nototheniae from the Southern Islands. The latter has been considered a possible synonym of *Ichthyobdella tentaculata*, which is described from South America. The doubtful early record of *Haemadipsa limbata* still stands unconfirmed.

To the above list can be added a species of *Ichthyobdella* known only from a single specimen taken at 80 fathoms in Cook Strait; specimens of the genus *Platybdella* from Cook Strait; and a Glossiphonid which is common at least in shallow coastal lakes. These are all in process of description. The Glossiphonid is of the genus *Glossiphonia*, a member of the *heteroclita* group, but so far not referable to a known species.

The characters of the leech fauna can be briefly summarised. There are at least four marine species representing the genera: *Pontobdella, Ichthyobdella, Platybdella*, and *Branchellion*. Three, if not all four, are distinct species, a point of interest in view of the strong endemic element among the coastal fishes, particularly the elasmobranchs. These genera are all known from Australia, South America, the Antarctic, and the northern oceans.

The freshwater leeches are of more interest. *L. australis* is a voracious sanguivore, formerly a medicinal leech, and in all probability introduced into this country. This fall, I received specimens which had come alive through the mail from Australia. *H. antipodum* seems a valid endemic species of an Australasian genus. The genus *Oligobdella* occurs at least in the Americas as well as here.

The knowledge of our leech fauna is progressing, but cannot yet be considered complete. Even in its present state, it shows features which are important and can reasonably be taken into account at this time. In particular there is the remarkable absence of species and genera which have achieved extensive dispersal. Most noteworthy is the absence of the voracious terrestrial sanguivores, the Haemadipsinae which, while primarily Indo-Malayan, are present in the Pacific, occurring in Fiji, and are even represented in South America. The absence of non-sanguivorous land leeches, excepting *O. edentula*, is also important.

This country is in frequent contact with lands to the north and north-west. The number of migratory birds arriving at and departing from these shores each year is great. The number of species is not high. The number of species making the journey with limited immersion in salt water is less, but the degree and nature of this contact is still sufficiently good for us to expect that we would share a leech fauna with the lands along the flight paths of these birds if bird-transport is significant in leech dispersal.

This certainly does not appear to be the case. The distribution of leeches through the South Pacific islands may result from carriage on short-range migrants not reaching this distance; but certainly many hundreds of years of active migration does not seem to have established any links with the Indo-Malayan or oceanic leeches in this country.

Briefly, the known freshwater leeches present in this country share no particular habit favouring their transport by birds either as adults or eggs. The many species which could on the basis of distribution and habits more reasonably be expected to be carried here by birds are absent from the fauna. The known facts do not warrant continued support of the concept of bird transport as an effective means of animal dispersal.

There is real need of an extensive knowledge of the leeches of this country and of the South Pacific islands. The leeches are a small group with definite habits. An intimate knowledge of their systematics, distribution and habits will provide a most valuable circumscribed body of facts useful in the testing of our concepts of the methods of animal dispersion.

THE SPECIES PROBLEM IN NEW ZEALAND LAND SNAILS

By A. W. B. Powell, Auckland Institute and Museum.

This paper is a composite one, for the final results will appear in three separate contributions. During an investigation into native snail populations, spread over the last twenty years, many interesting data have accumulated which have a definite bearing upon the species concept. The evidence is more in the nature of clues than watertight conclusions. Therefore I present my interpretation of this evidence for what it is worth, and invite criticism.

The snail groups dealt with are the large carnivorous species of *Paryphanta* and the equally large-sized herbivorous snails, *Placostylus*.

THE GENUS *Paryphanta*.

Paryphanta snails are carnivorous, feeding almost exclusively upon earthworms. They are restricted to some areas of high rainfall and certain species are confined to the higher levels of from 2,000–4,000 ft. They range from the Otago Cold Lakes to the tip of the North Auckland Peninsula, but they are by no means generally distributed. They occupy more or less the geologically old parts of the country that have escaped glaciation.

In a series of five papers published in the *Records of the Auckland Museum*, I have already made known no less than 36 species and subspecies, all of which are isolated by topographical boundaries.

In addition to these there are small aberrant populations which have scarcely the value of subspecies, but are nevertheless distinctive to the areas they occupy. These incipient species are of interest, for they stimulate conjecture as to the mode of development of new forms.

Intense localization of certain land snails was first observed in the Hawaiian Islands, where the tree snail, *Achatinella*, was found to consist of large numbers of distinct forms, each occupying a narrowly delimited zone. Recent work by Welch, 1938, on one species from the Waianae Mountains has resulted in the recognition of 25 subspecies. The areas occupied by these subspecies vary from 20 sq. ft. to 200 sq. ft.

Recent researches have shown that the snails of most tropical and subtropical lands are represented by large numbers of localized subspecies. In fact, only under the rigorous conditions of the palaearctic do we encounter extensive areas of snail distribution without apparent subspeciation.

Mokihinui Area.

In January of 1947, accompanied by Mr. A. C. O'Connor, of Wellington, and Mr. W. H. Johnston, of Seddonville, a fairly extensive search was made to locate as many *Paryphanta* populations as possible within a radius of 10 to 15 miles of Seddonville. Since then Mr. Johnston has generously devoted his whole time towards completing the field work.

The species and subspecies of the area are as follows:

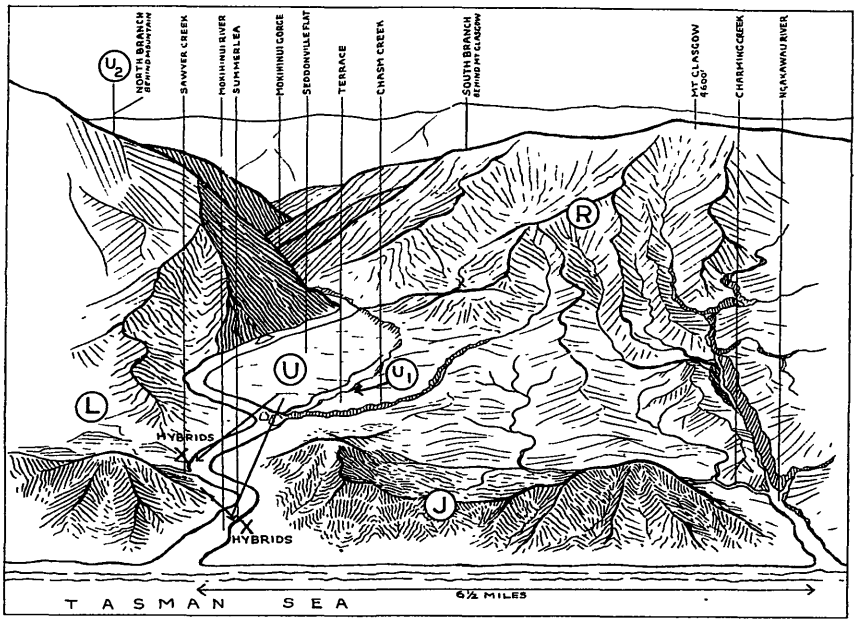
1. *lignaria*—radially streaked in dark brown on a yellowish base. North side of Mokihinui River.
2. *unicolorata*—plain khaki coloured. South side of Mokihinui River, between South Branch and Seddonville, on the river flats.
3. *unicolorata rotella*—spiral colour lines on top and sparse radial bands on base. Western drainage of Mount Glasgow.
4. *unicolorata johnstoni*—spiral colour lines top and base. On high-level silver pine "pakihis." Isolated block bounded by Mokihinui River to the north, Ngakawau to the south, the sea to the west, and two deeply cut streams to the east, Chasm Creek and Charming Creek.

Incipient Species by Isolation of Small Numbers from a Large Population.

Contrary to expectation, it has been demonstrated that *Paryphanta* snails will survive severe floods, even prolonged submergence. Mr. Johnston has supplied the information that the flood resultant from the 1929 Murchison earthquake submerged the Seddonville flat to a depth of over 10 ft. for a period of at least 10 hours and that floods involving inundation of Seddonville flat are of not uncommon occurrence. Also he has observed living *Paryphanta* snails in the flooded river on several occasions.

Although a large river such as the Mokihinui is primarily a fairly efficient barrier between two distinct species of snails, the above shows that it is also capable at irregular intervals of the chance intermixing of stock. Most examples washed into the flooded river would perish by being transported out to sea, but nevertheless some individuals caught up in eddies are given a chance to land and survive. At Sawyer Creek, on the north side of the Mokihinui River, at a big bend, a small colony of hybrids was located—actually amongst a large population of *lignaria*. The hybrids exhibited the *unicolorata* features of size, ground colour and surface granulation coupled with the radial colour pattern of *lignaria*.*

* Since the above was written I found a living example of *unicolorata* under driftwood at Sawyer Creek bend, where without doubt it had been deposited as the result of a recent flood.



Approximate diagram of Mokihinui west coast, looking east from the sea. The letter symbols are: L = *lignaria*, U = *unicolorata unicolorata*, U1 and U2 = *unicolorata* n.subspp., J = *unicolorata johnstoni*, R = *unicolorata rotella*.

Sixteen of these hybrids were taken and the entire area occupied was apparently no more than 400 sq. yds. The chances are that these hybrids will be rapidly absorbed by the numerical strength of the *lignaria* population with which they are associated. These hybrids could only develop as an incipient new subspecies if an isolation factor operated also.

On the river flat, south side of the Mokihinui River near the mouth, Mr. Johnston recently discovered a thriving colony of snails which are predominantly *lignaria* except for a slight *unicolorata* influence. This colony undoubtedly owes its origin to flood survivors of *lignaria*, a species which is abundant on the opposite bank, plus odd examples of *unicolorata* brought down from higher up the river in the vicinity of Seddonville.†

Unfortunately, there is no evidence to show when this colony was first established, but it is most likely resultant from the flood associated with the Murchison earthquake of 1929. It is of special interest, however, for the surrounding country is otherwise without large snails, and the colony may well be considered an incipient species. That is if the colony achieves sufficient numerical strength to absorb or control further chance accessions by flood-borne stock. In any case the mere fact of a *lignaria* colony chopped off by the river from the main population is sufficient to visualise its ultimate development of differentiating characteristics.

It would seem therefore that the numerically superior populations more or less isolated by topographic boundaries preserve their individuality by pressure of numbers, and that new forms arise primarily and under exceptional conditions through the accidents of small numbers becoming isolated from the main areas of distribution.

Development of Subspecific Forms within a Large Area of Distribution.

The species *lignaria* occupies a considerable area of virgin forest in a block of about 400 square miles situated between the Mokihinui River and the Karamea River.

† Further investigation of this locality shows that hybrid colonies extend in a narrow strip for about half a mile along the river bank and that the proportion of *lignaria* and *unicolorata* factors varies so that on the whole the *unicolorata* influence is dominant and more than one colonisation is indicated.

Although the forest is continuous, the snails are not generally distributed, but are in scattered concentrations determined by the availability or not of their basic food, earthworms. Earthworms and snails are best developed in the warmer areas where there is a good depth of leaf mould. Stony and steep ground is not usually favoured by these snails. Nevertheless, some intercommunication between snail concentrations in the area is likely, for the snails are capable of crawling distances under moist conditions. For instance, in rainy weather they have been observed crawling across metal roads.

An interesting feature of the *lignaria* distribution is that there is a distinct colour difference in the snails distributed respectively north and south of the range which more or less transversely divides the area into a northern and a southern aspect. Snail colonies on the Mokihinui or southern side of the divide have a greenish-yellow ground, while those of the north side have a reddish-brown ground. There are several possible explanations:

1. *Clinal Variation.* The area occupied by *lignaria* is very large for a species with such limited means of dispersal. Both colour forms could be considered clines if there was a gradient between them, but so far no intermediate colour forms have been seen. Each colony so far examined has been either one colour or the other, and strictly in relation to the other colonies of the side of the range it occupies.

An almost parallel case is the distribution of *Paryphanta hochstetteri* over the conjoined mountain systems, the Pikikiruna Range and the Tasman Range. The extremities of these ranges have noticeably different colour forms which I have ranked as subspecies, *hochstetteri* typical on the Pikikiruna Range and *hochstetteri anatokiensis* on the Tasman Range. Differentiation was probably facilitated in this case by a "bottle-neck" at the point of divergence of the Tasman from the Pikikiruna Range.

An undoubted case of clinal variation is presented by the large distribution of *Paryphanta busbyi* over the North Auckland Peninsula. Apart from the geographically isolated distinct species *watti* from the northernmost block, no regional form of *busbyi* has been found other than slight size variation—those from the higher rainfall areas of the west being noticeably larger.

To return to *lignaria*, there is a greater rainfall on the southern side of the range, but from the above one would expect a size difference rather than a colour change. There is no size difference, and, as pointed out already, the change from one colour to the other is sudden, not a gradient.

2. *Probable Polymorphic Condition of the Species.* The ability of a large population to absorb stragglers from a contiguous area has already been suggested. Therefore: *Is the greenish yellow ground colour of lignaria from the Mokihinui side the result of infiltration by the plain khaki-coloured unicolorata from the south side of the river?* And, by the same criterion, *Is the reddish-brown ground colour of lignaria from the Karamea side the result of former contact with the deep reddish-brown annectens, which now occupies the block from the Karamea River northwards to the Heaphy?* It should be noted that under existing conditions, in the coastal area at least, there is a buffer zone of 12 miles without *Paryphanta* snails between the *lignaria* and *annectens* distributions.

Visualising a prior more effective isolation than under present conditions, there were evidently three isolated major populations.

A. *lignaria*—Mokihinui to Karamea.

B. *unicolorata*—Mokihinui to Buller.

C. *annectens*—Karamea to Heaphy.

These presumed long-standing populations I would tentatively term species.* Subsequent isolating factors, i.e., progressive deep cutting of gorges in the minor streams, Chasm and Charming Creeks, are considered to have caused further isolation within a species group, i.e.—

B1. *unicolorata* typical. 100 per cent. pure on south side of Mokihinui from South Branch to end of gorge. Carried down plus *rotella* to form a mixture on Seddonville Flat, the type locality.

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* The separation between *lignaria* and *annectens* is absolute, but I have shown that *lignaria* and *unicolorata*, which under conditions of isolation are quite distinct both in colour and in form, will freely hybridise when brought together. It is likely therefore that a reconsideration of values may result in the admission of fewer species and more subspecies and that my groups (i.e., *busbyi, traversi, hochstetteri, gilliesi, lignaria* and *rossiana*) will represent the species.

B2. *unicolorata* n.subsp. (1). Belongs to the Seddonville high-level terrace south side of the Mokihinui from the gorge to Chasm Creek. Scarcely affected by floods.

B3. *unicolorata rotella.* Silver-pine pakihis on radial spurs, western slopes of Mount Glasgow.

B4. *unicolorata johnstoni.* Silver-pine pakihis on the isolated block bounded by Mokihinui River, Tasman Sea, Ngakawau River, Charming and Chasm Creeks.

B5. *unicolorata* n.subsp. (2). Eastern side of North Branch of the Mokihinui River with influences down north bank of Mokihinui to below Seddonville.

These I would term subspecies, since each is more or less bounded by obvious topographic boundaries, yet all can be grouped under a more broadly defined form which collectively occupies a larger but clear-cut area. Regarding the two-colour forms of *lignaria,* A1 and A2, a designation of lesser value than subspecies is indicated.

The adoption of a quadrinomial system of nomenclature is essential if relative values are to be adequately expressed. The fourth name would then apply to forms or "microgeographic species" as Dobzhansky has termed them. Until a quadrinomial system is generally accepted, which is inevitable, it is my contention that forms should be named if for no other purpose than to keep them under notice.

Mayr, 1942, in his *Systematics and the Origin of Species,* gives the following definition of a subspecies: *"The subspecies or geographic race is a geographically localized subdivision of the species, which differs genetically and taxonomically from other subdivisions of the species."*

Pilsbry, 1939, in his *Monograph of the Land Mollusca of North America,* gave a definition very applicable to my New Zealand problem. *"Subspecies are theoretically races showing some intergradation with neighbouring forms in a small proportion of the individuals, but characterized by having a definably different distribution, geographic or ecologic. This distribution may be contiguous to that of conspecific races, or it may be isolated by geologic, climatic or other conditions, as when races are confined to calcareous soils, to humid places in an arid region, or are insular. Most subspecies are recognisably differentiated populations which are not considered sufficiently distinct to be called species. They are merely incipient species, in which the discontinuity is incomplete, or is not strongly pronounced."*

Horowhenua Area.

In the *Records of the Auckland Museum,* Vol. 3, No. 2, published February, 1946. I recorded the results of an intensive survey of *Paryphanta* populations on the Horowhenua Plain, extending from Otaki to the Manawatu River. Five subspecies were recognised. Two of them, however, showed intergradation where their respective boundaries were contiguous, although the present boundary is a sizeable river.

However, after reviewing the geological evidence presented in a paper by Mr. G. L. Adkin, 1911, *The Post-tertiary Geological History of the Ohau River and of the Adjacent Coastal Plain, Horowhenua County,* the reason for this only partially effective separation of two subspecies is at once apparent, for there have been two prior courses of the Ohau River, and snail populations along its banks have been subjected to a "give and take" operation on at least three separate occasions during and since the Pleistocene.

Other Considerations. 1. Within the past fifty years vast areas of forest have been removed and once-compact snail populations now exist as a series of artificially isolated colonies. Will these artificially isolated colonies now develop individualistic trends, and if so, what space of time will be required for such possible trends to become apparent?

2. In order to facilitate future investigation, a hundred snails from a large population in the foothills of the Tararuas have been removed to a lowland area of bush near Levin not containing other snails. The test is that representatives of a form recognisably different from the subspecies of the lowland area has been artificially established in that area.

Will the induced colony continue to breed true to type, or will it eventually take on the characteristics of the form from the surrounding lowland area?

If my contention is correct, it will do neither, but will develop independent characteristics on the observed principal *that small communities almost invariably give rise to new forms because of their inability to suppress or control radical trends by weight of numbers.*

3. Unfortunately, controlled genetical experiments are not practical because of the slow growth and relatively long life of these snails—at least 15 years to a generation; also the difficulty of maintaining absolutely natural conditions over such a lengthy period.

THE GENUS *Placostylus.*

Placostylus snails are vegetarian, feeding almost exclusively on the fallen leaves of karaka and mahoe except for one instance at the Three Kings Islands, where a colony has adapted itself to ngaio leaves.

These snails are restricted to the coastal headlands of the east and north coasts of North Auckland from Whangarei northward, and on certain of the outlying islands of this area.

An interesting study is presented by the remnant colonies which have persisted under very adverse conditions at the Three Kings Islands. On Great Island, which is one and a-quarter miles in length and roughly hour-glass shaped, there are three small colonies of the large land snail, *Placostylus bollonsi*, and each has developed individualistic characteristics.

No. 1 colony from the north-east end is short and broad.

No. 2 colony from the cliff faces of the narrow divide is small and slender, and

No. 3 colony from the south-west cliff face is very large and slender.

It is at once apparent that the vegetation on Great Island has been greatly modified. Great Island, in spite of its being well watered, is the one semi-arid member of the group. By contrast with the other islands, the division between the rocky cliffs and the vegetation shows barren expanses of yellow and reddish earth and greyish shingle screes. There can be little doubt that Great Island once resembled the other members where the giant puka, *Meryta sinclairi*, is a dominant feature, but now Great Island is largely a monotonous expanse of kanuka and stunted pohutukawa.

The factors causing this change in character of the vegetation of Great Island are presumed to be:

(1) The long residence in former times of a moderately large Maori population. These Maoris probably occupied the island for over three centuries. At the time of Tasman's discovery of the islands in 1643 the Maoris were in occupation, and Tasman noted in his journal that most of the more accessible parts were under cultivation. 'This was probably the factor that reduced the snail populations to the perimeter of more or less inaccessible cliff faces and caused the initial segregation of these snails into at least three separate colonies.

(2) The present marked deterioration of the vegetation when compared with Cheeseman's description of the island in 1889 is directly attributable to the depredation of goats introduced at about the time of Cheeseman's visit. Prior to the extermination of the goats in 1946 by Internal Affairs, the succulent vegetation had been reduced to odd large-leaf trees in a general expanse of kanuka.

Colony No. 1. This colony was found at the north-east end of Great Island and consisted of only eleven snails. The colony was restricted to the leaf-spread area afforded by a group of seven trees of wharangi (*Melicope ternata*) and one of mahoe (*Melicytus ramiflorus*). This colony exists solely within the leaf-spread area of this grove, which is from 5 to 10 ft. wide and 30 ft. long down a slope of 45°.

Colony No. 2. Probably about 25 snails occupying a similar grove on the south-west side of the island.

Colony No. 3. About 40 living snails and over 200 dead ones were taken by Mr. E. G. Turbott in April last year. These were from a ngaio grove high up on the north-west landing slope. About 30 of the dead snails were comparatively fresh, and probably died during the drought of a few months prior to Mr. Turbott's visit.

The island was systematically combed by Mr. Turbott and the members of the expedition sent by Internal Affairs to exterminate the goats, with the result that no further colonies were found.

Colony No. 4. In December, 1946, Major G. A. Buddle succeeded in landing upon the formerly considered inaccessible North-East Island, which lies immediately to the North-East of Great Island. Here, amidst luxuriant vegetation dominated by the large puka, Major Buddle found *Placostylus bollonsi* to be quite abundant.

A point of special interest is that these snails are identical with those of the north-east colony on Great Island, in spite of the intervening waterway. North-East Island, however, showed abundant evidence of Maori occupation, and so it seems very probable that the Maoris either intentionally or unintentionally were responsible for acclimatising the snails to this island. The South-West King was visited by Major Buddle also, but no *Placostylus* was seen.

Considerations.

If the differentiation into three forms of *Placostylus* on Great Island is the result of induced isolation caused by Maori occupation during a period of at least three centuries, why is the North-East Island population identical with one of the colonies on Great Island? A probable reason may be that the utilization of the almost inaccessible North-East Island as a kitchen garden by the Maoris was a late development after the land on Great Island had deteriorated through over-cultivation.* The presence of stone contour walls to retard the washing away of the soil on the steep slopes of Great Island is sufficient evidence of the problem that beset the former Maori occupants.

GENERAL.

With all work on snail populations the determination of the length of time requisite for the development of a new form is the most difficult to assess. My present work, which is largely descriptive of existing colonies, provides a basis for future checks, but it is anticipated that the lapse of many years will be required to show any marked differences.

To return to *Paryphanta unicolorata* of the Seddonville flat, it may be noted that the type specimen collected in 1906, when the locality was in virgin bush, can be matched exactly with the present population of the area, which is persisting under greatly altered conditions.

THE CONSTITUTION AND RELATIONS OF THE NEW ZEALAND ECHINODERM FAUNA

By H. BARRACLOUGH FELL, Victoria University College, Wellington

External Relations of the Fauna.

TH. MORTENSEN (1925) has already given reasons for including in the New Zealand faunal region the Kermadec and Auckland–Campbell Islands as well as the Chathams and the main islands. Within the region thus defined, and taking into account eight species awaiting publication, there are known to occur 177 species. As is shown in the histogram (Fig. 1), 141 species (c. 80%) are endemic, 29 (c. 16%) comprise Australian and Indo-Pacific species, 4 (c. 2%) are Magellanic, and 3 (c. 2%) are cosmopolitan. The high proportion of endemic species may be correlated with the supposed prolonged isolation of the region; the external relations are chiefly with the Australian-Indo-Pacific faunas; the relation to the Magellanic region is very weak—and as shown later in this paper —occurs in the southern provinces only and in an area of mixed waters.

The above figures confirm Mortensen's earlier deductions, and as he has discussed the external relations in some detail, the main part of this paper is devoted to a survey of the internal constitution of the faunal region, based on fuller data on the distribution of echinoderms which are now available. It is obviously desirable to establish whether the echinoderms provide any evidence as to the existence of marine provinces within the New Zealand region. If such can be shown to exist, their relation to the distribution of other recent groups will be of interest; at the same time some further guide may be provided for palaeontological studies since echinoids are commonly found in the fossil state.

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*D'Entrecasteaux observed smoke rising from North-East Island in 1792.