence (fine dots), and Miocene-Recent synorogenic deposits of Kaikoura Orogeny (coarse dots). (Redrawn from Grindley, 1974)

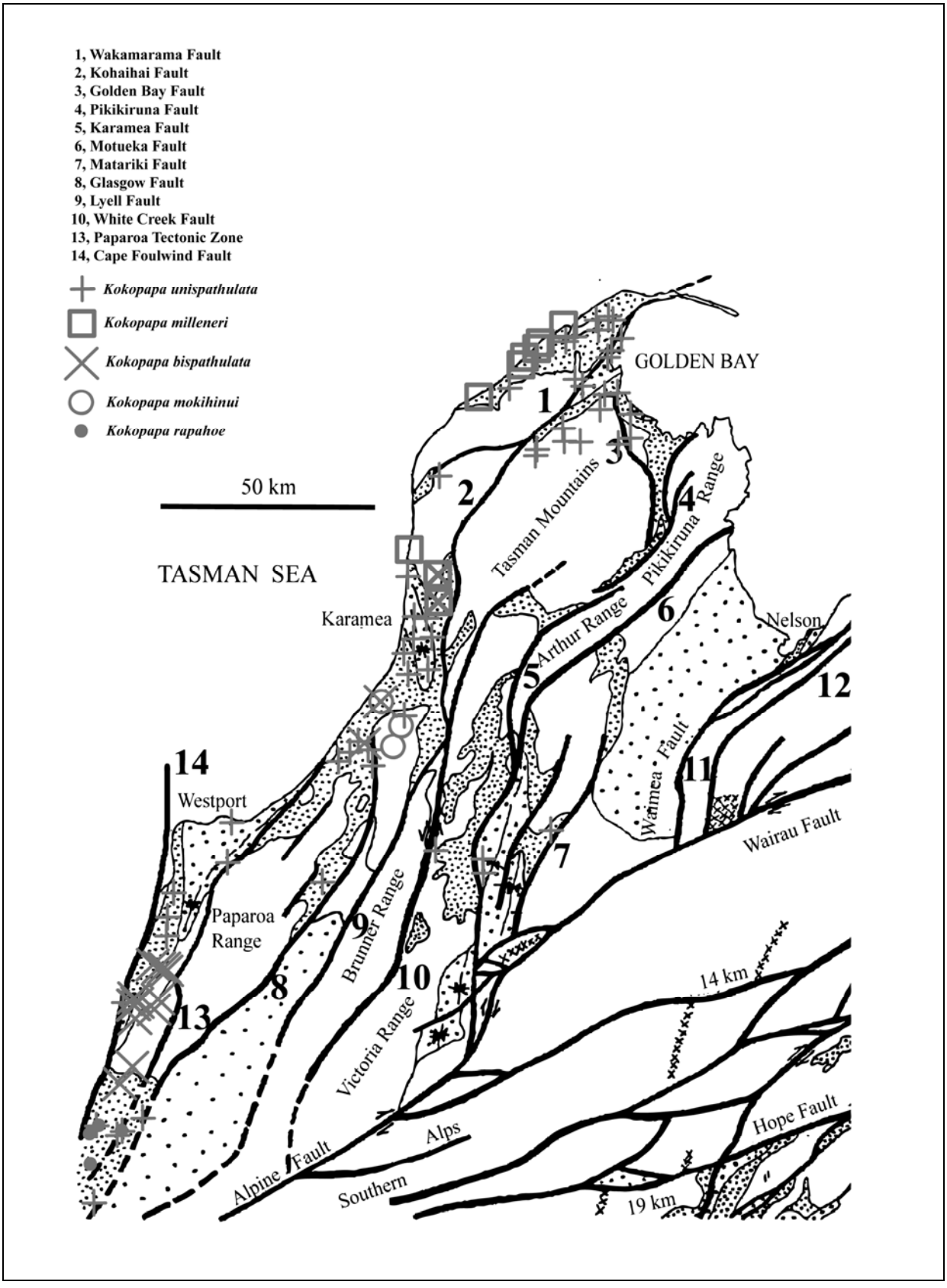

Fig. 8. Land snail species pairs showing Alpine Fault (black line) disjunction: top left, *Powelliphanta superba* (Powell, 1930), *Powelliphanta annectens* (Powell, 1930) and *Powelliphanta spedeni lateumbilicata* (Powell, 1946); top right, Charopidae sp. 3 and Charopidae sp. 4; middle left, *Ptychodon roscoei* Climo, 1978 and *Ptychodon blacki* Dell, 1955; middle right, Charopidae sp. 48 and Charopidae sp. 49; bottom left, *Zelandiscus*

elevata (Climo, 1978), Charopidae sp. 133 and *Zelandiscus worthyi* Climo, 1990; bottom right, *Flammulina* aff. *lateaperta* n. sp. and *Flammulina lateaperta* Dell, 1955.

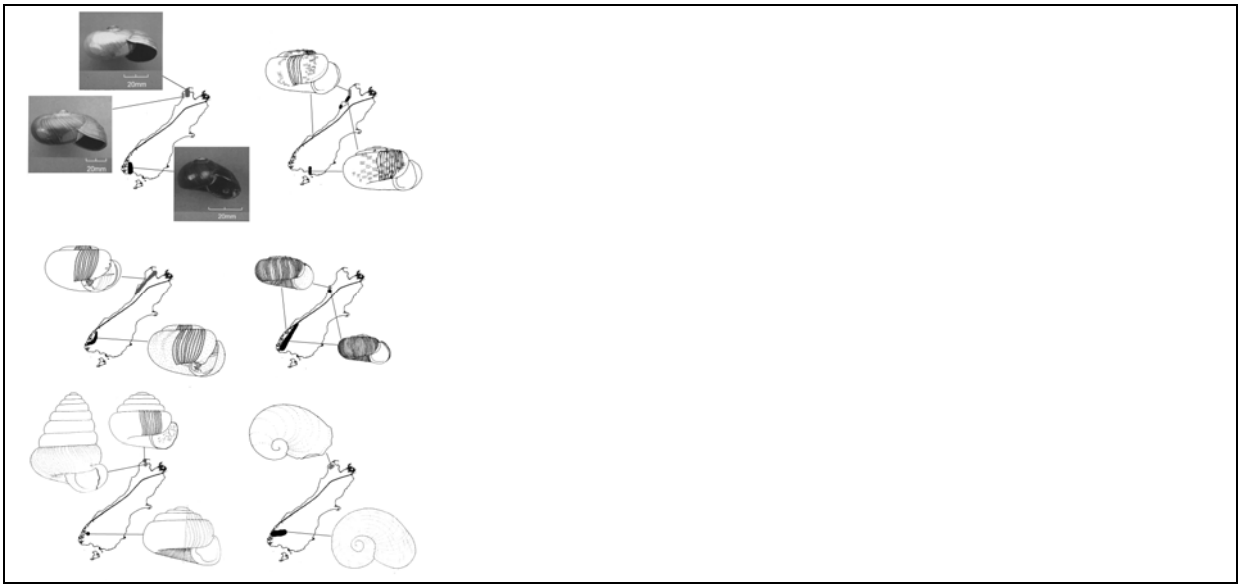

Fig. 9. Map of localities mentioned in the text.

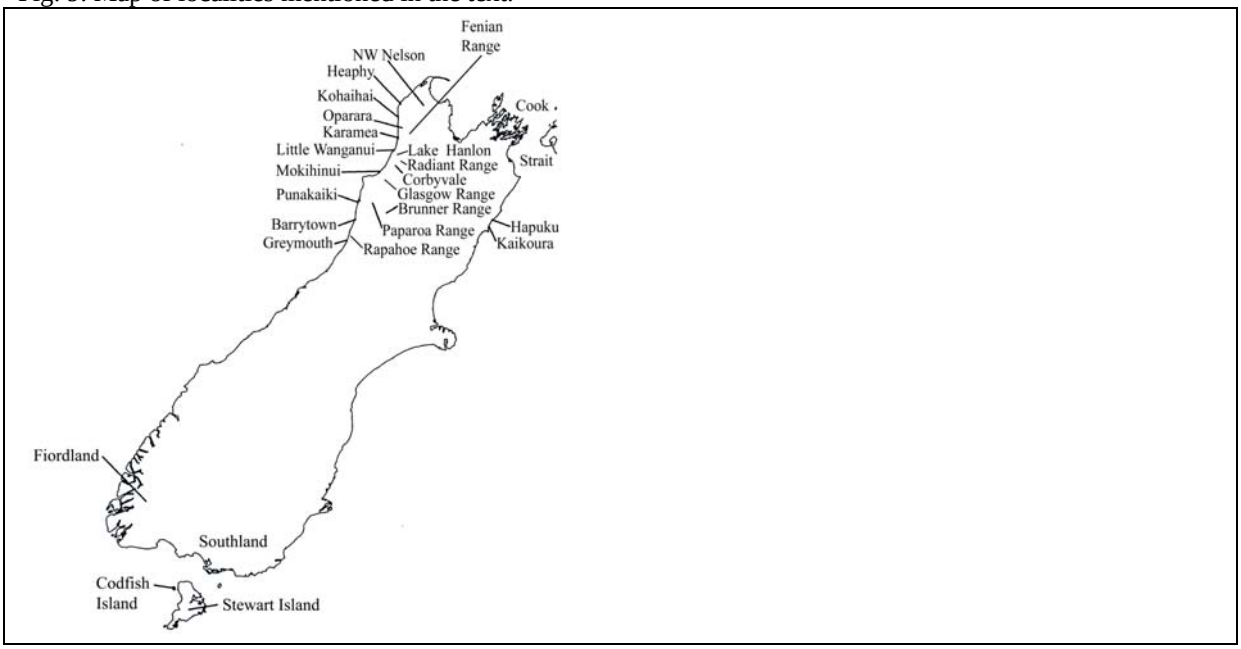

Plate 1. A, *Kokopapa bispathulata* n. sp., Scotchmans Creek, S of Punakaiki (NMNZ M.55543); B, *K. bispathulata*, Pororari, Punakaiki; C, D, *Kokopapa matarua* n. sp., beside Lake Hankinson, Middle Fiord, Lake Te Anau (NMNZ M.86111); E, F, *Kokopapa unispathulata* n. sp., island in Tennyson Inlet, Marlborough (NMNZ M.25469); G, *Kokopapa unispathulata*, Waimate; H, *Kokopapa unispathulata*, between Jetty & Ocean Beach, Glory Cove, Stewart Island (NMNZ M.68373). Scale bars = 100 µm.

Plate 2. *Kokopapa mokihinui* n. sp. (left), holotype (NMNZ M.77777); *Kokopapa matarua* n. sp. (middle), holotype (NMNZ M.86307); *Kokopapa rapahoe* n. sp. (right), holotype (NMNZ M.98776).