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SOME NEW ZEALAND SUBFOSSIL LAND MOLLUSCA

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Abstract

Rhytida yaldwyni n.sp. is described from caves near Dannevirke. Subfossil *Paryphanta* shells from Punipaua and numerous North Island localities, especially in the Wairarapa are described, and the distribution of *Geminoropa (Cavellioropa) spelaea* Powell is outlined. The distribution of these subfossil land shells is discussed in relation to the origins of the *Paryphanta* species in the southern part of the North Island, and to post-Pleistocene zoogeography.

INTRODUCTION

Recent work on caves in limestone country in the Wairarapa and Hawkes Bay has brought to light an interesting molluscan fauna associated with bird bones. A full report on the subfossil land mollusca is in course of preparation and full faunal lists will eventually be published. Several forms are of special interest and will be discussed here.

The writer is indebted to Messrs. J. C. Yaldwyn and W. H. Hartree for the collection of some of the material, to Mr. M. J. G. Smart of the Wanganui Museum for the loan of specimens and to Dr. C. A. Fleming and Mr. M. T. Te Punga for helpful discussions.

In the descriptions that follow the following measurements and indices are used:—

W.T. .... Whorl Thickness—the distance from suture to base of body whorl, measured parallel to the axis of the shell.

W.T.I. Whorl Thickness Index—the whorl thickness expressed as a percentage of the major diameter.

R.I. .... Riblet Index—the number of riblets on the body whorl divided by the diameter in mm.

H.I. .... Height Index—the height expressed as a percentage of the major diameter.

SYSTEMATICS

Rhytida yaldwyni n.sp. (Figs. 2, 3, 4)

This species is allied to *oconnori* and *hadfieldi* but is readily distinguishable by the very narrow umbilicus and the sculpture. The sculpture consists of irregular radial folds, strongest near the suture, and distinct fine concentric spiral threads. Rather irregular oblique wrinkles are also developed, some 13 to 16 on the body whorl. These are considerably more oblique than in either the *hadfieldi* or the *greenwoodi* series and much more numerous. The outline of the body whorl varies. In the holotype it is somewhat compressed, but in the three other incomplete specimens available it is more rounded. The umbilicus is very small and is partly closed by the reflexed inner lip.

Locality: Waewaepa Cave No. 9, Puketoi Ranges, near Dannevirke, c. 2000 feet, coll. J. C. Yaldwyn, —/1/1953; Martinborough Cave No. 1, Ruakokopatuna, Lower Wairarapa, c. 2000 feet, broken shell, 1920.

Holotype M.5720 and three paratypes (M.5721) in Dominion Museum.

In his original description of *Rhytida spelaea,* Powell stated, "Mr. W. H. Hill, of Hamilton, has a similar specimen which was collected

by Mr. H. Hamilton in the Coonoor Cave, near Woodville, in 1914." This specimen is not available for examination but it was probably referable to *R. yaldwyni* rather than to *R. spelaea*.

Powell (1949, p. 363) has shown from an examination of the radula that *Rhytida hadfieldi* belongs to the southern *patula* group. The new species described above (allied to *oconnori* and *hadfieldi*) is the first record of the *patula* group in the North Island.

	Maj. Diam. mm.	Ht. mm.	W.T. mm.	Umbilicus mm.	Whorls
R. yaldwyni n.sp. Holotype	24·0	16·2	11·0	1·3	3½
Paratype	24+	17·1+	11·7	1·2	3½
Paratype	21·8	16·1	10·8	1·2	3½
R. hadfieldi (Powell)	33·4	19·2	11·1	4·5	3¾
R. hadfieldi (young)	25·1	16·5	9·2	3·2	
R. oconnori	25·7	16·1	9·6	2·4	

Paryphanta (Powelliphanta)

The systematics of the living species of *Paryphanta* (*Powelliphanta*) are of necessity based upon features such as colour pattern, callus texture and colour, and to a minor extent on shell form. Such details as colour and texture disappear as the chitinous material of the shell is removed in weathering. Subfossil specimens of *Paryphanta*

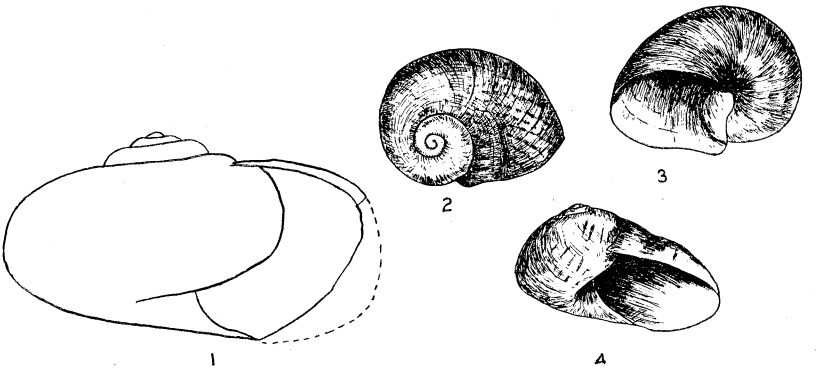


FIG. 1.—Wairarapa Paryphanta, Cave No. 1, Ruakokopatuna, 38·6 × 23·0 mm.
FIGS. 2, 3, and 4.—*Rhytida yaldwyni* n.sp. Holotype. 24·0 × 16·2 mm.

therefore present few diagnostic characters and have usually been neglected. A series from limestone areas ranging from the Wairarapa to Napier show a high degree of uniformity and raise the question of past distribution. The position of these subfossil shells has therefore been re-examined. The writer does not believe that the nomination of such forms within the normal nomenclatural classification can serve any useful purpose for the following reasons:—Although the shell shape is comparatively uniform, the original colour pattern may have been very diverse in the forms from different localities and while one species may have been present (as the writer believes) there is no way of deciding what subspecies may have been present originally. Nor does it appear that determination of original subspecies will ever be possible. For the same reason it will probably never be possible to correlate these subfossil shells with living subspecies with any certainty. However, knowledge of the past distribution of the genus will assist in

understanding the present distribution and some information may also be ascertained concerning the probable affinities of the subfossil shells. For these reasons it becomes necessary to devise some method of reference outside the nomenclatural framework. It is therefore proposed to designate such forms by non-technical vernacular names such as the "Wairarapa *Paryphanta*", the "Punipaua *Paryphanta*", etc.

The Wairarapa *Paryphanta*

This shell is of medium size, comparatively complete shells of 4 to 5 whorls attaining a major diameter of 38 mm., but broken fragments indicate that it grows slightly larger. The umbilical area is usually damaged but the umbilicus appears to be little less than one seventh the major diameter of the base. Spire comparatively elevated. Body whorl evenly rounded. There are distinct, somewhat irregular raised spiral threads on both upper surface and base of body whorl. Shells of this form have been found in limestone areas from the lower Wairarapa to Napier. The relative homogeneity of the specimens from these localities is shown by the measurements and indices given below.

Locality: Clay, "bone-matrix" floor of Martinborough cave No. 1, Ruakokopatuna, Lower Wairarapa, J. C. Yaldwyn and E. W. Dawson, 1/3/1952. Also several specimens from this area in the old Museum collection, detailed localities not given; Waewaepa Caves Nos. 2, 7, and 9, J. C. Yaldwyn, —/1/1953: Coonoor (fragment); Patoka, Hawke's Bay, W. H. Hartree, —/9/1952.

Measurements of Wairarapa Paryphanta

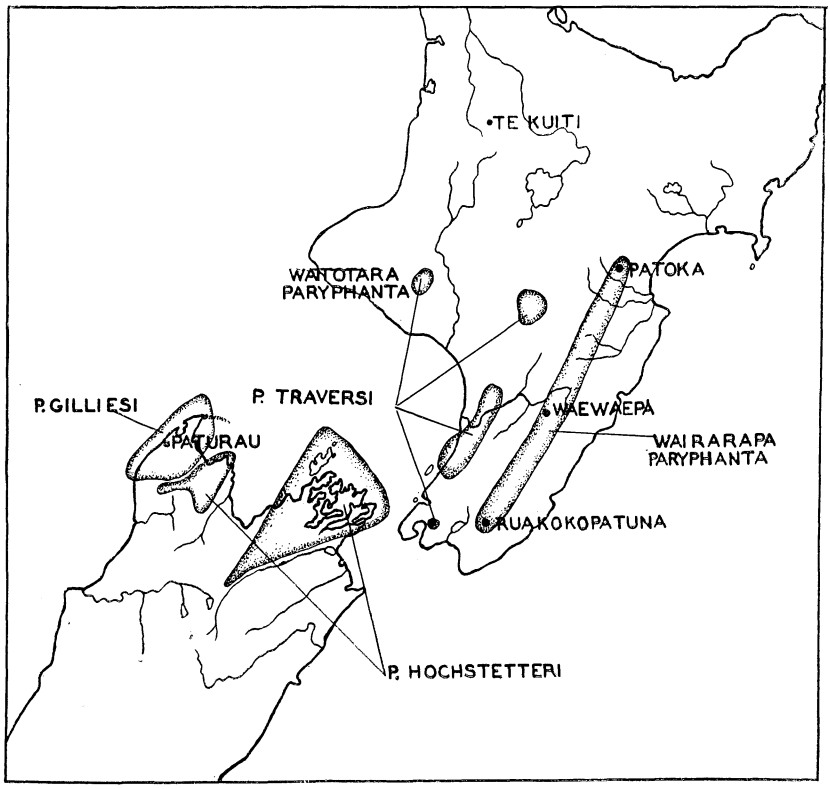
	Diam.	Height	W.T.	Umbilicus Diam.	Whorls
	mm.	mm.	mm.	mm.	
Ruakokopatuna	38·6	23·0	16·0	4·9	5
Waewaepa	32·2	18·0	12·7	—	5
,,	30·9	18·1	12·8	—	4½
,,	29·2	18·4	12·2	—	4½
,,	24·2	16·1	10·0	—	4½
Patoka	34·0	23·4	14·9	—	4½
,,	27·6	—	12·6	—	—

Indices for Wairarapa Paryphanta

	H.I.	W.T.I.
Ruakokopatuna	59	41
Waewaepa	56	39
,,	58	41
,,	63	42
,,	66	41
Patoka	69	44
,,	—	45

The ranges and mean for the Height Index are 56–69 (62), and those for the Whorl Thickness Index 39–45 (42). It would appear that one species is involved though this may have been originally divided into several subspecies.

The relationships of the Wairarapa *Paryphanta* are difficult to determine. Powell in his first paper on the group (1930, p. 34) described



Outline map showing localities and distribution patterns.

two basic shell shapes for the southern species of *Paryphanta* (i.e. the subgenus *Powelliphanta*). Shell shape A has a relatively high body whorl as seen in the *hochstetteri* series, shape B a relatively low body whorl as in the *gilliesi* series. The lowland North Island form *traversi* was referred to the group B on the basis of shell shape. Later Powell (1932, p. 158) described *Paryphanta marchanti* which on the basis of shell shape (Group A) he considered allied to the *hochstetteri* series rather than to the *traversi* series. This posed a number of zoogeographical puzzles which have never been satisfactorily explained. In attempting to decide the relationships of the Wairarapa *Paryphanta* the writer re-examined the *marchanti-traversi* series. On all grounds other than shell shape, *marchanti* appears to be closely related to the *traversi* series. Geographically, *marchanti* is not as isolated as has been previously considered. The writer has specimens of snails of the *traversi* series from the Kahuterawa Valley, south of Palmerston North and from the Ruahine Ranges near Umutoi. There are also two specimens in the Wanganui Museum of a large *Paryphanta* allied to *marchanti* from the upper Waitotara River. The differences in shell and callus colour between the northern members of the *traversi* series, such as *koputaroa* and *tararuaensis,* the Kahuturawa Valley and Umutoi shells mentioned above, and *marchanti* are, apart from the whorl shape, differences of degree rather than kind. The colour pat-

tern, tone and texture are essentially the same throughout. Geographically and morphologically, except for whorl shape, *marchanti* would belong to the *traversi* series. But on examination and measurement the two types of shell shape originally described by Powell do not appear to be distinct, or basic enough to justify the differentiation of the two series.

Whorl thickness indices have been calculated for series of *marchanti, hochstetteri, traversi,* and *gilliesi.* In the last three cases a number of the polytypic forms included in the species were measured. On comparing ranges and means of these indices it was readily apparent that there was no clear cut distinction between the *gilliesi* and *hochstetteri* types but rather that there was a gradation throughout. No clear-cut division between the *hochstetteri, traversi,* and *marchanti* series is apparent from the above analysis. The writer therefore concludes that the relationships of *marchanti* are, as distributional and morphological features indicate, with the *traversi* series rather than with *hochstetteri,* although the whole *traversi* series would appear to have been derived from a *hochstetteri* stock, or perhaps both groups were derived from a common stock.

Whorl Thickness Indices for *Paryphanta* series. Ranges and Means.

Wairarapa *Paryphanta* (7 specimens)	39–45 (42)
P. marchanti (10 specimens)	36–45 (39)
P. hochstetteri (10 specimens)	35–46 (38)
P. traversi (21 specimens)	35–42 (38)
P. gilliesi (10 specimens)	33–40 (36)
Mungaroa *Paryphanta* (5 specimens)	37–39 (38)

The distribution pattern and shell features of the Wairarapa *Paryphanta* throw some light on this matter. The present distribution of the fossil remains in limestone areas from Ruakokopatuna to Patoka may be sporadic only because of accidental preservation in suitable limestone areas. The original distribution may well have been continuous over this area. The geological age of the limestone has no particular significance; the important feature would appear to be the geographical distribution of these limestone areas to the east of the dividing range. It is, of course, quite probable that original distribution of the *Paryphanta* was related to limestone outcrops, the association of land snails with limestone formations being fairly well established. The whorl thickness indices for the Wairarapa *Paryphanta* are comparatively high; and although the ranges fall within those for *marchanti* the mean is considerably higher. It is not suggested that the Wairarapa *Paryphanta* represents an ancestral form to *traversi* and *marchanti* but rather that it existed contemporaneously with the ancestors of these last two species groups. The existence of a high whorled form to the east of the dividing range, where no living *Paryphanta* are known to occur is of considerable value in envisaging the past distribution pattern of the genus in the North Island.

The Waitotara *Paryphanta*

Two large Paryphanta shells from the upper Waitotara district in the Wanganui Museum have been examined through the courtesy of

Mr. M. J. G. Smart. One was found in the Makakaho Stream, a few miles upstream from its junction with the Waitotara River, at 1267 feet and was presented to the Museum by Mrs. Jones. The other came from the bank of the Makowai Stream, Ngamatapouri, a tributary of the upper Waitotara River, at 1500 feet and was collected by Mr. G. Matthews. Both are large shells, blackish-green in colour (apparently as a result of post-mortem changes), with fine, irregular, incised spirals on the upper surface, the bases smooth with traces of dark spiral colour bands. Practically all the limy material of the shell has disappeared and both the specimens consist of the thick outer chitinous layer and are somewhat distorted. Mr. J. Moreland has informed me (personal communication) that the second specimen was discovered beside a mudhole. The condition of the specimens is such that they could either be derived from a living population between the headwaters of the Makowai and the Makakaho Streams, or both could have been washed out from small swamps or mudholes and thus represent an extinct population.

	Diam. mm.	Ht. mm.	W.T. mm.	Umbilicus Diam. mm.	H.I.	W.T.I
Makowai	52·8	25+	20·5	7·3	47	39
Makakaho	64·7	29·5	25·0	10·4	45	38

The Whorl Thickness Indices correspond to the mean for *P. marchanti* and there seems little doubt, both from morphological similarity and distributional contiguity, that these Waitotara specimens are closely allied to *marchanti*.

The Punipaua *Paryphanta*

The late Mr. A. C. O'Connor collected one almost complete shell and a number of juveniles of a *Paryphanta* from a limestone cave at Punipaua Creek, near the Paturau River, West Nelson. Diam. 35·5 mm., height 18·9 mm., whorl thickness 13·6 mm. There are 4½ whorls and the shell surface bears distinct spiral threads. There are two subspecies of *gilliesi* living near the Paturau River at present, *P. gilliesi aurea* Powell and *P. gilliesi brunnea* Powell. Height and whorl thickness indices have been calculated for five specimens of each of these forms for comparison with the Punipaua subfossil.

	Height Index	Whorl Thickness Index
P. gilliesi aurea Powell	54–61 (58)	38–41 (40)
P. gilliesi brunnea Powell	52–60 (56·5)	36–40 (38)
Punipaua *Paryphanta*	53	38

From the above there seems no reason to doubt that the Punipaua *Paryphanta* represents a form ancestral to one, if not to both the subspecies of *gilliesi* at present living in the vicinity of the Paturau River.

The Mungaroa *Paryphanta*

Powell (1946, p. 122) recorded the occurrence of "collapsed shells of a *Paryphanta* closely resembling a small *obscura* . . . at the Wallaceville Swamp, an area of peat bog in the Mangaroa Valley just east of

the main Hutt Valley, Wellington. They were on the surface of the peat, not embedded, under cover of a derelict *Phormium* plantation." When first collected these shells are completely flattened, all trace of lime having vanished. They do retain much of the colour pattern although original tonal values have, no doubt, been altered. Some of the better preserved shells have been soaked in hot water and restored to approximately their normal shape. The upper whorls are generally damaged but the body whorl is sometimes well enough restored to allow measurements to be taken of diameter and whorl thickness. Measurements for five specimens are given below.

Mungaroa *Paryphanta*

Diam. mm.	W.T. mm.	Umbilicus Diam. mm.	W.T.I.
42·5	15·8	5·9	37
42·7	16·3	6·0	38
44·7	17·5	6·4	39
40·1	15·6	5·0	38
42·7	16·5	5·2	38

There is considerable uniformity as regards whorl thickness, the range of the Whorl Thickness Index being 37 to 39, mean 38. A series of five *Paryphanta traversi otakia* Powell (including the type) have a range of 36 to 37 (mean 36). The colour pattern is essentially the same as *otakia* with a spiral pattern of narrow, closely spaced lines on the dorsal surface, broken by the growth lines. The ventral surface is uniformly dark with faint traces of spirals (as are many *otakia*) and irregularly developed sub-peripheral bands. The writer concludes that the Mungaroa *Paryphanta* is closely allied to *otakia* and was probably derived from the *traversi* stock.

Harris (1951, p. 6) has stated that the swamp is "probably not more than about 7,000 years old."

Geminoropa (Cavellioropa) spelaea (Powell)

The writer has already given some details of this species (Dell 1952, pp. 92, 94) and recorded it from Punipaua and the type locality which is the old moa bone caves at Coonoor. Recent collections made by Mr. J. C. Yaldwyn from Waewaepa, close to Coonoor, include additional specimens. It has also been collected by Mr. W. H. Hartree at Patoka.

As previously shown the Punipaua specimens differ slightly from North Island topotypes in having more ribs on the body whorl. Peculiarly enough the Patoka specimens are closer to the Punipaua specimens in this respect than to the Waewaepa series.

Ranges and Means of Riblet Indices

Waewaepa and Coonoor	(5 specimens)	18–21 (19)
Punipaua	(2 specimens)	24–27 (25·5)
Patoka	(5 specimens)	26–29 (27)

These differences could be of systematic value but examination of specimens from intermediate localities is necessary to elucidate the matter. All the adult specimens show the characteristic flattening of the upper part of the body whorl.

DISCUSSION

The major interest of the subfossil snails described above lies in their association in a number of widely separated areas. The forms found at the various localities are as follows:—

Punipaua

Rhytida oconnori Powell, the Punipaua *Paryphanta, Geminoropa (Cavellioropa) spelaea* (Powell).

Ruakokopatuna

Rhytida yaldwyni Dell, the Wairarapa *Paryphanta.* The *Cavellioropa* has not as yet been recorded from this area but may well occur there as the collections have so far been made mainly from the deeper bird deposits.

Waewaepa and Coonoor

Rhytida yaldwyni Dell, the Wairarapa *Paryphanta, Geminoropa (Cavellioropa) spelaea* (Powell).

Patoka

Rhytida cf. greenwoodi Gray (too broken for specific determination but of the *greenwoodi* type), the Wairarapa *Paryphanta, Geminoropa (Cavellioropa) spelaea* (Powell).

Paryphanta is thus represented by an ancestral *gilliesi* form at Punipaua and a different form in the North Island localities (though these latter shells may well have been subspecifically differentiated). *Rhytida* has a representative at Punipaua, with a related form at Ruakokopatuna and at Waewaepa and a representative of a completely different line at Patoka. *Geminoropa (Cavellioropa) spelaea* (Powell) has been recorded from all these localities except Ruakokopatuna, where, however, it may well occur.

The age of these deposits cannot be estimated very exactly. The Punipaua *Paryphanta* may not have been very different from the two *gilliesi* forms living in the region at present; the Wairarapa *Paryphanta, Rhytida oconnori, R. yaldwyni,* and *Cavellioropa spelaea* are all extinct. The clearing of the bush cover after European settlement can hardly be the cause of extinction as suitable areas of bush still exist near Punipaua so that this fauna could have persisted there. In addition quite extensive collections were made in the Forty-mile Bush and the Seventy-mile Bush before their destruction and such large snails would undoubtedly have been recorded if present. Two large species of *Cavellioropa, C. huttoni* (Suter) and *C. moussoni* (Suter), the latter closely related to *spelaea,* occur as living shells in the same general area (type locality for both, Forty-mile Bush). Judging by the data accompanying collections, the shells have been collected from surface or subsurface layers in all cases. In most cases bird bones were associated. More intensive work on the sequence of bird remains will give a better basis for a sub-recent chronology. Until this is achieved the true stratigraphic position of the associated mollusca cannot be adequately discussed. The mollusca appear to be present mainly in the top layers. The four molluscan deposits discussed seem to be contemporaneous judged by the fossil evidence. *Cavellioropa* ranges throughout, *Rhytida* is represented by two related forms in the

three southern areas, and the Wairarapa *Paryphanta* is common to the three northern localities. The species should therefore prove to be good indicators for the upper levels of the bird deposits in this area. *Geminoropa* (*Cavellioropa*) *spelaea* (Powell) in particular would appear to be an excellent indicator fossil.

The date of the fossils is certainly post-Pleistocene. Correlation of such terrestrial cave deposits with swamp and marine deposits is very difficult in an area such as New Zealand with few time markers. The zoogeographical position at the time represented by these deposits is as follows. *Cavellioropa spelaea* had been established over the whole area from Punipaua to Patoka. This is the widest distribution pattern represented. Two very different types of *Paryphanta* had developed, the Punipaua *Paryphanta* in the South Island locality, and the Wairarapa *Paryphanta* in the three northern areas (though this may have been represented by regional subspecies). A *Rhytida* of the southern *patula* type (allied to, but distinct from, the Punipaua subfossil *R. oconnori*), was established in the North Island as far north as Waewaepa. In the north at Patoka a *Rhytida* of the northern *greenwoodi* series (possibly *spelaea* Powell, known from coastal sand dunes in Hawkes' Bay) took its place.

This distribution pattern demands first of all a continuous or semi-continuous land mass between Punipaua and Patoka to allow the *Cavellioropa* to establish its range and to allow the ancestors of *Rhytida yaldwyni* and possibly of the Wairarapa *Paryphanta* (or the species themselves) to become established. The Wairarapa *Paryphanta* was probably derived from a *hochstetteri* stock in the north-eastern portion of the South Island. Faunal barriers had already allowed the separation of different stocks at Punipaua and in the area now dominated by *hochstetteri*. These faunal barriers must have been at some stage, selective, to allow the passage of *Cavellioropa* while segregating *Paryphanta*. A faunal barrier must then have been established between the north-eastern section of the South Island and the Wairarapa (possibly a "Cook Strait" Bight occupying the area between Cloudy Bay and Palliser Bay). This would allow the segregation of the Wairarapa *Paryphanta* and the *Rhytida*, which, isolated from the South Island stocks, attained their distinctive characters. The *Paryphanta* extended its range as far north as Patoka on the East Coast and possibly as far north as Te Kuiti (Powell, 1946, p. 103). Such an extension of range presupposes no continuous faunal barrier to the north but some faunal barrier (approximately in the position of the Manawatu Strait) must then have come into operation to prevent any extension of the range of *Rhytida yaldwyni* so that *R. yaldwyni* was isolated south of Waewaepa and *Rhytida spelaea* (derived from a *greenwoodi* stock) became established in Hawke's Bay).

It is reasonable to suppose that the central ranges of the southern North Island prevented an interchange of *Paryphanta* from east to west. The *traversi* series could then be derived as Powell has suggested (1946, p. 122) from a *hochstetteri bicolor* × *obscura* cross giving forms like *traversi otakia* and the Mangaroa subfossil in the southern part of the western coast of the North Island. From this stock the *traversi* series could have been derived by adaptive radiation,

extension of range to the north, and subsequent partial or complete isolation. Such an invasion of the North Island could have taken place by a more westerly trans-Cook Strait land connection than that postulated for the Wairarapa *Paryphanta* (Te Punga, 1953).

Whatever the true phylogenetic relationship of *Paryphanta marchanti* Powell may be i.e. whether derived from the *traversi* series (as the writer believes) or whether more directly related to *hochstetteri* as Powell originally stated, its zoogeographical position now becomes explicable. If it has been derived from the *traversi* series as its morphological characters and the distributional data tend to show, it is not unreasonable to suppose that as a geographical extreme derived from a hybrid *hochstetteri* cross it should present some of the characters of its ancestors. On the other hand *P. marchanti* could have been derived at the same time and from the same stock as the Wairarapa *Paryphanta*. In other words, both the *traversi* series and the Wairarapa *Paryphanta* were probably derived from a rather similar *hochstetteri* stock but at different times and *P. marchanti* could have been derived from either source.

One urgent need in establishing a chronology of the post-Pliocene in New Zealand would be the working out of the stratigraphy of the cave bird bone deposits. This in itself, together with a few radiocarbon determinations would supply a basis upon which such conjectures as the above could be more accurately documented.

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