

TRANSACTIONS
OF THE
ROYAL SOCIETY OF NEW ZEALAND

ZOOLOGY

VOL. 1

No. 30

FEBRUARY 12, 1962

[Continued from *Transactions of the Royal Society of N.Z.*, Volume 88, Part 4.]

Paleogeographic History Reflected in Speciation Trends of
the New Zealand Ribbed Pulmonate *Charopa coma* (Gray)
(Charopidae)

By R. A. CUMBER

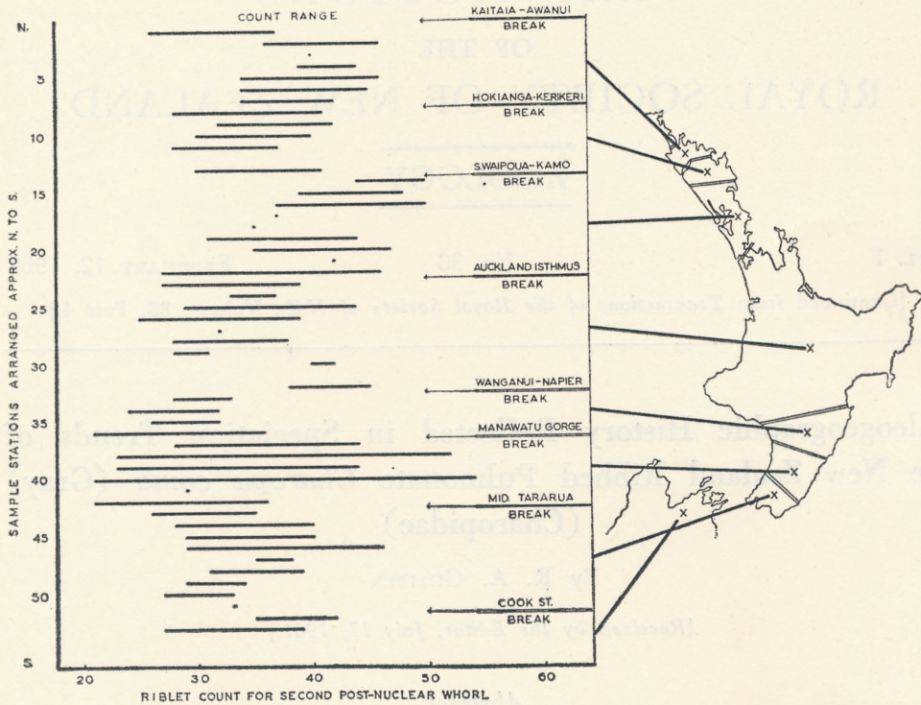
[Received by the Editor, July 17, 1961.]

Abstract

VARIATION in riblet frequency in the second post-nuclear whorl of *Charopa coma* (Gray) has been studied in 53 samples (over 700 specimens) taken from the vicinity of Kaitaia, in the far north, to the Nelson districts, in the north of the South Island. Trends in frequencies of a north-south clinal nature are indicated. Strongly bimodal frequencies however, manifest in the Manawatu area, are explained on the basis of paleogeographic history which indicates that this species may well have become separated into large northern and southern populations by the Pliocene depressions which produced the Manawatu Straits. Subsequent geographic reunion at this point has produced a reuniting of such populations after a period approaching that necessary to produce reproductive isolation. This period of about 10 million years fits suggested ideas on speciation rates in terrestrial Mollusca. If a period of 2-5 million years for subspecific speciation is accepted, there are grounds for suggesting separation in the Cook Strait area for such a period.

INTRODUCTION

LIVING animals which reflect past land frontiers with some precision are by no means common. The further we delve into the past, the more we must look to the lower organisms whose stability has enabled them to survive relatively unaltered until the present day. But not only "lowliness" is concerned here. Of equal importance in such organisms is their immobility—their relative resistance to dispersal. Terrestrial Mollusca are admirably suited for such studies. Amongst these pulmonates, those species which possess distinct radial riblets are particularly suited, for here is a statistic which is easily and accurately assessed.



TEXT-FIG. 1.—Count ranges for the second post nuclear whorl in samples of *C. coma* taken from Oruaiti in the north to Nelson districts in the south and arranged approximately in that order. Sample numbers refer to: 1—Oruaiti, 22.9.58 (4 specimens); 2—Ahipara Saddle, 1.10.57 (3); 3—Herekino, 22.9.58 (1); 4—Otangaroa, 23.2.59 (3); 5—Kao Hill, 19.9.58 (4); 6—Waiare, 19.9.58 (16); 7—Mangamuka, 23.9.58 (4); 8—Paihia, 12.1.49 (26); 9—Waikare, 24.9.60 (2); 10—Aramahoe (B.O.I.), 19.1.57 (3); 11—Kaikohe, 1948 (4); 12—Omapere (Hokianga), 3.10.57 (1); 13—Waipoua Forest, 26.9.58 (10); 14—Maunganui Bluff, 19.1.57 (3); 15—Mangakahia, 25.9.58 (7); 16—Bream Head, 6.1.57 (8); 17—Paparaoa, 29.9.58 (1); 18—Wellsford, 13.1.58 (1); 19—Pukapuka, 18.3.59 (5); 20—Warkworth, 3.7.48 (10); 21—Puhoi, 25.12.59 (1); 22—Titirangi, —.12.37 (22); 23—Clevedon, 9.7.58 (21); 24—Te Aroha, 7.7.59 (3); 25—Te Kawa, 19.3.59 (2); 26—Mapiu, 10.7.58 (3); 27—Awakino, 24.9.59 (1); 28—Turangakumu, 12.2.57 (11); 29—Tangoio Hill, 9.2.59 (2); 30—Tarata, 3.4.57 (2); 31—Stratford, 28.11.48 (1); 32—Kai Iwi, 28.1.48 (2); 33—Pohangina, 13.4.61 (20); 34—Huntermville, 28.3.57 (5); 35—Wharite, 15.5.58 (8); 36—Waewaepa Ra. (Puketoi Ra.), 29.3.57 (9); 37—Ballance Bridge, 28.1.59 (8); 38—Pahiatua Track, 29.7.58 (19); 39—Pahiatua, 15.6.58 (56); 40—Kahuterawa, 27.4.61 (307); 41—Castlepoint, —.6.59 (1); 42—Mt Bruce, 20.1.61 (24); 43—Paraparaumu, 1938 (26); 44—Tauherenikau Valley, 25.4.38 (10); 45—Porirua, —.2.40 (6); 46—Wilton's Bush, Wellington, 1938 (39); 47—Wellington-Hutt Waterfront, 1938 (3); 48—Lowry Bay, —.2.40 (8); 49—Wainuiomata, —.8.38 (8); 50—Miramar Peninsula, 1938 (3); 51—Haurangi Ra. (Aorangi Ra.), 24.1.59 (1); 52—Durville Island, 1941 (2); 53—Nelson Districts, 1948 (32). The indicated breaks are based on apparent range trends in *C. coma*, modern geographic features, and less apparent geographic features which appear to have barrier value in other pulmonates.

Charopa coma (Gray) (Fig. 1) is such a ribbed species. This snail is peculiar to New Zealand, where it occurs from the vicinity of Kaitaia in the far north to Stewart Island in the south. Apparently it does not exist on the Three Kings Islands, in the North Cape Area, or on the Subantarctic Islands. Its usual habitat is the densely bushed areas where it may be found beneath rotting wood, under bark, or under matted fallen vegetation. It often persists, however, beneath wood in dwindling bush remnants providing the under cover is not severely disturbed.

Suter (1913) in his re-description of this species, remarks on the variability in riblet frequency, and in addition, recognised the subspecies *globosa* which has a "more elevated, broadly rounded conoidal spire, and narrower umbilicus" recording this from Wanganui, Dannevirke, Mauriceville, Paekakariki, and Wellington. The species *C. multicostrata* (Murdoch) and *C. pseudocoma* (Suter), the former from Wanganui, Ruatahuna, Motu River Valley, and the latter from Poverty Bay, Akaroa, Little River, Dyer's Pass, Riccarton Bush, may best be considered at most as subspecies or varieties in view of the variation shown for *C. coma* in the present paper.

More recently Whitten (1956) studied variation in the riblet index (ratio of total number of riblets on the body whorl to major diameter in mm) of *C. coma* in some ten localities ranging from Whangarei to Stewart Island. He was not able to illustrate any clear trends in variation and concluded that "in most localities there is considerable variation in the number of riblets amongst individuals from the one locality. The mean riblet index, however, does not show much variation between the various localities. A larger series of specimens from each locality could alter the mean index a little, but probably not very much."

The writer (1960) in statistical studies on representative species of six ribbed genera in New Zealand, was able to show that considerable advantages were to be obtained through the use of the second post-nuclear whorl. This whorl was shown to possess moderate relative stability and significant correlations with riblet frequencies in other post-nuclear whorls. The use of this whorl obviates the disadvantages presented by the frequently weathered first post-nuclear whorl and the indefinitely and closely ribbed aged whorls. It also allows the fuller use of samples in that younger specimens may be utilized. The speciation trends studied in the present account are based on statistical studies of riblet counts in the second post-nuclear whorl.

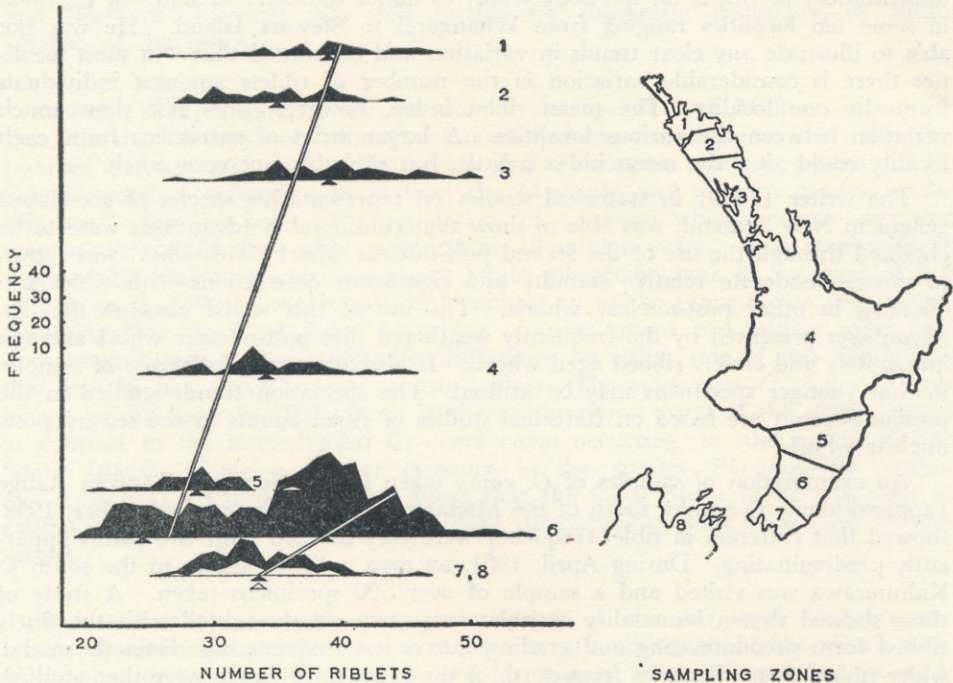
An examination of samples of *C. coma* taken in the Northern Tararua Range (approximately five miles south of the Manawatu Gorge) during September, 1958, showed that extremes in riblet frequency were very marked with two forms apparently predominating. During April, 1961, an area a little further to the south at Kahuterawa was visited and a sample of over 300 specimens taken. A study of these showed that a bimodality in riblet frequency clearly existed with the finely ribbed form predominating and grading into a less frequent but distinctly modal, wider-ribbed form. Samples from north of the Manawatu Gorge were then studied, and here it was found that only the widely ribbed form apparently existed. It was then decided to analyse all samples in the writer's collection. These have accumulated over the last 25 years and are fairly fully representative from Kaitaia in the far north to the northern districts of the South Island. The assemblage and study of more southern materials would have added to the value of the present paper, but it is doubtful whether these areas are as yet adequately sampled. The present materials studied, however, would appear to cover the more significant and interesting section of the species' range.

RESULTS

The materials studied were collected from more than 53 sampling stations and involve over 700 specimens. The Nelson sample (53) comprises material from five localities between the Whangamoia Range and Takaka Hill.

The information obtained from riblet counts of the second post-nuclear whorl is summarized in Text-figures 1 and 2. Text-figure 1 indicates the count range, the samples being placed in an approximately north to south sequence. The sampling localities, dates of collections, and numbers of specimens studied are given in the caption. A number of breaks along this north-south range of samples

are indicated. The position of these has been determined partly by the range trends which are evident, partly by obvious modern geographic features, and partly by less apparent geographic features which apparently limit distributions of other pulmonates. The samples falling between these breaks have been grouped and their frequencies plotted in Text-fig. 2. The graphed frequencies have been spaced to conform with strictly north-south distances separating the centres of adjacent zones. Means and fitted linear regressions show the trends. With the exception of zone 6, distributions appear to be normal. The anomalous bimodal distribution shown in this zone, involving as it does the indicated trends, strongly suggests a re-uniting of two long separated populations.



TEXT-FIG. 2.—Frequency distribution for riblet counts of the second post-nuclear whorl of *C. coma* in samples falling within the indicated zones. These frequencies are spaced in accordance with the strictly north-south distances separating zone centres. The means (triangles) and linear regressions are shown. Zone means and S.E.'s are as follows: Zone 1, 39.0 ± 0.7 ; 2, 34.9 ± 0.6 ; 3, 39.1 ± 0.5 ; 4, 34.1 ± 0.5 ; 5, 28.6 ± 0.6 ; 6 (lower modality), 24.5 ± 0.4 ; 6 (upper modality), 38.7 ± 0.3 ; 7, 33.5 ± 0.5 ; 8, 33.6 ± 0.8 .

DISCUSSION

The data present three interesting considerations. Firstly there is the apparent north-south clinal tendency; secondly there is the obvious re-uniting of two populations which paleogeography must explain; and thirdly there is the theoretical consideration of time required for two large separated populations to reach a condition where they cannot interbreed, and so become separate species.

It could be epostulated that riblet frequency is strictly related to temperature, and that the cooler the climate the greater is the interval between the laying down of riblets. But the situation is not simply this as evidenced by mixed populations at the one site. If the indicated clinal trend is basically conditioned by climatic variation, there are obviously other factors inherent in the zones which over-ride

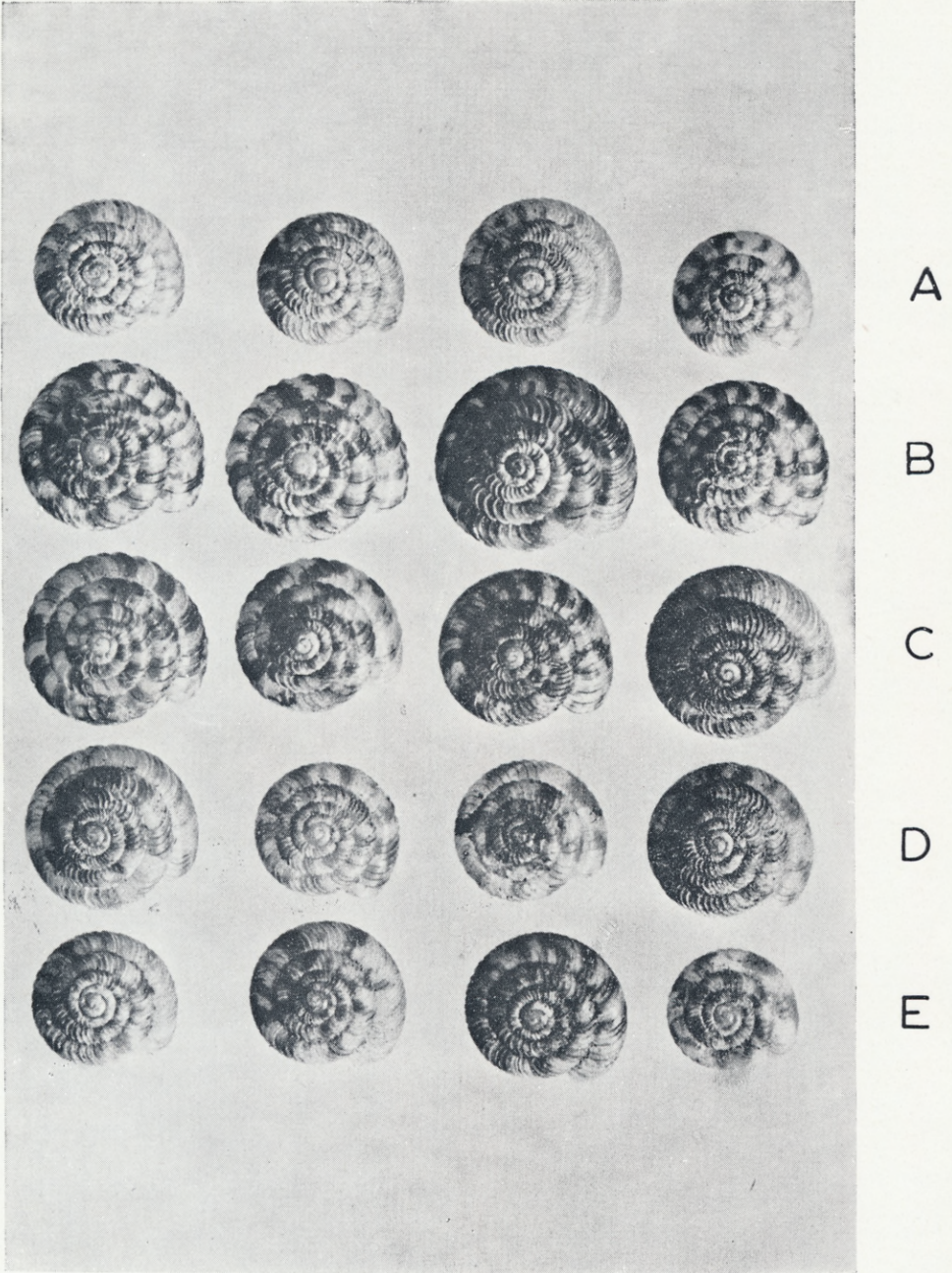


FIG. 1.—Typical riblet frequency of *C. coma* from: A, Mid-North Auckland area; B, Ruahine-Manawatu Gorge area; C, Kahuterawa area; D, Wellington area; E, Nelson area, showing varying degrees of frequency. The extreme forms co-exist in the Kahuterawa area (C).

Photo: M. Soulsby.

a strictly overall north-south linear manifestation of this trend. Perhaps temperature thresholds, past climatic history, and the size and degree of isolation of the various populations are important here. Reference to Text-fig. 1 shows that sample 1 from Oruaiti in the far north has a rather different range from that of its neighbours. This may well be related to a relatively small population originally isolated in an area now represented by the peninsula separating Doubtless Bay and Ranganui Harbour, and the peninsula immediately north of Wanganui Harbour.



TEXT-FIG. 3.—The interpretation of New Zealand geography in the early Wanganui Epoch (? early Pliocene) as evidenced partly by the presence of marine fossiliferous rocks: based on G.S. 641 (1946) reproduced by Fleming (1949).

The re-uniting of two long isolated populations along the Manawatu Gorge line would appear to be adequately explained by a consideration of New Zealand's paleogeography during the past 10–15 million years. This is outlined by Fleming (1949). Text-fig. 3 is a reproduction of his figure showing paleogeography during the early Wanganui period based on the occurrence of marine sediments of the Opoitian and Waitotaran stages. It would seem that the great Pliocene depressions commenced as a strait or straits across the Ruahine-Tararua axis during the Kapitean (latest Miocene)—i.e., perhaps 10–15 million years ago. The dispersal of basic stocks of *C. coma* must have preceded this break. The geographic reunion of the Manawatu Straits may have taken place at about the time that Cook Strait was breached—i.e., perhaps two million years ago.

It would seem that on the disappearance of the Manawatu Straits the southernmost forms of the northern population (widely spaced ribs) began mingling with the northernmost (narrowly spaced ribs) representatives of the southern population. On present evidence this mingling is apparent only to the south of the Manawatu Gorge. Eastern outlying areas such as the Waewaepa Range and Mt Bruce belong rather to the northern population, indicating that the Manawatu Straits may have turned relatively sharply southwards at their eastern margin.

There is no doubt that the isolation of these northern and southern populations has resulted in generic differences of a magnitude approaching those necessary for specific distinction. A statistical analysis of a sample of 312 specimens from Kahuterawa confirms significant bimodality (Chi sq. = 119.0 for 23. d.f. *** p. less than 0.001: normal distributions satisfactorily fit the separate distributions). It may be that the separation has been sufficient to produce reproductive isolation and that in fact two species do now co-exist. Only experiment will clear this point. However, the extreme variability of the species throughout its range and the moderately large number of intermediate forms in the zone of mingling suggest that isolation does at least not exist for proportions of the populations. The widely-spaced riblet form from the Southern Ruahines and Northern Tararuas may well qualify for subspecific distinction in future revision of the genus.

Solem (1959) reviewing the question of the age of land Mollusca concludes that "in the Tertiary only minor evolutionary changes took place . . . Modern families were present in the Cretaceous and Paleocene; modern genera in the Eocene; modern subgenera in at least the Miocene; and modern species in the Pliocene." On this basis large populations of a species which become separated may attain specific rank after a period of 10 million years. It is reasonable to suppose that similar populations might attain subspecific rank in a period of 2-5 million years. These conclusions would appear to fit the present case very nicely. Assuming that the Cook Strait breaching occurred about two million years ago, one would expect to find subspecific differences on either side of this break, and this does in fact occur in the present species. The subspecies *C. coma globosa* recognised by Suter in 1892 occurs in the southernmost parts of the North Island in contrast to the more typical *C. coma coma* occurring in the north of the South Island. There is further evidence in the species *Phenacohelix stokesi* (E. A. Smith). Cumber (1961) shows that the Cook Strait break has been in existence for a period sufficient to produce differences of subspecific rank in this species.

It is generally true today that the majority of our terrestrial Mollusca are associated with substantial bush coverage. In attempting to fit the distribution of these animals into Pleistocene geographic history, it should not be assumed, however, that these have always been their requirements. The question of humidity is all important. Sparse vegetation at 4,000ft today is doubtless a far better habitat than the same degree of vegetation near sea-level in most areas. There are few detailed studies on the food requirements of snails, but it seems probable that with the exception of a relatively few carnivorous species, most browse on decaying vegetation, fungae, algae, lichens, mosses, and perhaps ferns. The association of the different species with different plants may well be due to the epiphytes on these plants, which are dependent upon conditions of humidity. Some species today live beneath moss and lichen covered rock well above the bush line, just as successfully as do others beneath logs in the densely wooded areas of the genus.

New Zealand possesses a large and varied fauna of terrestrial Mollusca. Close studies of distribution and variation in other species will certainly yield information of great interest to both geographer and biologist, and will place our systematics on a firm basis. There is an urgency to collect adequately our fast dwindling areas of original vegetation before the opportunities for such studies are lost for all time.

ACKNOWLEDGMENTS

The collection of the materials on which the present account is based has taken place at intervals over the last 25 years. During this period many people have contributed to the present result by means of discussion and assistance in the field. This assistance is gratefully acknowledged—the kindness on many occasions of the late Mr A. C. O'Connor is especially remembered. The assistance of Miss M. Soulsby, photographer, and Mr A. C. Glenday, statistician, of the Department of Scientific and Industrial Research, Palmerston North, is also acknowledged.

REFERENCES

- CUMBER, R. A., 1960. Riblet Frequency as a Taxonomic Character in New Zealand Terrestrial Mollusca. *Trans. roy. Soc. N.Z.* 88 (1): 99-103.
- 1961. A Revision of the Genus *Phenacohelix* Suter 1892 (Mollusca: Flammulinidae) with Description of a New Species, and Studies on Variation, Distribution, and Ecology. *Ibid. Zool.* 1: 163-96.
- FLEMING, C. A., 1949. The Geological History of New Zealand (with Reference to the Origin and History of the Fauna and Flora). *Tuatara* II (2): 72-90.
- SOLEM, A., 1959. Zoogeography of the Land and Fresh-Water Mollusca of the New Hebrides. *Fieldiana Zoology* 43 (2): 241-359.
- SUTER, H., 1913. "Manual of New Zealand Mollusca." *N.Z. Govt. Printer, Wellington.* 1120 pp.
- WHITTEN, H. E., 1956. Some Variations in the Species *Charopa coma* (Gray). *Conch. Sect. Auck. Mus. Bull.* 12: 17-20.

R. A. CUMBER,
489 Albert Street,
Palmerston North.