The Fresh-water Mollusca of New Zealand. Parts II and III.

Part II.—The Species Previously Assigned to the Genera Limnaea and Myxas.

By R. K. Dell Dominion Musuem, Wellington

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Abstract

EXAMINATION of the type material of the species of fresh-water mollusca previously classified as Limnaea in New Zealand has shown that L. tenella Hutton is a juvenile of the introduced L. stagnalis, L. pucilla Hutton is indeterminate, while L. tomentosa Pfr. and L. leptosoma Hutton belong to the genus Simlimnea Iredale. L. alfredi Suter is best left in Limnaea (s.l.) until animals can be obtained. An ancestral subspecies to L. alfredi is described from Hamilton's Swamp. All the living species previously classed as Myxas are shown to belong to one variable species, the earliest available name for which is tomentosa Pfr The generic name for this group should be Simlimnea Iredale.

Introduction

THE species of the genus Limnaea recorded from New Zealand and their discrimination from Myxas have been a stumbling block for local conchologists for the last half century. Pfeiffer described Succinea tomentosa (subsequently referred to Limnaea) in 1855. Hutton described leptosoma, pucilla and tenella in 1885, all from restricted areas. Specimens identified as tomentosa were sent to Hutton by Gillies and the radulae of these specimens were described (1885). In the Hutton collection in the Canterbury Museum there are specimens labelled tomentosa from Auckland. These do not agree with the type of Pfeiffer's species. There do not appear to be any subsequent records of Hutton's three species nor of tomentosa, the specimens in other collections being misidentified or having been distributed from the original lots. Suter's alfredi, described in 1890, was recorded from a number of South Island localities, but again does not appear to have been re-collected during the last 50 years. The forms classed as Amphipeplea by Suter have not been revised since 1913. Finlay (1926, p. 443) publicised Kennard and Woodward's conclusion that Myxas Sowerby had priority over Amphipeplea Nilsson, and this name has since been used for the New Zealand forms. Shell morphology in itself is of little use in determining relationships in this group, and no anatomical comparison between the European Myxas glutinosa (Muller) and the New Zealand forms has been made. Three New Zealand forms were recognised by Suter, ampulla Hutton, ampulla globosa Suter and arguta Hutton. Cumber (1941) has more recently described a subfossil form from the Waikare Moa Swamp as ampulla waikariensis. These forms are all diagnosed on shell shape and outline, although Hutton originally indicated radular differences between his arguta and ampulla. Suter (1905, p. 250) has, however, shown that the radulae of "arguta" from four different localities varies very considerably from that described by Hutton. Suter's usage in his own collection appears most confused, his conception of ampulla for example being very different from the type series His proposition of globosa as a variety of ampulla is based upon this confusion, globosa being more closely related to true arguta. The elevation of Suter's varietal names for mollusca to the status of sub-species in the fresh-water mollusca as elsewhere has added to the general confusion.

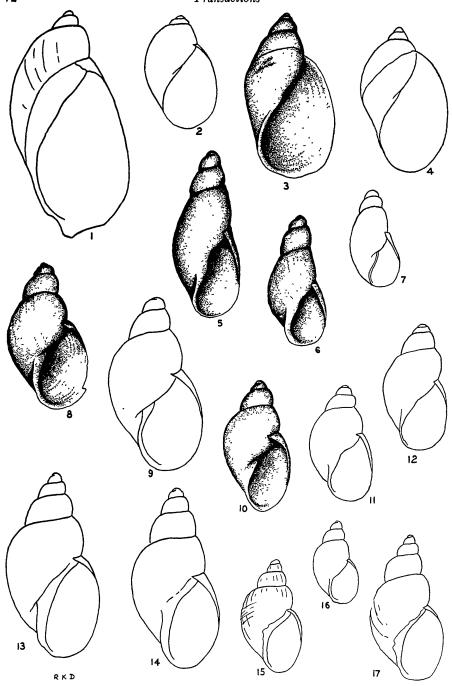


Fig. 1—Succinea tomentosa Pfeisfer, outline taken from a photograph of the type, supplied by the British Museum (Natural History). Fig. 2.—Simlimnea tomentosa (Pfr.) specimen in the Canterbury Museum, accepted as tomentosa by Hutton. Fig. 3—Simlimnea tomentosa (Pfr.) Type of Limnaca leptosoma Hutton Fig. 4—Simlimnea tomentosa (Pfr.), specimen of "leptosoma Hutton" in the Dominion Museum Fig. 5—Limnaca stagnalis (L.) juvenile from lake on Hokio Rd., Levin. Fig. 6.—Type of Limnaca tenella Hutton (to same scale as Fig. 5) Fig. 7.—Limnaca tenella Hutton, from the type series Fig. 8—Limnaca (sl) alfredi Suter, lectotype. Figs. 9, 11, 12.—Limnaca (sl) alfredi Suter, from the type series Fig. 10—Limnaca fincilla Hutton, type. Figs. 13, 14—Limnaca (Galba) truncatula (Muller), Grunenwald, Germany. Figs. 15, 16—Simlimnea alfredi hamilton: n.subsp. paratypes. Fig. 17—Simlimnea alfredi hamilton: n.subsp., holotype

In other parts of the world variation among members of the Limnaeidae has been long recognized. Work on the variation of such forms as the European Limnaea peregra for example has shown the varied shell forms that can result from the interaction of different environmental conditions upon diverse genetical material within one species. No one knowing of this work could consider the three accepted forms of Myxas, their scattered and sporadic distribution pattern, and their apparent lack of ecological preference without seriously doubting the advisability of maintaining the forms as separate on the basis of intergrading shell characters. The position is further complicated by the fact that two other "species", Succinea tomentosa Pfr. and Limnaea leptosoma Hutton, both previously grouped under Limnaea, should also be included in this group.

An examination of all the material available, including the types or photographs of the types has made possible some clarification of the problem. The writer is indebted to Dr. W. J. Rees, of the British Museum (Natural History) for a photograph of the type of Succinea tomentosa Pfr. and to the Director of the Canterbury Museum

for the loan of Hutton's material.

THE FORMS PREVIOUSLY CLASSIFIED AS LIMNAEA

Limnaea (s.s.) stagnalis (Linnaeus, 1758), Figs. 5, 6, 7.
1758. Helix stagnalis Linnaeus Syst. Nat., ed. 10, p. 774.
1926. Limnaea stagnalis (Linnaeus); Kennard and Woodward, Syn. Brit. Non-Marine Moll, p 43.

1885. Limnaea tenella Hutton, Trans. N.Z Inst, Vol. 17, p 55 1913. Lymnoea tenella Hutton; Suter, Man. N.Z. Moll. p. 606.

The type series of Limnaea tenella Hutton shows that this species is undoubtedly based upon juveniles of the introduced Limnaea stagnalis (L). The largest syntype of tenella is figured for comparison with a juvenile stagnalis from a small lake off Hokio Road, Levin The similarity is so striking that there can be no doubt of the specific identity. Hutton himself records that stagnalis was abundant in the River Avon in 1881, four years before tenella was described from the same locality (Hutton, 1882, p. 157). He seems to have had some doubts as to the specific differentiation of the New Zealand shells as he says (1885, p 54): "I have to thank Mr. H. M. Gwatkin for sending me odontophores of the British Limnaeidae without which I should have hesitated to name some of our species." Hutton gives some details of the radula of tenella but does not compare it specifically with stagnalis, and his figures are unfortunately too small for comparison.

Limnaea tenella Hutton must therefore disappear from the indigenous New Zealand faunal list, and the name becomes a synonym of stagnalis. Limnaea stagnalis (L.) is now widely distributed in sluggish streams and particularly in lakes throughout

New Zealand.

Limnaea pucilla Hutton, 1885.

1885. Limnaea pucilla Hutton, Trans. N.Z. Inst., vol. 17, p. 56.
1893. Limnaea pusilla Hutton (emend): Hedley and Suter, Proc. Linn Soc N.S.W. (Ser. 2), Vol. 7, p. 625. 1913. Lymnoea pusilla Hutton: Suter, Man. N.Z. Moll., p. 605.

Hutton's Limnaea pucilla (emended to pusilla by Hedley and Suter with no explanation) was based upon two specimens, both immature shells, from Auckland. The larger of the syntypes in the Canterbury Museum is here figured (Fig. 10). There have been no subsequent records of this species. Actually it is quite close to the subsequently described alfredi Suter, and pucilla may well be based on a juvenile shell of this form. Suter distinguished alfredi from pucilla by the presence of an umbilical chink in the former. Such a feature is, of course, quite often lacking in an immature shell The general whorl shape of the two forms and all other major shell characters agree very closely If the locality "Auckland" is correct for pucilla there are very good geographical grounds for considering the two forms distinct since alfredi has only been recorded from restricted areas in the South Island. Any decision upon the specific identity of the two forms under such circumstances could only be subjective and would raise more difficulties than it would solve. In addition, if the forms were considered identical the name pucilla Hutton based upon two juvenile shells and a rather dubious type locality would take precedence over alfredi Suter, for which an adequate type series is available and for which the type locality is well documented. There is also the possibility that the types of pucilla are juveniles of introduced or even foreign shells, which never lived in New Zealand.

The writer therefore recommends that the name pucilla be considered indeter-

minate, and that it should be dropped from the local faunal list.

Limnaea (s.l.) alfredi Suter, 1890.

1890. Limnaea alfredi Suter, Trans. N.Z. Inst., Vol. 22, p. 229.

1913. Lymnoea alfredi Suter, Manual of N.Z. Moll., p. 604.

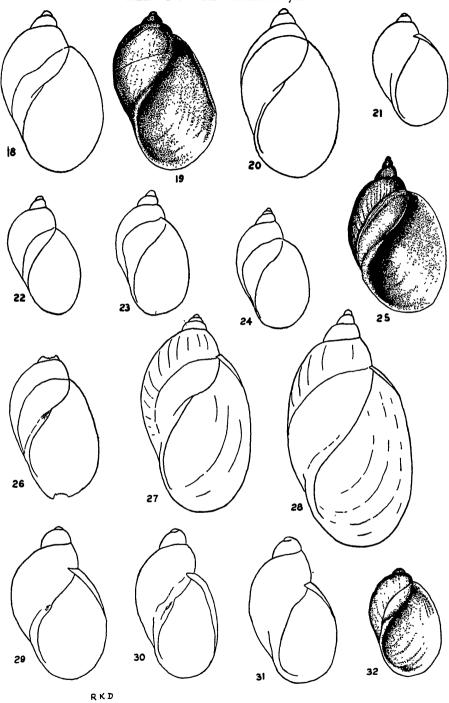
This species was recorded by Suter from a number of localities in Canterbury and Otago, but it has not been re-collected in recent years. For instance no species of *Limnaea* was collected in the survey of New Zealand lakes carried out by Lucas and Hodgkin in 1902.

Comparison of the type series of alfredi with the European truncatula Muller shows that the two forms are very similar as regards all shell features. The New Zealand shell has a rather more oblique and more expanded aperture which gives it a rather different outline. The two species are, however, very close conchologically. In the absence of other evidence there would be quite strong grounds for considering the New Zealand form to have been derived from an introduction of the European species. The strong shell similarity, the restricted and sporadic distribution, and the apparent early extinction of the form would all be in accordance with such a supposition. Two additional lines of evidence, in addition to the fact that the shells, though superficially similar, are separable, indicate the morphological distinctness of the New Zealand form, and hence its indigenous status. Suter (1892, Pl. 23, Fig. 56) figured the radula of alfredi, and although the drawing is on a very small scale, the central tooth is obviously bicuspid. A bicuspid central does not appear to be usual in Limnaea though it occurs in other genera in the family. In the Canterbury Museum there are some sub-fossil specimens of a Limnaea from the moa swamp at Hamilton, North Otago These shells are smaller, with a comparatively longer spire and less expanded aperture, and probably represent an ancestral form. They undoubtedly indicate that the alfredi type of shell has had a history in New Zealand that pre-dates European influence and that it is a truly indigenous form.

DISTRIBUTION. Governor's Bush, Hooker Valley (type); Lagoon at Birch Hill

Station, Tasman Valley; Lake on Arthur's Pass; Ashburton.

The generic name to be used for these New Zealand forms cannot be satisfactorily determined until animals are obtained. The old genus Limnaea has been split into a number of subgenera on anatomical grounds in Europe and North America. The Australian forms have been provided with four generic names; Peplimnea Iredale 1943, Austropeplea Cotton 1942, Simlimnea Iredale 1943 and Glacilimnea Iredale 1943. Neither Austropeplea nor Glacilimnea appear to be applicable for the New Zealand shells. The Australian species classified under Simlimnea have shorter spires and similarly expanded body whorls to the New Zealand shells previously classified under Myxas, and this usage is tentatively recommended later in this paper. None of our species agree with the type of Peplimnea, although some of the Australian forms included under this genus by Iredale (1943) are close in general appearance. In the meantime it seems more reasonable to continue the use of Limnaea (s.l.) for alfredi especially as the animal is unknown. The comparatively long spire distinguishes this species from the "Myxas" group in New Zealand This is the only distinguishing feature as far as is known, and the gap is partly bridged by "Myxas ampulla Hutton", so that the two groups may ultimately prove to be congeneric. The discovery of living specimens of alfredi will provide the only solution to this problem.



Figs. 18, 19, 20—Simlimnea tomentosa (Pfr.), syntypes of globosa Suter Fig. 21.—Simlimnea tomentosa (Pfr.) Auckland, Canterbury Museum. Figs 23, 24.—Simlimnea tomentosa (Pfr.) from specimens in the Dominion Museum labelled "leptosoma Hutton" (M 28). Fig. 25—Holotype of Simlimnea tomentosa waikariensis (Cumber). Figs 22, 26, 32—Simlimnea tomentosa (Pfr.) syntypes of Limnaea arguita Hutton Fig 27—Simlimnea tomentosa (Pfr.) Turanganiu, Wairarapa, probably same type of population as the types of "Limnaea leptosoma Hutton" Fig. 28—Austropeplea aruntalis Cotton and Godfrey, near Adelaide. Figs 29, 30, 31.—Simlimnea tomentosa (Pfr.) syntypes of Limnaea ampulla Hutton

Limnaea (s.l.) alfredi hamiltoni n.subsp. Figs. 15, 16, 17.

Shell small, close to alfredi Suter but differing in the relatively smaller spire and the considerably less expanded aperture. The spire may be slightly shorter than the height of the aperture but it is usually taller. Aperture but little expanded, axis vertical (usually oblique in alfredi). The sculpture consists of rather regular, close-spaced growth lines, and occasionally broad, irregular spiral folds are developed.

Height, 6.9 mm; height of spire, 3.7 mm; diameter, 3.6 mm (holotype).

Holotypes and paratypes in Canterbury Museum, paratypes in Dominion Museum. Locality. Moa Swamp, Hamilton's, North Otago (subfossil).

THE FORMS PREVIOUSLY CLASSIFIED AS MYXAS

The generic name to be used for the forms previously classified as Myxas in New Zealand requires discussion. One of the major features of the type of the genus Myxas, M. glutinosa (Muller) is that the mantle is reflected over the shell, which it almost completely covers when the animals are active. In the New Zealand forms the mantle barely covers the edge of the shell. The type of the Australian genus Austropeplea Cotton and Godfrey (A. aruntalis Cotton and Godfrey) is similar to Myxas glutinosa in this respect. Two other species have been classified in this genus, Austropeplea huonensis (Tenison-Woods) and A. launcestonensis (Tenison-Woods). No information seems to be available about the animals of these two species. On shell characters it would be difficult to separate specimens of launcestonensis from the type series of the New Zealand globosa Suter. If launcestonensis proves to have a widely reflected mantle there can be no close relationship, and this is just another example of convergence of shell characters in unrelated groups of the fresh-water mollusca If on the other hand the animal of launcestonensis proves to be comparable with the New Zealand forms it should be removed from Austropeplea. Of the other Australian genera, the only one that requires comparison with the New Zealand shells is Simlimnea Iredale. The mantle in Simlimnea seems comparable with that in the New Zealand forms, and the shells are of similar size and shape. The use of Simlimnea is here advocated for the New Zealand forms, at least until anatomical comparison can be made. At least one of the Australian species, S. victoriae (Smith) has a high spire and it is possible that Limnaea alfredi could also be placed in this genus.

Simlimnea brazieri (Smith) is one of the major Australian intermediate hosts for the Liver Fluke and forms, identified as Myxas ampulla (Hutton) have been

found to be hosts for the same fluke in New Zealand.

Simlimnea Iredale 1943. Austral. Zool. vol. 10, p. 213.

Type species of the genus (o.d.) Limnaea brazieri Smith.

There does not appear to be more than one rather variable species living in New Zealand. Considering type series alone shell shape varies from the Succinoid type of tomentosa through ampulla and the rather generalized, evenly rounded arguta and leptosoma to the widely expanded globosa. Figures are here presented of the types or representatives of the type series of all the named forms. As will be shown, the name tomentosa has priority and will be used for the whole series.

Simlimnea tomentosa (Pfeiffer, 1855)

1855. Succinea tomentosa Pfeiffer, Proc. Zool. Soc. London, 1854, p. 297.

1885. Limnaea (Amphipeplea) arguta Hutton, Trans. N.Z. Inst., Vol. 17, p. 54. 1885. Limnaea (Amphipeplea?) ampulla Hutton, Trans. N.Z Inst., Vol. 17, p 55.

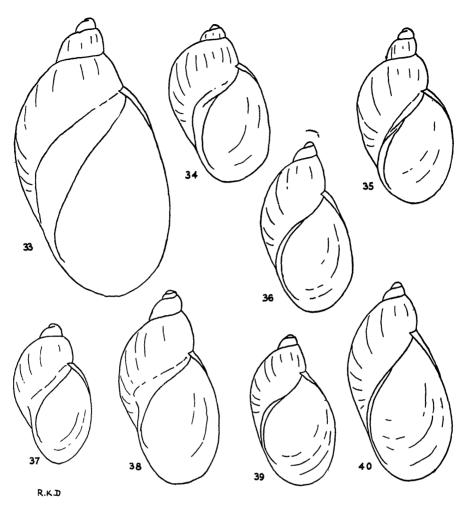
1885 Limnaea tomentosa Pfeiffer; Hutton, Trans. N.Z. Inst., Vol. 17, p 55.

1885. Limnaea tomentosa Fienter; flutton, Irans. N.Z. Inst., Vol. 17, p. 55.
1881. Limnaea leptosoma Hutton, Trans N.Z. Inst., Vol. 17, p. 55.
1891. Amphipeplea ampulla var. globosa Suter, Trans. N.Z. Inst., 23, p. 93.
1905. Amphipeplea arguta Hutton; Suter, Trans. N.Z. Inst., Vol. 37, p. 250.
1913. Lymnoea leptosoma Hutton; Suter, Man. N.Z. Moll., p. 605.
1913. Lymnoea tomentosa Pfeiffer; Suter, Man. N.Z. Moll., p. 606.

1914. Amphipeplea arguta Hutton; Suter, Man. N.Z. Moll., p. 606.

1913. Amphipeplea ampulla Hutton; Suter, Man. N.Z. Moll., p. 607 1913. Amphipeplea ampulla var globosa Suter; Man. N.Z. Moll., p. 608

1913. Amphipeplea arguta Hutton; Suter, Man. N.Z. Moll., p. 608.



Figs. 33, 37, 38.—Simlimnea tomentosa (Pfr.) growth series from Sandringham, Auckland. Figs. 34, 35, 36.—Simlimnea tomentosa (Pfr.) Lake Takapuna, Suter Collection Figs. 39, 40.—Simlimnea tomentosa (Pfr.) Lower Waikato River, O'Connor Collection.

Examination of a photograph of the type of tomentosa Pfr. kindly supplied by Dr. W. J. Rees, of the British Museum (Natural History) shows that it is a succinoid type of shell (Fig. 1) quite unlike specimens labelled "tomentosa" in the Hutton Collection in the Canterbury Museum. No similar shell has been recorded from New Zealand since 1855, and it has seemed highly probable that the original locality was incorrect However, a number of shells of a very similar type have now come to light and the position can now be discussed more decisively. In the O'Connor Collection there is a small series of shells collected from the lower reaches of the Waikato River by Mrs I. Worthy, in 1940. These prove to be very close to the type of tomentosa in outline (Figs. 39, 40) and the population is fairly constant. In a series of shells from Lake Takapuna in the Suter Collection a few of similar shape are present (Figs 34, 35, 36). If this elongated succincid shell was constant there would be grounds for considering tomentosa a separate species of Simlimnea. Populations of Simlimnea are, however, sufficiently variable to consider this form only an extreme variant. The Lake Takapuna population itself is very variable, and there does not seem to be any systematic grounds for separating the extremely elongated shell. There is a tendency for the occasional development of similar succinoid forms in other populations—e.g., one from Sandringham, Auckland (Fig. 38). Pfeiffer's tomentosa therefore appears to be based on an extreme variant of the common Auckland Simlimnea. As such the name tomentosa would take preference over all the other described forms of this genus in New Zealand. Superficially this would appear to be a case to be submitted to the International Commission on Zoological Nomenclature with the request that the name Succinea tomentosa should be suppressed under the newly adopted Principle of Conservation. Fuller consideration shows that the name tomentosa has been used up to the present time in all Manuals and Checklists of the New Zealand fauna, and that the evidence for its true application (the type specimen) has been in existence and available at the British Museum. It is hardly, therefore, a case for the application of the Principle of Conservation, but rather a systematic problem of the true application of the name. The matter is stressed here because it is typical of a number of other very similar cases that must be considered in a revision of the New Zealand fresh-water and terrestrial mollusca.

Limnaea leptosoma Hutton was based upon two dead shells from Wellington (fide Hutton). There are, however, two additional specimens in the Suter Collection (No. 3881) which are labelled "Syntypes" and were presumably distributed to Suter by Hutton. In the Dominion Museum there are 14 specimens labelled "leptosoma Hutton, Wellington". This lot has the registered number M 28 and is almost certainly the source of Hutton's original specimens and indirectly of Suter's. The larger shell of Hutton's type pair in the Canterbury Museum is rather abnormal compared with the rest of the series. The whole series is undoubtedly better referred to the "Myxas" group rather than to Limnaea, the continued use of Limnaea being almost certainly due to examination of the larger abnormal type specimen. This is but another example of the danger of relying on a type specimen rather than a series when studying the fresh-water mollusca. A syntype of leptosoma Hutton in the Suter Collection is quite indistinguishable from specimens labelled ampulla globosa in the same collection.

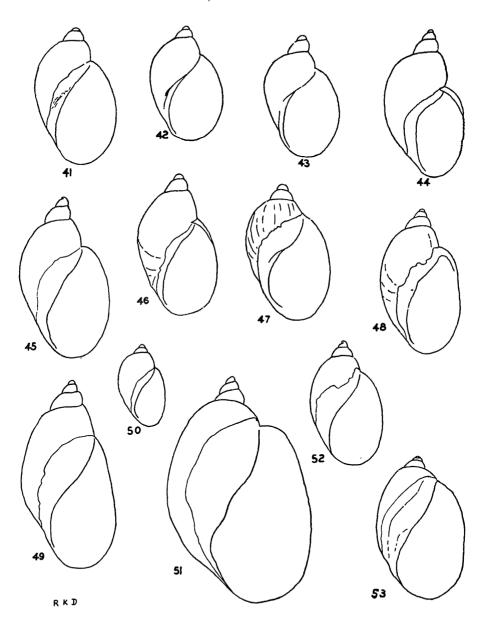
Suter differentiated ampulla from arguta by shell colour and the relative height of the spire compared with that of the aperture. Shell colour is certainly not constant in the group, and is not a good taxonomic character. The relative height of the spire is exceptionally variable. As in all species with a widely expanded aperture, the variation in this respect is largely a function of growth. The type series of ampulla represents an obtusely spired population, and no other specimens have been seen that match them closely. All other populations examined are narrow-spired. The name ampulla could perhaps be preserved for populations similar to the type series. Until animals of this form are obtained, however, it seems preferable to combine all the New Zealand "Myxas"—like forms under the one name in view of the wide variation present. Suter's globosa was proposed as a varietal name for shells in which the aperture was widely expanded, and the use of this name in a subspecific sense is quite unwarranted.

A number of other examples are figured to illustrate the range af variation present. Three specimens from Sandringham, Auckland, show the growth stages in this

population.

DISTRIBUTION. Simlimnea tomentosa is found in a variety of habitats. In larger bodies of standing water it is not commonly found, but it has been recorded from Lake Wakatipu in depths from 30 to 300 feet and sporadically in other lakes such as Lake Taupo, Lake Omapere and Lake Takapuna. In smaller bodies of standing water it occurs more frequently, being one of the mollusca that occurs in ephemeral winter pools. It has also been recorded from swampy water-covered ground, especially when the surface is broken with cattle hoof prints. In running waters it is less frequently seen, but it does occur in small, swiftly running streams where algae are abundant, and is often found in numbers in side channels along the edges of rivers. The general ecology is, however, largely unknown.

Its occurrence in any locality is likely to be sporadic in time, and although locally abundant it is often confined to very restricted areas. For these reasons its detailed distribution throughout New Zealand is not well recorded. It is represented in collections from near Ninety Mile Beach in the north to Otago in the south, but there are no records from large intermediate areas such as in the vicinity of East Cape, Fiordland and Marlborough. It does not appear to have colonized the off-shore islands such as Great Barrier Island. Stewart Island nor the Chathams.



Figs. 41, 42, 43, 44 — Simlimnea tomentosa (Pfr.) subfossil, Wanaka. Figs. 45, 46, 47, 48 — Simlimnea tomentosa (Pfr.) subfossil, Hamilton's Moa Swamp. Figs. 49, 50, 51, 52, 53.—Simlimnea tomentosa waikariensis (Cumber) topotypes.

SUBFOSSIL FORMS

Subfossil forms of Simlimnea are known from a number of localities in the South Island, and specimens from one of these have been described by Cumber (1941) as Myxas ampulla waikariensis. This was differentiated from M. ampulla globosa by its more solid nature. It proves to be a most variable shell and will be discussed more fully below. Small collections are also available from Hamilton's Moa Swamp, Otago, in the Canterbury Museum and from G.S.5036, Pleistocene Lake Marl, Wanaka (presented to the Dominion Museum by the N.Z. Geological Survey). These latter tend to have a higher spire than populations of the living tomentosa, but this is not a constant feature, and the populations are so variable that they cannot be clearly distinguished from the living forms. Better series especially of the Wanaka shells may show more definite points of difference. The shells of all the subfossil forms are much more solid than any of the living shells. This does not appear to be due to post-mortem deposition of lime, as surface sculptural details are still very clear. It is, of course, probable that only shells with a comparatively thick calcareous layer would be preserved.

Simlimnea tomentosa waikariensis (Cumber, 1941). Figs. 49, 50, 51, 52, 53. 1941. Myxas ampulla waikariensis Cumber, Rec. Cant. Mus., Vol. 4, p. 360.

Large topotypic collections of this shell have been available from the Canterbury Museum. There is a very wide range of variation. Some of the shells have a very irregular, distorted outline. The aperture is widely inflated in many of the specimens There is a close morphological relationship with the "globosa" form of tomentosa though a much larger size is attained and the spire appears to be considerably more developed than it is usually in living shells with wide apertures. Young shells have a more regular shape and are close to the "leptosoma" form. The large shells have all the characters of a gerontic population. The form may be differentiated by the above-mentioned characters from living populations. This is not a very strong set of differentiating characters and the differences may well be due to peculiar ecological conditions.

Conclusions

The changes in nomenclature herein proposed may be summarized as tollows:—

Present Status.

Limnaea tenella Hutton
L. pucilla Hutton
L. alfredi Suter
L. tomentosa (Pfr.)
L. leptosoma Hutton
Myxas arguta Hutton
M. ampulla Hutton
M ampulla globosa Suter
M. ampulla waikariensis Cumber

Juvenile L. stagnalis (L). Indeterminate L. (s.l.) alfredi Suter

Simlimnea tomentosa (Pfr.)

Simlimnea tomentosa waikariensis (Cumber)

This represents a considerable reduction in the number of forms recognized. The species of *Limnaea* previously listed have been a constant source of annoyance to conchologists since at least 1913. The species could not be re-collected, nor could any reasonable explanation be given for their disappearance. The listing of five living species of *Limnaea* in faunal lists has seemed an absurdity to every collector of freshwater mollusca.

In the case of "Myxas" the separation of arguta and ampulla has always appeared to be a subjective matter, and the use of the name globosa proposed originally in a varietal sense, as a geographical subspecies without any geographic basis has further complicated the issue. The continued use of the name Myxas has not assisted the solution of biogeographical problems. It is believed that the recognition of one valid species of Limnaea (s.l.) and one living species of Simlimnea approaches much more nearly the position found in nature.

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Part III.—The Genus Physastra

Abstract

THE name Isidora is not applicable to New Zealand fresh water mollusca, and (following Prashad and Hubendick) the use of the name Physastra Tapparone-Canefri is advocated in its place. The New Zealand living forms present a pattern of continuous variation, and one specific name should be used for the whole series. The earliest available name is variabilis Gray. The subfossil series available are discussed

Introduction

The freshwater mollusca previously known as *Isidora* in New Zealand have always proved exceptionally difficult to classify. In the course of a revision of the freshwater mollusca the writer has had the benefit of access to the Suter Collection and the collection made by the late A. C. O'Connor, in addition to the Museum collections. The writer is indebted to Dr. R. S. Duff for the loan of all freshwater mollusca in the Canterbury Museum. In addition he has had access to the collections in the Auckland Museum. Dr. W. J. Rees, of the British Museum (Natural History) has supplied photographs of the relevant types held in that institution.

Physastra Tapparone-Canefri 1883.

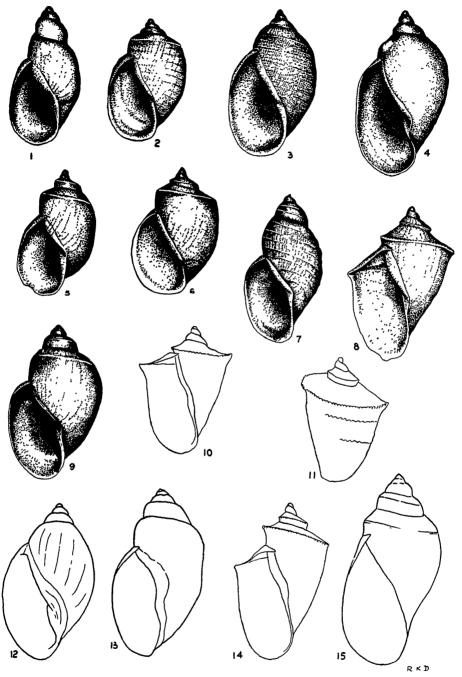
Ann. Mus. Civ. Genova, vol. 19, p. 245.

Type Species. Physastra vestita Tapparone-Canefri. New Guinea.

Kennard and Woodward (1920, pp. 86–88) noted that *Isidora* Ehrenberg, 1831, was proposed for certain Egyptian and Syrian physoids, and that the Australasian forms showed sufficient differences to be grouped under different genera. *Ameria* H. Adams and *Isidorella* Tate were available for Australian species, but the New Zealand forms should receive a new name. These facts seem to have been overlooked by New Zealand conchologists. Prashad (1921, pp. 474–5) suggested the use of *Physastra* Tapparone-Canefri, proposed for *Physastra vestita* Tapparone-Canefri from Great Kei Island, near New Guinea, for a series of shells from the Dutch East Indies, New Guinea, Australia and New Zealand.

Hubendick (1948) studied the anatomy of a number of species of *Bulinus* (auct) and attempted a revision of the generic nomenclature of the group. His treatment of the Australasian forms was based upon anatomical study of three Australian species. He has apparently placed all the New Zealand forms in *Physastra* although it should be noted that he has given no evidence that he had examined animals from New Zealand.

The species classified under *Lenameria* and *Tasmadora* in Australia; "Isidora" in New Zealand; and *Physastra* appear on shell characters, and from their distribution, to form one series and until the results of anatomical investigation can be



Text-fic. 1—Fig 1—Physastra variabilis (Gray) (Type of Physa antipodea Sowerby, from a photograph). Fig. 2—Physastra variabilis (Gray) (Type of Isdora lirata conferta Sutcr) Fig. 3—Physastra variabilis (Gray) (Suter's specimen of conferta from Wairau) Fig. 4—Physastra variabilis (Gray) (Type of Physa moesta Adams, from a photograph) Fig 5—Physastra variabilis (Gray) (Type of Physa moesta Adams, from a photograph) Fig 6—Physastra variabilis (Gray) (Type of Physa dould, from a photograph) Fig. 7—Physastra oconnori (Cumber), Holotype. Fig 9—Physastra variabilis Sowerby, type from photograph Figs. 8, 10, 11, 14—Physastra variabilis (Gray), Lake Brunner. Fig 12—Physa cf. fontinalis L, Silverstream, Wellington Fig 13—Physastra variabilis (Gray), from Tenison-Woods' figure of Physa guyonenis Tenison-Woods Fig 15—Physastra variabilis (Gray), from Tenison-Woods' figure of Physa lirata Tenisor-Woods

used to confirm or deny the practice, the name *Physastra* may well be used to cover the New Zealand forms.

The last general revision of the group in New Zealand was published by Suter in 1905, and the groupings and nomenclature there advocated were followed by him in the Manual in 1913. One subfossil species was described by Cumber (1941). but otherwise the most recent Checklist (Powell, 1946) follows Suter. Many of the early forms were described with no more precise locality than "New Zealand," and some were never figured from type material. Some of these early species were wrongly ascribed to New Zealand, but these have already been removed from our list-e.g., cumingi Adams, wilsoni Tryon and novaeseelandiac Clessin. Some Australian workers (Iredale, 1943 and Cotton, 1943) have advocated the dismissal of all names which were not described from a definite type locality. Such an action would simplify the nomenclatural problems, but under the present Nomenclatural Rules there is no mechanism whereby such a course could be justified, particularly when a type specimen is still in existence. The subsequent selection of a type locality appears to be the only mechanism to be followed in such a case. The type concept in systematics has proved of inestimable value, but its value is drastically reduced in the so-called "difficult" groups where systematics must perforce be based upon populations rather than upon individuals. This is particularly marked in the case of the freshwater mollusca, where in many respects an exact type locality is more important in practice than a single type specimen. Of the names available for New Zealand forms the following were not originally assigned a type locality: variabilis Sowerby, antipodea Sowerby, hochstetteri Dunker and novaezelandiae Sowerby. Suter (1905, p. 269) wrote of variabilis Gray, "The very short diagnosis, unaccompanied by a figure, has in my opinion been the curse of the New Zealand conchologists. From the many species judged to be synonyms of this unfortunate variabilis it can be gathered that no one ever knew what Gray's species is—perhaps not even Gray himself, for his diagnosis fits nearly all of our species . . . I reject it as insufficiently described, unfigured, and embracing perhaps several distinct species."

Unfortunately, perhaps, the type specimen is still in existence in the British Museum, and by courtesy of Dr. W. J. Rees I have been able to examine a photograph (a drawing from which is presented here (Text-fig. 1, Fig. 9). This at least

places variabilis on a similar footing to the other species mentioned above.

The determination of specific limits in this group is so difficult that it is doubtful if any finality will ever be reached on strictly morphological grounds. Members of obviously discrete populations vary amongst themselves to such a degree that normal measuring techniques cannot convey an adequate picture of the variation present. There is some evidence to show that populations vary on occasions from generation to generation. Some of the shell variation is undoubtedly ecologically controlled, but it is quite obvious that some of the major variations within populations is genetical in origin. The occurrence of these molluscs in New Zealand is often sporadic, and long series even then are difficult to collect. The position is made even more obscure as it is obvious that snails of diverse origin have been purposely or accidentally liberated from aquarium stock and have become established in habitats such as artificial ponds, private and public lily ponds, and even in natural stream systems. It is at present very difficult, and in the future may be completely impossible to differentiate between indigenous and introduced forms.

There appear to be few characters or groups of characters by which populations may be differentiated into discontinuously varying groups or species. The main varying characters which appear to be useful for discrimination are diameter relative to total height, height of spire and aperture, absence or presence and degree of develop-

ment of a keel and the degree of development of spiral sculpture.

Suter's conception of some of the species is not in accord with the characters of the type specimens—e.g., tabulata Gould, and novaezelandiae Sowerby. Unfor-

tunately it has not been possible to obtain photographs of the type of hochstetteri Dunker (supposedly in the Natural History Museum, Vienna) and the location of the type of lirata Tenison Woods has not been traced. There are, however, syntypes of this latter species in the Canterbury Museum. The type of Physa hochstetteri Dunker has never been figured, but Suter managed to equate hochstetteri with guyonensis Tenison Woods, through identification by Dohrn of specimens from Lake Guyon as hochstetteri. Topotypes (possibly syntypes) of guyonensis are available in Canterbury Museum, and this conception of hochstetteri must of necessity, in the meantime be accepted. With this one exception all the named species of this group are here figured from type material. Regardless of the conclusions reached herein by the present writer these figures should provide an accurate basis for any additional systematic work on the group.

Study of the large number of New Zealand Physastra available shows that they

may be divided into a number of poorly defined groups.

GROUP 1. Shells of comparatively large size occurring in Northland and South Auckland localities, usually in lakes. The shell is often coated with a black or brownish deposit. There is a tendency for the whorls to be evenly concave or slightly shouldered, but a rather obscure keel which is usually most apparent on the spire whorls is quite usual, and some shells may show a strongly developed keel. The height of the spire varies rather considerably. It is undoubtedly to this group that the names variabilis Gray and novaezelandiae Sowerby and probably hochstetteri Dunker apply. Gray's variabilis has priority and the group will be referred to as the variabilis group.

GROUP 2. Shells of medium size occurring mainly in Northland in streams and swamps. The spire is comparatively low, the aperture widely expanded, and the shell wide in proportion to its height. On clean shells microscopic incised spirals are usually present. The shells are usually prominently keeled and the body whorl usually has a straight, more or less parallel sided, outline below the keel. The names tabulata Gould 1948 and moesta H. Adams 1861 apply to the group. Photographs of the type specimens show that there is no basis for separating these two names,

and they should be considered synonymous, tabulata having priority.

GROUP 3. Small to medium shells with strong to moderately strong, raised spiral sculpture. The shell is sometimes strongly keeled in addition. The group of *lirata* Tenison Woods, from which *conferta* Suter cannot be separated. Distribution somewhat scattered.

GROUP 4. The subfossil oconnori Cumber, which is characterised by a very

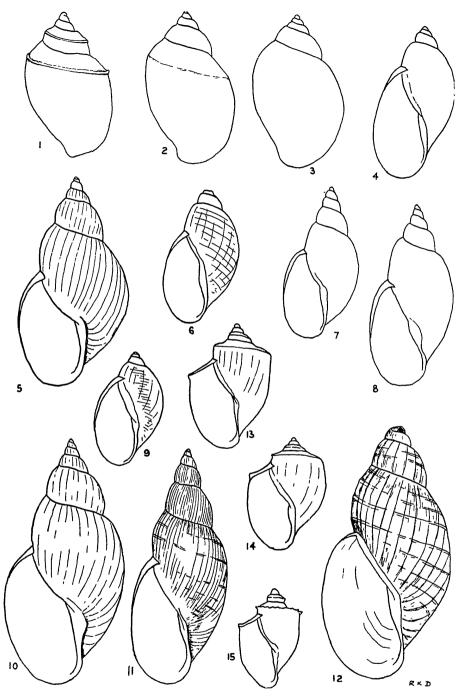
elongate spire, combined with a very narrow shell.

GROUP 5. A group of medium sized shells with a very concave outline from the apex to the body whorl. A keel is hardly ever developed. Shell often shining and polished if clean. Microscopic spiral sculpture unevenly developed. This is the common form in the central lakes of the North land. None of the available names appears to apply directly to this group, though antipodea is probably an extremely elongated form of this. For the purposes of discussion this will be designated the Central Lakes Group. Populations of this group are often comparatively constant.

Superficially there would be a certain amount of justification in regarding these groups as of specific, or in some cases subspecific value. Unfortunately, even after the populations representing these groups had been segregated, a very large number of populations would remain with characters intermediate in some respects and quite

divergent in others.

The tabulata group is developed particularly in localities in the Bay of Islands, and shells may be selected from these populations that match the types of tabulata and moesta. Shells from the vicinity of Auckland and the Waikato River, however, show a complete transition to those of the variabilis group. Shells from Lake Brunner have the same biconic outline as juveniles of tabulata, but retain this shape at least in shells 8 mm high. Juveniles of the lirata group have a similar shape in some



Text-fig. 2—Figs 1, 2, 3—Physastra variabilis (Gray), series from Kaikohe, to show different degrees of development of the keel within one population Fig 4—Physastra variabilis (Gray), Lake Rototti 1 fathom, Suter Collection. Figs 5, 10, 11, 12—Physastra oconnori (Cumber), Topotypes Fig 6—Physastra variabilis (Gray), Lake Waikaremoana, 8 fathoms, Suter collection Figs 7, 8—Physastra cf oconnori (Cumber) Pleistocene, Wanaka Fig 9—Physastra variabilis (Gray), Lake Taupo, 8 fathoms, Suter Collection Figs 13, 14, 15—Physastra variabilis (Gray), Moera, Bay of Islands, growth stages in "tabulata Gould' All to same scale

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areas. This shape is an unusual one in New Zealand *Physastra*, and its presence in a number of populations probably indicates closer relationship than the differences in adult shape would infer. Other populations in the northern part of the North Island show variation from the typical *tabulata* towards a much narrower shell. The *tabulata* group, though well differentiated in the Bay of Islands area, cannot be satisfactorily separated from *variabilis* on the one hand and the narrower northern series on the other.

The lirata group has been characterized by the strong development of spiral sculpture. The type (from Taieri River) cannot be traced, but an outline drawing taken from a figure by Tenison-Woods is given here (Text-fig. 1, Fig. 15). Suter used this name for any shell showing distinct spiral sculpture, and by far the largest number of specimen lots of this genus were labelled "lirata" in his collection. None of the characters given by Suter as characteristic of this form has proved constant. The types of Isidora lirata conferta Suter (from Otorohanga) are not distinguishable from tabulata and the two names should be considered synonymous. In practically every population of New Zealand Physastra that has been studied spiral sculpture is present on clean shells. Practically every gradation exists from the strong raised spiral folds of oconnori to the irregular, microscopic incised spirals of "tabulata". No satisfactory basis exists for the separation of lirata.

The variabilis group is differentiated mainly on the basis of size. These large shells occur sporadically throughout New Zealand, though they seem more common in the North. It seems very likely that, as with many other freshwater gastropods (e.g., Lymnaea stagnalis) the life span of a normal population of Physastra is about one year. There is little direct evidence as yet, but snails kept in aquaria take about a year to reach normal size for their population. In addition, populations in the field are usually of one size group. It is possible that if some snails do not die off at the end of the first year they may continue to grow and so achieve the variabilis form. The fact that such populations are commoner in the warmer northern areas seems additional evidence for such a supposition. The occurrence of similar shells in southern localities is sporadic and usually only a few specimens are obtained. Shells have been seen from Lake Rerewhakaitu (Central volcanic district), Wanganui, and Lake Wakatipu (Suter Collection). The fact that large shells of this type may develop from very different populations is a strong argument against the granting of specific status to such a form. Such "over-grown" forms may be considered gerontic in relation to the mean of local populations and wide variation in regard to shell characters in such forms would be expected. This group of shells could be given full specific status in northern areas, but the sporadic occurrence in diverse southern populations would then be inexplicable. It is difficult to see how the group may be separated, especially as South Auckland populations—e.g., Waiuku and Lake Waikare, are intermediate in size between the northern shells and southern populations.

The Central Lakes group seems to consist of fairly stable populations, most of which Suter had labelled as "lirata" in his own collection. They give rise to occasional shells of the variabilis type. It appears to grade into a rather similarly shaped shell with a glossy hyaline surface which is found in streams, pools and lakes in the Wellington area and the southern Wairarapa. Rather similar shells occur in the Christchurch area, but here a high percentage of the shells are keeled. These latter approach very closely to the type of lirata Tenison-Woods. Similar forms occur in the Canterbury rivers. Physa antipodea Sowerby, judging by a photograph of the type kindly supplied by Dr. W. J. Rees, is a development of this type of shell in which the spire has become elongate. The form appears to be rare and apart from the type, the only specimen that has come to notice is one collected by Professor Percival in a small lake in Takahe Valley, west of Lake Te Anau

The preceding discussion has been presented in some detail, as it has seemed advisable to demonstrate as fully as space will permit the extreme difficulty of limiting

morphologically even the few comparatively stable groups of *Physastra*. From his study of the New Zealand members of this group, the writer has concluded that only one species should be recognised amongst living populations, and that no subspecies can as yet be separated. The name to be used would be the earliest available one, *variabilis* Gray, with all the other names based upon living material synonyms . . . Such a course may seem extreme, particularly to those who have never attempted to identify specimens of this genus. That no conchologist since Suter has been satisfied with any identifications in this group, and the fact that Suter himself could not use his own classification consistently, would indicate that the bases for differentiation were very slight. There is ample precedent for such action in variable groups of the freshwater mollusca. The common European species *Limnaea* (*Radix*) pereger Mueller is credited with at least 50 different synonyms by Kennard and Woodward (1926).

The alternative possibility for which some evidence can be advanced would be to recognise the following forms:—

1. P. tabulata Gould (= moesta Dunker) confined to North Auckland.

2. P. variabilis Gray (= hochstetteri Dunker = novaezelandiae Sowerby) occurring in Northland and north of the Central Lakes in the North Island.

3. P. lirata Tenison-Woods (of which antipodea Sowerby is probably an extreme variant). The common form in the South Island, extending as far north as Welling-

ton and perhaps including the Central Lakes form.

This latter course seems completely unrealistic in face of completely overlapping shell characters. Until intensive anatomical research can demonstrate the presence or absence of differences in the animal correlated with definable differences in the shell characters, the writer advocates the usage of *Physastra variabilus* (Gray) to cover all the living forms. All the names so far proposed have been based upon shell characters, and the demonstration that the distinctions cannot be upheld on shell characters at least leaves the field open for a more complete investigation of the problem by means of anatomical study, controlled breeding experiments and detailed ecological studies.

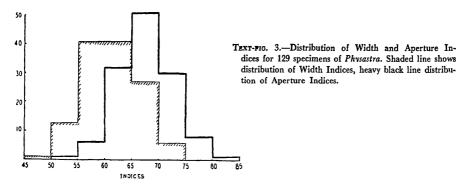
To supply some objective basis for the discussion on variability, the ranges and means of Width and Aperture Indices for 25 populations have been tabulated below.

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	Height		
	mm.	W.I	Ap.I.
Russell Lake (10)	14.5-17.2	58-67 (63)	63-73 (68)
Tuakau (10)	12 -20	57–65 (60)	
Kaipara Heads (4)	14 -18	60-67 (63)	67–76 (72)
Moera, Bay of Islands (10)	8.5-10	65-73 (69)	67-72 (70)
Huntly (5)	10.5-14.5	67-73 (69)	67–76 (69)
Western Springs (5)	12.5-14.5	64-72 (68)	64-72 (69)
L Rerewhakaitu (4)	14 –18	55-64 (61)	65–73 (71)
Lake Taupo (Suter Coll) (6)	10 -12	55-68 (62)	75–82 (77)
Lake Taupo (O'Connor) (10)	11.5-13.5	58-67 (60)	67–75 (71)
Murchison (4)	12 –15	50-58 (54)	
Near East Cape (4)	13 - 14.5		
Botanical Gardens, Wellington (Suter) (3)	11.5–12	56–61 (61)	70–74 (72)
Botanical Gardens (O'Connor) (5)	11 5–15	52–58 (55)	60–70 (67)
Waikato Heads (3)	12 - 12.5	56–58 (57)	58-62 (60)
Toko, Stratford (3)	12.5-13.5	64–67 (65)	63–72 (68)
River Heathcote (3)	11 –12	58-59 (58)	
Birch Hill (4)	11 –12	61–63 (62)	
West Lake, Wairarapa (5)	9 5–12	57–58 (57)	63–76 (69)
Waiuku (3)	14.4–17.4	59–65 (63)	61–66 (63)
Poutu, Kaipara (4)	15.0–16.8	61–67 (63)	61–70 (67)
Kaikohe (8)	9.0–16.6	59–68 (65)	6378 (70)
Lake Wakatipu (2)	16.8–18.2	59–60 (59)	65–68 (66)
Patumahoe (6)	12.4-15.5	60–68 (64)	62-72 (66)
St Albans (4)	9 –10	51–56 (54)	62–65 (64)
P. oconnori (10)	16.5–22 5	45–56 (50)	49–59 (53)

The number of specimens measured in each population is given in parentheses immediately after the locality. W.I. is the Width Index-i.e., the diameter expressed as a percentage of the height, and Ap.I. is the Aperture Index-i.e., the

height of the aperture expressed as a percentage of the height.

The distribution of the means for both Width Index and Aperture Index of these 25 populations appears to follow a normal curve of distribution. The actual indices obtained for the 129 specimens measured to derive the above range and mean tables have been plotted on distribution tables (Text-fig. 3). It becomes obvious from this that the New Zealand forms of Physastra cannot be satisfactorily differentiated on the basis of shell proportions.



The following reasons have therefore influenced the writer in advocating the use of one name for all the living New Zealand forms of Physastra.

- I. An analysis of shell shape in a wide range of populations has shown normal distribution of variation with no indication of the existence of separable forms.
- II. Single populations exhibit very wide ranges of shell proportions.
- III. The presence or absence of a keel has no systematic importance Many populations include shells with strongly developed keels, and others with no trace of a keel, together with intermediate types.
- IV. The presence and strength of spiral sculpture appears to vary independently of other characters.
- V. Insufficient anatomical study of the animal has been made to assist in systematic differentiation. Living shells are difficult to obtain. All the names so far proposed have been based on shell characters.

Physastra variabilis (Gray, 1843)

- 1843. Physa variabilis Gray, in Dieffenbach, Travels in N.Z, vol. 2, p. 245. 1848. Physa tabulata Gould, Proc. Boston Soc. Nat. Hist., vol. 2, p. 214.
- 1861. Physa moesta H. Adams, Proc. Zool. Soc. London. 1861, p. 144. 1862. Physa hochstetteri Dunker, Malak. Blatter, vol. 9, p. 150. 1862. Physa coramandelicus Dunker. Malak. Blatter, vol. 9, p. 150. 1873. Physa novaezelandiae Sowerby, Conch. Icon. vol. 19, f. 29.

- 1873. Physa antipodea Sowerby, Conch. Icon., vol. 19, f. 37.
- 1879. Physa lirata Tenison-Woods, Proc. Linn. Soc. N.S.W., vol. 3, p. 138.
- 1879. Physa guyonensis Tenison-Woods, Proc. Linn. Soc. N.S.W., vol. 3, p. 138 1905. Isidora lirata conferta Suter, Trans. N.Z. Inst., vol. 37, p. 275

Only an abridged synonymy is presented above, as practically all other references may be obtained from Suter (1913).

Insufficient material has been collected to attempt to analyse the detailed local distribution of the genus in New Zealand, but records exist for most major regions in the North and South Islands from Awanui to Fiordland. No records are known from Stewart Island or the Chathams. Forms of the genus may be found in fresh waters of practically every type, from the deeper lakes to stagnant drains. The general preference is for still waters.

Physa cf. fontinalis

Several series are available from lily ponds from a variety of areas, including Auckland, Hawke's Bay and Wellington. These shells are obviously of diverse origin and probably represent forms introduced from several sources. Determination of places of origin and specific identity will be a long task. It is, however, important to realise that such introductions exist. One group has a fairly uniform appearance with a glossy polished surface, evenly convex whorls, a low spire, and no sign of keeling. Unfortunately only the shells are available in most cases. A population of similar animals has been studied in an apparently natural habitat, associated with Simlimnea tomentosa in the Hutt River at Silverstream, Wellington. The shells occur in shallow channels and pools in the main river bed but separated from the main river flow. These snails have a digitate mantle edge, with the side rows of the radula set at a considerable angle. This is in marked contrast with Physastra, where the animal has a straight edge to the mantle and where the two sides of the radula form a straight line. There is no doubt that this population represents a Physa-like form, and it is probable that the forms from artificial habitats will prove to be similar. It is very probable that these forms have been introduced as aquarium stock and represent another introduced animal that has successfully established itself in New Zealand. The actual final determination of the identity of this form will undoubtedly be a lengthy process, but it is very close indeed to the European Physa fontinalis L. Shells of this type are known to the writer from: Hutt River, Silverstream, Wellington; fish ponds, Hastings.

SUBFOSSIL FORMS

Subfossil specimens of *Physastra* are known from a number of swamp and lake deposits.

Physastra oconnori (Cumber, 1941)

1941. Isidora oconnori Cumber, Rec. Cant. Mus., 4, p. 359.

This species is differentiated from all living shells by the comparatively large size, and long spire combined with a very narrow shell. Widely spaced, irregular spiral folds are usually developed. A large number of topotypes have been available for examination from the Canterbury Museum. As in recent populations there is considerable variation in general shape, but the major distinguishing characters cited remain comparatively constant. It is in fact the most consistent population examined, and its full specific status is therefore retained.

Physastra aff. oconnori (Cumber)

Shells from Pleistocene lake marl, Glendhu Rd., Lake Wanaka (G.S. 5036). presented to the Museum by the Geological Survey have some of the characters of *Physastra oconnori* Cumber. The shell is comparatively narrow, though not so narrow on the average as is *oconnori*, and the spire is comparatively high, although the population is approaching *variabilis* in this respect. The shell surface is either smooth or marked with growth lines, and completely lacks the wide raised spirals of *oconnori*.

Physastra cf. variabilis (Sowerby).

Shells from a peat lake at Poukawa, near Te Aute, in the O'Connor Collection are wider still on the average than the Wanaka shells, and have a comparable spire development. They thus fall within the lower limits of variation of living variabilis although no population of variabilis sampled has the same combination of narrow shell and high spire. These shells have the same raised spiral ridges as seen in oconnori.

Speculation as to the probable relations of these subfossil forms is premature at the moment, since so few localities have been sampled and nothing is known of the relative ages of the deposits. The following table of range and means of width and aperture indices shows the relationships of shell shape in these populations.

	Height	W.I.	Ap.I.
oconnori (10)	 16.5–22.5	45-56 (50)	49–59 (53)
Lake Wanaka (8)	10.4–13.7	50-56 (52)	55–61 (58)
Poukawa (5)	14.0–16.2	49-65 (56)	55–64 (58)

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R. K. Dell, B.A., M.Sc., Dip.Ed., Dominion Museum, Private Bag, Wellington.