XVII. MOLLUSCA: GASTROPODA

By Fritz Haas (*Chicago Natural History Museum*)

(28 text-figures)

[Read 21 April 1955]

Our knowledge of the fresh-water gastropods of the lakes on the high Andean plateau is very scanty and rests mostly upon such occasional contributions as those of D'Orbigny (1835–47), Pilsbry and Vanatta (1896), Bavay (1906), and Pilsbry (1924). The gastropods made known by these authors were collected almost exclusively in Lake Titicaca; Bavay alone also describes material from Lake Poopó. The known localities thus excluded the marginal lagoons and lakes in the greater Titicaca basin, and the recorded gastropods included, strangely enough, almost all the pulmonates known to this day from the region and only a few prosobranchs compared with the number since discovered. This fact is due, as we know now, to almost exclusive shore and shallow water collecting, which gave no reason to hope that a rather rich and specialized indigenous gastropod fauna might exist in the deeper waters of Lake Titicaca or in the neighbouring lakes and lagoons.

Thus the rich and carefully collected material of the Percy Sladen Expedition contains an unexpected variety of endemic prosobranch genera described below. Another important result of the expedition is that the long series of shells from many individual localities permit a linking together of forms previously described as different species or even genera, but now shown to be merely extremes of an unexpectedly wide range of variation.

The drawings of the species described or discussed in this paper have been made by Miss Margaret Bradbury, artist of the department of Zoology in the Chicago Natural History Museum. I must also express my sincere thanks to Mr G. I. Crawford for the privilege of being entrusted with the study of the gastropods of the Percy Sladen Expedition to Lake Titicaca. Topographical and other information about the localities from which the collections came will be found in Gilson (1939).

DESCRIPTION OF SPECIES

1. *Tropicorbis* (*Lateorbis*) *canonicus* (Cousin)

Planorbis canonicus Cousin 1887, p. 264, Pl. 4, fig. 11.
Helisoma canonicum Pilsbry 1935*b*, p. 88.
Tropicorbis (*Lateorbis*) *canonicus* Baker 1945, p. 85, Pl. 135, figs. 20–27.

This species, originally described from Ecuador, and later reported (Pilsbry 1935*b*) from Bogotá, Colombia, is also distributed over most of Peru, as will be seen from the list of the localities where it was found by the Percy Sladen Expedition; it must be stressed, however, that all the localities listed, with one single exception, are outside Lake Titicaca itself. They include waters on the Pacific slope, Andean tributaries of the Amazon on the Atlantic slope, and rivers, lakes and lagoons situated within the Titicaca basin. The few lots of *T. canonicus* from a locality in or on Lake Titicaca all come from

Capachica, near the mouth of a river emptying into the lake. The species was collected in very shallow water in ditches and in shallow lagoons as well as in deeper lakes from the surface down to a depth of 16 m. (in Lagunilla Saracocha) and even to 27 m. (in Lago Langui).

There is little variation exhibited in the available material, except that specimens from Lago Langui show a tendency toward a not very pronounced but unmistakable scalarism. While all other localities for *T. canonicus* contain fresh water, Lake Poopó is saline. Only a single immature specimen good enough for specific classification was collected there, and it does not provide any evidence of local variability as a result of life in an environment in which planorbids do not generally occur.

Localities: Lake Titicaca, near mouth of a river at Capachica; Laguna Yapupampa 0·5 m.; Laguna Arapa 0–0·7 m.; Hacienda Ylpa, outflow of Lake Umayo; Rio Desaguadero; Lake Poopó (one young specimen); Rio Ramis at Ayaviri 0·3 m.; Lagunilla Lagunilla 0·3–24·5 mm.; Lagunilla Saracocha 0–16 m.; Saracocha River, 1 km. below outlet; Lagunilla River; summit of "La Raya" pass 0·3 m.; Lago Langui 0–27 m.; Layo; Rio Langui; pond near Rio Huatanay 5 miles below Cuzco.

Taphius montanus (D'Orbigny) and other named forms of the group

This paragraph deals with what were formerly believed to be a number of distinct species, which I have been forced by conchological evidence to consider as merely forms

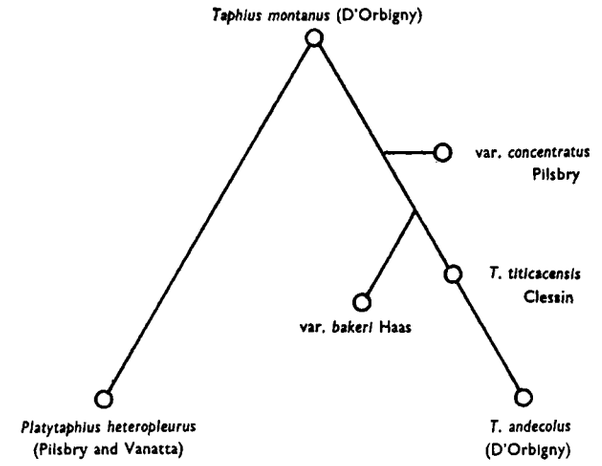

Fig. 1. Diagram of the relationships of the *Taphius montanus* group.

connected with one basic species, *Planorbis montanus* D'Orbigny. As we shall see again later in the case of *Littoridina culminea* (D'Orbigny), the Titicaca material presents a chain of forms linking together what at first appear to be several distinct species. In *L. culminea* the chain is linear, but in *Taphius montanus* it is bifurcated, and there are here two series of specializations arising from one unspecialized form. Before entering on a detailed account of these chains we must agree on names for this basic species and the derivatives from it with which we have to deal. Fortunately the primitive basic form was named before or at least not later than any of the other forms involved, so the name *T. montanus* (D'Orbigny) is available under the rules of nomenclature to designate the starting-point of our bifurcate list of forms. The other ends of the series represent two forms which were originally described as independent species, but which

are in fact connected by conchological intermediates with the basic species, and are referred to below as two forms of the basic species. Another described species represents a point on one of the prongs of the fork, and other forms distinguished by varietal or subspecific names by earlier writers are to be considered as side branches of this same prong. The relationships of the group are shown diagrammatically in Fig. 1. With this introduction I may present the following list of synonyms:

2. *Taphius montanus* (D'Orbigny) (Figs. 2–5)

Planorbis montanus D'Orbigny 1835, p. 26; 1840, p. 345, Pl. 44, figs. 5–8; Sowerby 1878, Pl. 13, fig. 107; Clessin 1841–86, p. 174, Pl. 26, fig. 2; Bavay 1904, p. 152, fig. 4; 1906, p. 142, fig. 26.
Taphius montanus Baker 1945, p. 79.
Planorbis (*Taphius*) *andecolus* form *montanus* Pilsbry 1924, p. 50, Pl. 4, figs. 5–6*b*.
Taphius andecolus montanus Baker 1945, Pl. 131, figs. 27–31.
Planorbis Andecolus D'Orbigny 1835, p. 26; 1840, p. 346, Pl. 44, figs. 1–4.
P. andecolus Sowerby 1878, Pl. 6, fig. 50; Clessin 1884, p. 134, Pl. 22, fig. 4; Bavay 1904, p. 152; 1906, p. 142.
P. (*Taphius*) *andecolus* Clessin 1841–86, p. 33; Pilsbry 1924, p. 49, Pl. 4, figs. 1–1*b*, 3–4*b*.
Taphius andecolus Baker 1945, p. 79, Pl. 77, figs. 13–15, Pl. 131, figs. 32–35, Pl. 137, figs. 1–13.
Planorbis (*Taphius*) *andecolus* form *concentratus* Pilsbry 1924, p. 50, Pl. 4, figs. 2–2*b*.
P. titicacensis Clessin 1841–86, p. 147, Pl. 12, figs. 23–25; Posnanski 1914, p. 34, Pl. 2, figs. 4 partim.
Taphius titicacensis Baker 1945, p. 79.
T. montanus Baker 1945, Pl. 137, figs. 1–3. (Not of D'Orbigny.)
Planorbis heteropleurus Pilsbry & Vanatta 1896, p. 562, Pl. 26, figs. 1–3.
P. (*Platytaphius*) *heteropleurus* Pilsbry 1924, p. 51.
Platytaphius heteropleurus Baker 1945, p. 120, Pl. 79, figs. 10–12.

Before describing the separate forms of this protean species, I must explain in more detail why I consider that they form a bifurcate rather than a linear series of connected forms. My reason is that in any attempted linear arrangement more highly specialized forms would apparently be connected via decreasingly specialized ones with the most primitive form, and through it again via increasingly specialized forms to the other extreme of specialization. This seems an unnatural arrangement, whereas one with the most primitive form at the vertex, and the two specialized forms diverging on either side, is a better representation of the true state of affairs. No speculations on the causes of specialization can be offered here; all we can say is that the specialization here observed may originally have arisen from the occupation of different ecological niches, *Taphius montanus* and *T. andecolus* being shallow water forms and *Platytaphius heteropleurus* living in greater depths, at least to 82 m.

We can now describe the various forms beginning with typical *Taphius montanus* (D'Orbigny). A set of eight specimens from Molinopampa, collected as dead shells at a depth of 25 m., correspond perfectly to D'Orbigny's original description and figure of his *Planorbis montanus*, though they considerably exceed the dimensions given by him, and attain a diameter of 21·9 mm. and a height of 9·8 mm., with $4\frac{1}{2}$ whorls as compared with 16 mm., 6 mm., and 4 whorls. This is the only sample in which typical *montanus* is represented. Pilsbry (1924), too, seems to have seen very few *T. montanus* proper in the material he used for the first ecological account of the Titicaca *Taphius*. Nothing is known, moreover, about the living conditions of this typical *montanus*, though there are conchological reasons to assume that it lives in rather sheltered habitats in shallow water. This form in its typical configuration has so much of a normal, unspecialized planorbid that one cannot but consider it as the common root, from which stem the two other forms with considerable specialization for life in lakes.

Most of the specimens belonging to this species which have been studied either by Pilsbry (1924) or now by me represent more or less acceptable intergradations toward *T. andecolus* (D'Orbigny), the first of the extreme forms to be discussed below. The intermediate steps in this transformation are often hardly perceptible and they vary considerably in degree even in specimens from one and the same locality. Thus, in a sample of thirteen specimens from Molinopampa, gathered dead in depths between 19 and 27 m., there are some which are almost identical with the "typical" *montanus* mentioned above, collected at the same locality, but in a depth of 25 m.; they even attain a similarly large size. Other specimens, however, of the same sample, show a much stronger basal angulation and consequently a more funnel-shaped underside; others, besides the features just mentioned, have a slight angulation of the whorls even on the upper side. The accentuation of these features leads gradually as we shall see to the form which D'Orbigny described as *T. andecolus*.

Pilsbry (1924, p. 49, Pl. 4) has given an admirable account of the variability of *T. montanus* and has shown with good figures its various forms, which properly arranged constitute an uninterrupted chain of forms, beginning with the almost round-whorled *montanus* form with its widely open umbilicus, and ending with the definitely keeled

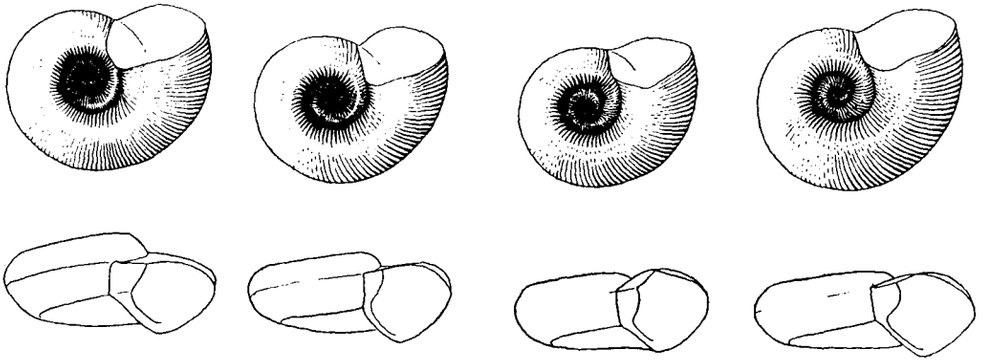

Fig. 2. Chain of forms linking *Taphius montanus* (D'Orbigny) with the form *andecolus* D'Orbigny. Seen from below and from the side. × 1·6.

andecolus form which is very narrowly umbilicate, indeed little more than perforate. The Titicaca material is in perfect agreement with Pilsbry's analysis, and even presents additional intermediate links between his two extremes. Though the pictures given by Pilsbry are conclusive and clear in support of his statement I have thought it desirable to represent the *montanus-andecolus* chain once more. Fig. 2 represents an even more complete series.

I should mention here that *Planorbis titicacensis* Clessin (1884) represents a form almost midway between *Taphius montanus* and *T. andecolus* and has no claim to be a distinct species; Pilsbry (1924, p. 50) reached the same conclusion. Here also is the place to discuss the form named *concentratus* by Pilsbry (1924, p. 50, Pl. 4, figs. 2–2*b*). It is characterized by very high whorls, rectangularly angulated both above and beneath, and by the ample and deeply excavated umbilicus. Pilsbry saw only three specimens of this form among a collection of about one hundred *Taphius* from Lake Titicaca, and they seemed to him distinct from the forms intermediate between *T. montanus* and *T. andecolus*. In the material studied by me I found some specimens referable to *T. concentratus*

and, at the same time, linked with the *montanus-andecolus* chain of forms; this side-chain, connecting *concentratus* with some link of the main chain close to *andecolus* is illustrated in Fig. 3 from specimens collected off Catachaca in Puno Bay at a depth of 13–15 m. The figure shows that Pilsbry's *T. concentratus* is not the end of this chain, for some of these specimens, which display all the shell characters of *T. concentratus*, show in addition a tumid keel at the latero-superior angle and, occasionally, a less pronounced one beneath, and a more distinct though blunt latero-inferior angulation. The place of this form is not within the *montanus-andecolus* chain of forms, but it is connected with it by a side-chain which branches off closer to, but still at some distance from *andecolus*.

Baker (1945, Pl. 137, figs. 25–27), has figured a shell under the name of *T. montanus* D'Orbigny, which obviously does not represent this form, but a distinct one close to *andecolus*, from which it differs in the acute peripheral keel which lends an angular outline to the last whorl. Among the material collected by the Percy Sladen Expedition,

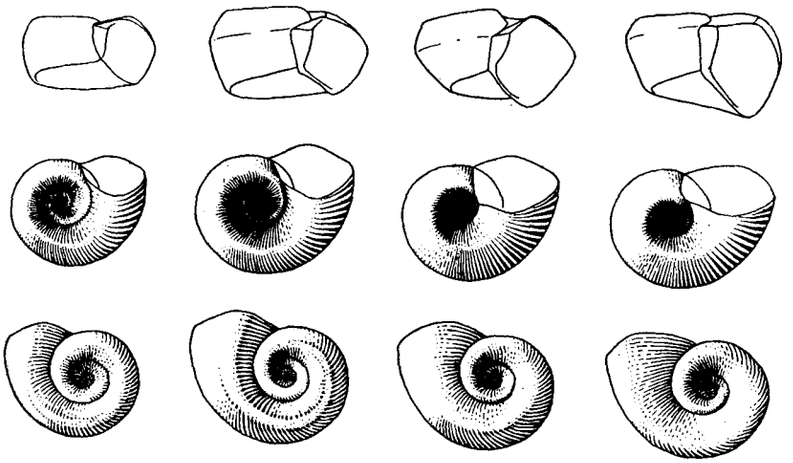

Fig. 3. Chain of forms linking *Taphius montanus* (D'Orbigny) with var. *concentratus* Pilsbry. Seen from the side, from below and from above. × 1·6.

a few specimens seem to belong to this form, which I cannot fit into the linear series of forms connecting *montanus* with *andecolus* and which appears, like var. *concentratus* discussed above, to be a lateral offshoot from a root very close to *andecolus*. Since the name of *montanus* bestowed by Baker on this form, is preoccupied I choose the new one of *bakeri* for it. The form *bakeri* thus represents a short side-chain of the main chain *montanus-andecolus*; the type specimen (Fig. 4), together with a few paratypes, was collected at Capachica in 3·5–6 m. of water; other paratypes come from near the mouth of the Ramis River and from Moho Bay, while Baker's specimen has the locality Duli. The entire shell characters of the *andecolus* form, including the forms *concentratus* and *bakeri*, seem to indicate, by the concentrated shape and the development of angles and keels, that the ecological niche occupied by it lies in shallow water exposed to wave action.

The wealth of material has enabled me also to link the primitive *T. montanus* (D'Orbigny) to another form, *Platytaphius heteropleurus* (Pilsbry & Vanatta) which is so different that Baker, in his monograph of the planorbids, considered it not merely as

a valid species, but as the representative of a genus of its own, *Platytaphius* Pilsbry (1924).

Before submitting the proof of my conclusion, I must explain why I am using a terminology which is slightly different from that of either Pilsbry or Baker. Both authors accept D'Orbigny's name *andecolus* as the basic one, and consequently, treat *montanus* as a subspecies or form of *andecolus*. No reason whatsoever—not even the discarded one of page priority—can justify this treatment, for, in the absence of insurmountable nomenclatorial difficulties, the less specialized form, which still reveals its taxonomic affinities, should be considered as the starting-point, and its name should be adopted for the entire chain of forms arising from it. In the present instance the *montanus* form not only passes gradually into that of *andecolus*, but as I shall now show, is the starting-point of another chain between the extremes *montanus* and *heteropleurus*. This justifies, in my view, the use of the name *montanus* to cover the entire connected series of forms.

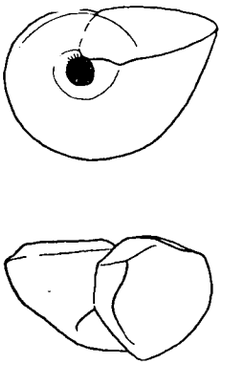

Fig. 4. *Taphius montanus* (D'Orbigny) var. *bakeri* n.var. From below and from the side. × 3·5.

The original diagnosis of *Platytaphius heteropleurus* (Pilsbry & Vanatta 1896, p. 562, Pl. 26, figs. 1–3) is based on an immature specimen of only $3\frac{1}{2}$ whorls and shell measurements of 11·5 × 4·5 mm., and with an unexpanded aperture, but revealing otherwise all the typical features. The specimen figured by Baker (1945, p. 79, fig. 10) is considerably higher than the type specimen, but equally fails to show the apertural features represented in fully mature ones. The largest shells of this form among the present collections (Fig. 5) come from Isla Suana at depths ranging between 14·2 and 14·6 m. Their measurements are given in Table I, and they may safely be assumed to be fully grown.

TABLE I. *Dimensions (mm) of* Platytaphius heteropleurus

Major diameter	Minor diameter	Height	Distance between highest and lowest points of aperture	Diameter of aperture
13·3	11·5	7·0	7·2	5·1
14·5	10·9	7·5	8·5	5·7
16·7	12·8	7·3	9·1	7·3

The angulation on the upper side of the whorls varies a good deal from a mere trace to a blunt keel, and so does the latero-inferior angle. Accordingly, the adjoining whorls may be convex and gently sloping toward the centre, more or less flat, or even hollowed and descending steeply toward the centre. It will be clear from this description, supported by reference to Fig. 5, that the least angulated form with convexly rounded whorls comes very close to *Taphius montanus*, while specimens with increasing angulation and carination and a resultant flattening or hollowing of the whorls approach *Platytaphius heteropleurus* and even pass beyond it, in the sense of earlier authors, whose specimens do not represent the extreme end of the series, but show only a few traces of the stronger angulation and of the concave upper surface of the whorls. In my largest specimens the

last whorl widens distinctly towards the aperture which thus becomes campanulate with spreading parietal, outer and basal walls. The peristome thus formed is somewhat protracted where the two angulations or keels end, but very little so peripherally; these protractions give the aperture a somewhat lozenge-like shape.

The *heteropleurus* form is characteristic of deeper water, where there would be little or no wave-action; all the localities lie between 10 and 82 m. in depth, except for a single collection from Ancoraimes, from between 3·4 and 4·7 m. The wide and flat shape of this form seems to show the influence of this ecological niche. There can be no doubt that the *heteropleurus* form in deep water has to resort for respiration to some other resource than the planorbid lung, for a migration or flotation to the surface seems rather improbable. It will be interesting to see whether a secondary gill has been developed in the pulmonary cavity, as has been recorded in Lymnaeids of deep lakes.

The species *Taphius montanus*, together with the two chains of forms branching off from it, is restricted to the Titicaca basin. Apart from its occurrence in Lagunilla

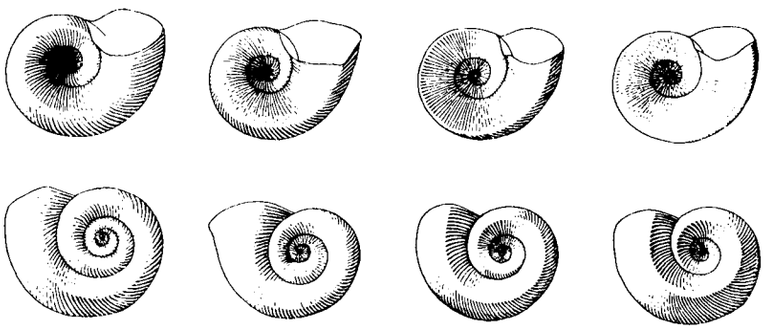

Fig. 5. Chain of forms linking *Taphius montanus* (D'Orbigny) with the form *heteropleurus* Pilsbry & Vanatta, seen from below and from above. × 1·5.

Saracocha, it is further restricted to the area in the immediate neighbourhood of the lake, formerly occupied by Titicaca when its level was higher and represented now by Lake Titicaca proper and the shallow lagoons which border it—Lagunas Tejane, Sunuco, and Arapa, and Lake Umayo. It is highly probable that forms of *montanus* will be found also in such marginal lagoons of Titicaca as Laguna Yapupampa, in which the Percy Sladen Expedition did not discover any, and in the Lagunilla Lagunilla. The centre of distribution, however, is Lake Titicaca, and only a few forms have succeeded in surviving in the marginal lagoons listed above, namely the *andecolus* form in the Lagunas Tejane, Sunuco, Arapa and in Lagunilla Saracocha, and the form *concentratus* in Lake Umayo. The following lists show the bathymetrical distribution of the various forms. Since the forms are linked by intermediates, the *andecolus* form is taken for this purpose to include all forms from extreme *T. andecolus* about halfway towards *T. montanus*, and the remaining half of the chain is included with the *montanus* form. As for the *heteropleurus* form, intermediates with *T. montanus* are known only from one locality, so these and the extreme *T. heteropleurus* are listed separately.

In the chain of forms stemming from *Littoridina andecola* (D'Orbigny), as we shall see, the extremes live side by side in the same locality, together with more or less

complete ranges of intermediate forms. Conditions are very different, however, in the case of *Taphius montanus* (D'Orbigny) and its chains of forms. In no case, as far as the material at hand is concerned, have the extreme forms been found living together, and from no single locality have complete series of connecting forms been seen. The existence of such complete chains must therefore be deduced from fragments of such chains pieced together. This does not invalidate the result of our investigations. There can be no doubt that conchologically the extreme forms of *montanus* can be derived from the basic *montanus* form.

The fact that all the intermediate forms are not found side by side must be attributed in this case to the attainment of a higher degree of speciation, in which some of the connecting links have already begun to disappear in some localities while persisting in others. The phenomenon is perhaps worth a special investigation, and the material available is sufficient and well enough preserved for statistical study. Lack of time, however, prevents me from taking up this fascinating topic, which I must leave to others. In all that I have written on *T. montanus* I have dealt only with conchological chains of forms. Final confirmation of the views here put forward must await the results of anatomical study of the material.

Localities:

2a. Taphius montanus montanus

Paton 4–5·5 m.; Sucuné 1·2 m.; Japitse; Capachica 0·2 m.; Uruñi Bay 0·9 m.; Isla Campanaria de Ccotos 0·2–0·6 m.; Molinopampa 10–25 m.; Isla Titicaca 2·5–7·8 m.; Coata Bay 1 m.; Esteves Island 1·4 m.; Puno Bay 0·7 m.; Catachaca 3 m.; Isla Taquiri 2·7–2·8 m.; Isla Suana 3–14·7 m.; off Rio Desaguadero 1–2·6 m.; off mouth of Rio Tiahuanaco 0·9–2·9 m.

2b. Taphius montanus andecolus

A. In Lake Titicaca (0–30 m.):

Ancoraimes 0·6–24 m.; Paton 2–11 m.; Sucuné 2·4–16 m.; Choccocoya 1·5–4·5 m.; Japitse 3·5–15 m.; Moho 1·7–30 m.; Jonsaní 15–20 m.; Piata 2–9 m.; Capachica 0·5–6 m.; Taman 0·5–30 m.; Uruñi Bay 0·5–11·3 m.; Isla Campanaria de Ccotos 1–20 m.; Molinopampa 3·4–27 m.; Isla Titicaca 0·5–3 m.; Siripata 6–16 m.; Esteves Island 0·5 m.; Chucuito 1–2·5 m.; Catachaca 13–15 m.; Isla Suana 0–14·3 m.; Guaqui and between Guaqui and Taraco 1·8–3·3 m.; off mouth of Rio Tiahuanaco 2·3–2·7 m.

B. In lagoons and lakes in the Titicaca basin:

Laguna Sunuco; Laguna Tejane near Piata 0–0·5 m.; Laguna Arapa 0·1–0·7 m.; Lagunilla Saracocha 0–18 m.

2c. Taphius montanus concentratus

Off Catachaca 13–15 m.; Taquiri Island 2·7–2·8 m.; Lake Umayo 0–1 m.

2d. Taphius montanus bakeri

Moho Bay 1–3 m.; off Rio Ramis 6 m.; off Capachica 3·5–6 m.

2e. Taphius montanus heteropleurus

Ancoraimes 3·4–24 m.; Paton 25–34 m.; Choccocoya 11–23 m.; Moho Bay 20–30 m.; Jonsaní 15–20 m.; Taman 15–82 m.; Molinopampa 10–27 m.; Coata Bay 12–30 m.; off Catachaca 13–15 m.; Isla Suana 14·2–14·6 m. (all in Lake Titicaca 3·4–82 m.).

3. *Anisancylus crequii* (Bavay) (Fig. 6)

Ancylus crequii Bavay 1904, p. 156, fig. 7; 1906, p. 146, fig. 29.
Anisancylus crequii Pilsbry 1924, p. 51.

Since it lacks an apical sculpture *Ancylus crequii* must be referred to *Anisancylus* Pilsbry. Bavay's original picture shows the apex as rather short and rounded, whereas in fact it is longer and pointed; furthermore, its upper surface is curiously flattened. Fig. 6 shows these features, as well as the considerable degree of variation in the outline of the shell. Viewed from the right side, the shell of *A. crequii*, with its concave right half, resembles a right valve of an *Arca* of the subgenus *Navicula*, and presents an appearance which is very unfamiliar in gastropods.

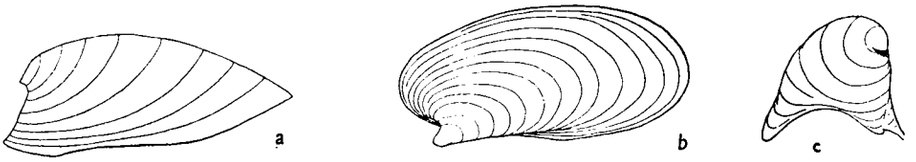

Fig. 6. *Anisancylus crequii* (Bavay), *a* from the side; *b* from above; *c* from behind. × 10.

The occurrence of *Anisancylus crequii* in Lake Langui so far distant from Lake Titicaca is noteworthy.

Localities:

A. Lake Titicaca:

Ancoraimes 5·5–14 m.; Paton 8–11 m.; Sucuné 1·2–16 m.; Choccocoya 1·5 m.; Japitse 4·5 m.; Piata 2–3 m.; Capachica 1·7–5·5 m.; Taman 0·4–30 m.; Chiflon Bay 0·3–0·6 m.; Uruñi Bay 0·9–3·6 m.; Molinopampa 3–27 m.; Siripata 16 m.; Isla Titicaca 1 m.; Esteves Island 0·5–4 m.; off Chucuito 1 m.; off Catachaca 1·3 m.; Isla Suana 14·2–14·6 m.; Guaqui 1–8 m.

B. Lagoons and rivers in the Titicaca Basin:

Saracocha River; Laguna Sunuco.

C. In the Amazon System:

Lago Langui, Urubamba Valley, about 4,000 m. alt., in 0·6–27 m. depth.

4. *Anisancylus lagunarum* sp.nov. (Fig. 7)

Diagnosis. An elliptical species with a comparatively high shell, apex projecting, at about three-quarters of the length, closer to the right side and pointing toward it.

Comparison. Of all South American species of ancylids, this new species seems to be closest to *A. crequii* from Lake Titicaca and Langui, with which it shares the unsculptured shell surface as well as such characters as the position and shape of the apex. It differs from it by the greater symmetry of the shell, for in *A. crequii*, the right side of the shell is compressed or even concave, and the extreme tip of the apex viewed from above may extend to the right-hand margin or even beyond it.

Description of the type. Length 4·4 mm., height 2·8 mm. Shell high, elongate-elliptical, almost completely symmetrical, slightly wider in front than behind. Apex at about 75 per cent. of the length, high, situated toward the right side and leaning over to it, pointed, flattened above and destitute of any sculpture. In profile, the anterior face is slightly, but unmistakably convex, the posterior face rather concave. The remnants of the periostracum are light brown, but most of the surface shows the uncovered, white, chalky shell-substance. No traces of radial sculpture are visible.

Discussion. The specimen described as the type and figured (Fig. 7) is almost completely symmetrical in outline, and so are many of the other specimens studied. Some, however, show their right side slightly flattened or almost straight, in which case the apex is further to the right; examples are some of the more elliptical specimens from Laguna Tejane. In *A. crequii* we see the extreme of such a reduction of the right side of the shell, for there it is even concave, and the shell consequently much more asymmetrical, with the tip of the apex overhanging the excavated slope of the right half of the shell. It may be asked whether *A. crequii* is not simply the extreme limnic form of what I am describing here as *A. lagunarum.* Since, however, this new species has not been found in the shallow lagoon-like parts of Lake Titicaca, where other species of fresh-water molluscs occur which are not limnically adapted to life in lakes, and since no *A. crequii* has yet been collected in the lagoons which contain *A. lagunarum*, I prefer to consider them, for

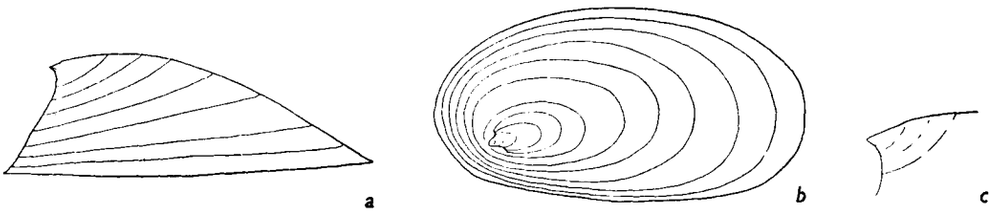

Fig. 7. *Anisancylus lagunarum* sp.nov. *a*, from the side, × 10; *b*, from above, × 10; *c*, lateral view of the apex, × 22.

the present at least, as two distinct but related species. The specimens of *A. lagunarum* from Laguna Tejane mentioned above show that under circumstances not yet understood, this new species may assume a shape very similar to that of *A. crequii* of Lake Titicaca.

Localities: Laguna Tejane 0–0·5 m.; Lagunilla Lagunilla 0·3–9·9 m.; Lagunilla Saracocha 0–16 m.; Lagunilla River.

5. *Hebetancylus* sp.

A comparatively large species, represented by three specimens preserved in alcohol, but all more or less damaged and so thin that the shell cracks in the progress of drying. This seems to be a new species of the group of *H. moricandi*, but it is somewhat broader, roundish ovate, and it lacks the radial striation of the surface. The short and blunt apex, inclined toward the right side, does not show any traces of sculpture.

The material at hand is too scanty and in too bad a shape to permit description. *Hebetancylus* sp. is known from Lago Langui, 0–0·6 m.

Ancylus titicacensis Posnanski, nomen nudum.

Posnanski 1914, p. 34, Pl. 2, fig. 4 partim.

No description accompanies the quotation of this shell in the text or on the plate, and that is as well for the corresponding part of fig. 4 on Pl. 2, the upper two shells on the left side of the upper row, represent specimens of the big *Pisidium* of Lake Titicaca! Thus Posnanski's *Ancylus titicacensis* may fall into well merited oblivion.

The credit of having called attention to Posnanski's generally ethnographic book as a source of information—or of misinformation—about the mollusc fauna of Lake Titicaca belongs to H. A. Pilsbry (1925), whose statements on the shells mentioned therein are in full accordance with the view expressed above.

Genus *LITTORIDINA* Souleyet

The generic name *Littoridina* was created by Souleyet in 1852 for a species of hydrobiid snail he had collected in the Guayaquil River in Ecuador, *L. gaudichaudii* Souleyet. The new genus embraced all the tiny fresh and brackish water hydrobiids of South America which formerly had been placed with *Paludina, Paludestrina* or *Hydrobia.* In 1865, Stimpson (p. 47) proposed the new generic name of *Heleobia* for *Paludestrina culminea* D'Orbigny and its allies, but failed to indicate the distinguishing features between his new genus and *Littoridina.* Pilsbry (1924, p. 52) took up Stimpson's name and used it in a subgeneric sense for all the Lake Titicaca *Littoridinas.* I hesitate to follow him in that, and I think that *Heleobia* can be used, if at all, only for the *culminea*-group and for *L. berryi* Pilsbry. These species, the giants of their genus, are certainly different from all the remaining *Littoridinas* of Lake Titicaca which resemble far more their fluviatile congeners. Yet I think it is premature to use the name *Heleobia* at all, before the species on which it is based have been anatomically studied and compared with true *Littoridinas.* The results of such an investigation which is in progress will show whether or not the name *Heleobia* can be employed and for which species it should be used. According to Thiele (1929), the genus *Littoridina* and a few of its relatives constitute a tribe Littoridineae of the subfamily Hydrobiinae of the family Hydrobiidae.

6. *Littoridina stiphra** sp.nov. (Fig. 8)

Description of the type. Height 4·2 mm., width 2·8 mm., height of aperture 1·4 mm., width of aperture 1·1 mm. Shell conical, thin, transparent, smooth, milky white, narrowly rimate. Whorls 6½, regularly increasing, separated by a shallow, marginate suture, last whorl about half of the entire height of the shell. Apex low, smooth, the first four whorls ventricose, the fifth much more flattened, the remaining 1½ whorls flat and ultimately even concave above and moderately convex below the periphery, which is characterized by a rounded angulation passing gradually toward the aperture into a low keel. Aperture irregularly rhombic, sharply pointed above, less sharply pointed and protracted at the periphery where the keel ends, and at the base, which is slightly protracted and effuse; between the columellar and the parietal sides there is a broadly rounded angle; columellar wall of aperture not appressed, bordering an umbilical chink. The straight, lipless peristome, by contrast with the remainder of the shell which is whitish, has a yellowish hue deeper on the columellar and parietal walls. Operculum deeply set, at least ½ whorl deep, paucispiral, very thin, horny.

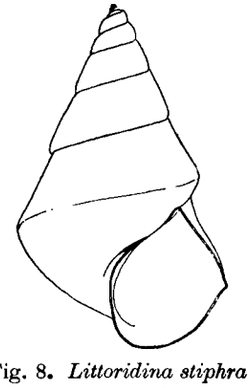

Fig. 8. *Littoridina stiphra* sp.nov. × 10.

Discussion. The type specimen described above represents about the centre of a range of variation which covers ecarinate specimens as well as more sharply carinate ones. Thus in some specimens the peripheral angulation starts only about one whorl from the aperture and is so low that it hardly deserves to be called a carina; at the other extreme,

* στιφρός, compact.

however, an angle, which almost immediately develops into a pronounced keel, is already present on the fourth whorl. All intermediate stages between these two extremes are present. As far as the shell dimensions are concerned, no perceptible variability can be found among the material before me.

I was not at first altogether sure that this new *Littoridina* was not the form described by Bavay as *Pyrgula neveui*, on account of the number of whorls ($6\frac{1}{2}$ in each case) and on account of the conical shape both of these specimens and of Bavay's figure. The condition of the keeled whorls, however, as well as the dimensions of the shell, suggest that *Littoridina stiphra* cannot be identified with *L. neveui*. Furthermore, it is more likely that the vastly more frequent species treated below as *L. neveui* really is that species, rather than the rarer *L. stiphra* which has been found only in a single locality, namely in Lake Titicaca at Molinopampa, at a depth of 3 m.

7. *Littoridina cumingii* (D'Orbigny) (Fig. 9)

Paludina Cumingii D'Orbigny 1835, p. 30.
Paludestrina Cumingii D'Orbigny 1840, p. 385, Pl. 47, figs. 14–16.
Hydrobia Cumingii Frauenfeld 1864, pp. 595 and 666.
Paludestrina Cumingiana Stimpson 1865, p. 46.
Littoridina cumingii Pilsbry 1911, p. 560; Biese 1944, p. 172, Pl. 1, fig. *b*.

This species has a very wide distribution, since it had been found near Callao in Peru and near Valparaiso in Chile, though Biese (1944, p. 175) is doubtful about the correct classification of the Valparaiso specimens. In the material collected by the Percy Sladen Expedition it is represented in waters draining into the Amazon as well as in the system of Lake Titicaca; it represents the only not endemic fresh-water prosobranch gastropod found in the lakes, lagoons and rivers tributary to Lake Titicaca. It was not found in the lake itself.

This species has only once been depicted and is figured here, together with the hitherto unknown operculum, which is deeply immersed, corneous, and paucispiral.

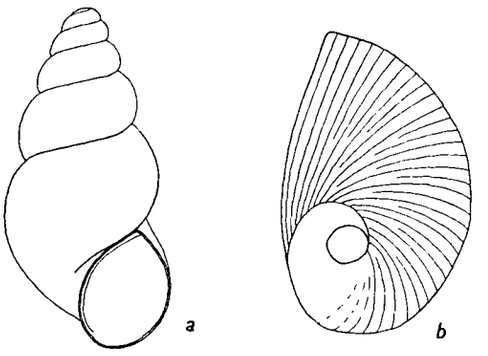

Fig. 9. *Littoridina cumingii* (D'Orbigny). *a*, shell, × 10; *b*, operculum, × 25.

Localities:

A. In the Titicaca Basin:

Rio Ramis at Puente Ramis 0·3 m.; Laguna Tejane near Piata 0 m.; Laguna Arapa 0·1–0·7 m.; Hacienda Ylpa on outflow of Lake Umayo 0–1 m.; Lake Umayo 0–0·8 m.; Lagunilla Lagunilla 0·1–24·5 m.; Lagunilla Saracocha 0–16 m.; Lagunilla River.

B. In the Urubamba valley (Amazon system):

Lago Langui 0–27 m.; Rio Langui 50 m. and 12–14 km. below outflow; Rio Urubamba at Pachar Station and at Ollyantaytambo Station.

8. *Littoridina cuzcoensis* Pilsbry

Littoridina cuzcoensis Pilsbry 1911, p. 560, figs. 10–11; Biese 1944, p. 172.

Only a few specimens from near Cuzco are at hand which do not allow a conclusion whether this is a valid species or just one of the many polymorphisms of the widely spread *Littoridina cumingii* (D'Orbigny), with which it is in any case closely related. The exact locality of the specimens of this form collected by the Percy Sladen Expedition is a pond 5 miles below Cuzco, near Rio Huatanay, in 0·15 m. of water.

9. *Littoridina lacustris* sp.nov. (Fig. 10)

Description of the type. Height 4·1 mm., width 2·7 mm., height of aperture 2·1 mm., width of aperture 1·7 mm. Shell broadly conical, perforate, greyish, translucent but rather solid, smooth. Whorls 6, the apical one swollen and planorboid, the following ones with gradually diminishing convexity, the last rather flat above and much swollen below the periphery; suture simple, rather shallow. Aperture ovate, pointed above and below and slightly effuse at the base; peristome simple, straight, brownish yellow, slightly expanded over the umbilical chink and adnate to the parietal wall. Operculum closing the shell at a distance of about $\frac{1}{3}$ whorl from the aperture, horny, thin, with about $3\frac{1}{2}$ whorls, paucispiral and with a subbasal nucleus.

Discussion. There is comparatively little variation in the height-width relation of this species, though the obesity can be slightly smaller or greater than in the type specimen. Apparently full-grown specimens only 4·0 mm. long are present as well as taller ones of a height of 4·3 mm.

Of other species of *Littoridina*, *L. berryi* Pilsbry seems to be closest to *L. lacustris*. It differs, however, from it by being less conical, having a narrower perforation and umbilical chink, attaining a greater length and having a greater number of whorls, at least 7. In *L. berryi*, the last whorl has either a flat or even a slightly concave outline just beneath the suture, while in *L. lacustris* the upper portion of the last whorl is always, if only slightly, convex.

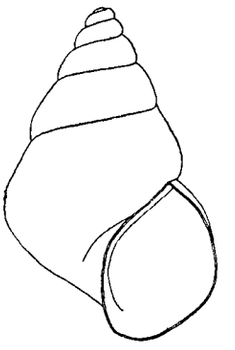

Fig. 10. *Littoridina lacustris* sp.nov. × 11.

Localities: Paton 2 m.; Sucuné 0·6–16 m.; Taman 0·5–66 m.; Chiflon Bay 0·3–0·6 m.; (all in Lake Titicaca).

10. *Littoridina languiensis* sp.nov. (Fig. 11)

Description of the type. Height 6·8 mm., width 3·9 mm., height of aperture 2·7 mm., width of aperture 1·7 mm. Shell large for the genus, conical, whitish, translucent, rimate, almost smooth. Whorls 7, regularly increasing, convex, with frequent very low hair-like perpendicular lamellae; suture simple, but deep. Apex flat, tip not sunk, last whorls evenly rounded; umbilical hole narrow, slightly covered by the expansion of the columellar lip. Aperture small, ovate, roundly pointed above, indistinctly effuse below; peristome continuous, somewhat thickened, brownish, very slightly expanded at the columellar margin, slightly but distinctly free from the parietal wall. Operculum immersed for about $\frac{1}{2}$ whorl, corneous, paucispiral.

Discussion. The height-width relation of the species shows little variation, but the whorls may be somewhat more or less convex than in the type, which represents an average shell. The freedom of the parietal margin of the peristome from the wall of the shell is apparently a feature of full-grown specimens only, and others, younger but not

smaller, do not show the thickening of the peristome; in such shells, the parietal callus of the peristome is still completely adnate to the preceding whorl.

Comparison. The locality of this species, Lake Langui, is not situated in the basin of Lake Titicaca, but empties into one of the Andean tributaries of the Amazon. *Littoridina languiensis* cannot, however, be compared with any of its Amazonian congeners, nor with any of the species of the Pacific slope, being far larger than all these. Its dimensions recall those of the big *Littoridina* species of Lake Titicaca, such as *L. culminea* and *L. berryi*, but apart from size no comparable features can be found. *L. languiensis* may thus be considered endemic to Lake Langui, where it was collected in 3–7 m.

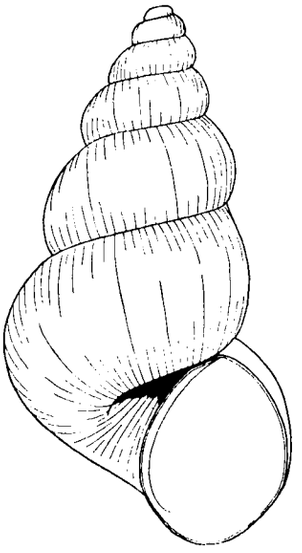

Fig. 11. *Littoridina languiensis* sp.nov. × 11.

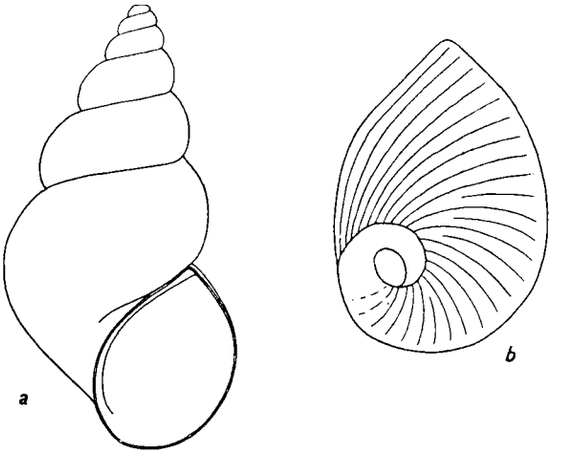

Fig. 12. *Littoridina popoensis* (Bavay). *a*, shell, × 11; *b*, operculum, × 20.

11. *Littoridina popoensis* (Bavay) (Fig. 12)

Paludestrina popoensis Bavay 1904, p. 154, fig. 5.
P. poopoensis Bavay 1906, p. 144, fig. 27.
Littoridina popoensis Pilsbry 1911, p. 560; Biese 1944, p. 172.

Bavay gave a fairly good description of this inconspicuous shell and made some remarks about its range of variation. My own examination of much richer material fully confirms his statements, and I need only add that this species may considerably exceed the length given by Bavay (5·0 mm.), since the largest specimen at hand has a height of 7·3 mm. and a width of 3·2 mm.

Apparently all Bavay's specimens were taken dead, for his description mentions neither the periostracum, which is deciduous, thin, greyish beige and silky; nor the operculum, which is thin, corneous, deeply immersed and paucispiral. The shell is almost smooth, with very faint even closely set low rugae, which show through the periostracum.

L. popoensis shows no relation to any of the endemic species of *Littoridina* in Lake Titicaca; it bears considerable resemblance to *L. cumingii* (D'Orbigny) and may constitute merely a local race of this widespread species. It seems to be restricted to Lake Poopó and its immediate vicinity.

Localities: Lake Poopó 0–1·8 m.; in a pond at La Yorona on the east shore of the lake.

12. *Littoridina profunda* sp.nov. (Fig. 13)

Description of the type. Height 3·7 mm., width 2·0 mm., height of aperture 1·7 mm., width of aperture 1·0 mm. Shell slender, broadly turreted, thin, imperforate, covered with a deciduous greyish periostracum, under which the surface is raised into low hair-like perpendicular lamellae. Whorls $6\frac{1}{2}$, regularly increasing, all of them very convex, the apex planorboid, the suture deeply incised, the last whorl equally swollen above and below the periphery. There is a pseudumbilical narrow chink. Aperture small, pear-shaped, oblique, pointed above, with a continuous peristome which is simple on the outer margin, slightly expanded at the base and over the columella, and adnate to the parietal wall. Operculum not known.

Discussion. This new species of *Littoridina* was collected at and near Taman, Lake Titicaca, in depths from 56 to 82 m. Only seven specimens were obtained in all, and only one of them, the one selected as the type, seems to be adult. It is a dead shell without operculum. Some of the younger specimens, however, were taken alive, and in them the operculum was shown to be immersed; it is apparently thin, horny and of the *Littoridina*-type, but this can be stated with certainty only when the anatomical study is completed. *L. profunda* differs from all other congeners from the High Andes, except *L. vestita* described below, in the fact that the outer surface is covered by an uneven, dirty grey periostracum, while in the other species it is smooth and whitish, and by its extremely convex whorls which are much more swollen than in any other known *Littoridina*.

Locality: Lake Titicaca at Taman in 56–82 m.

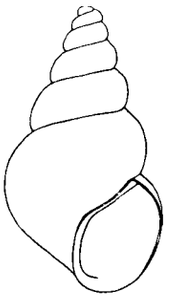

Fig. 13. *Littoridina profunda* sp.nov. × 11.

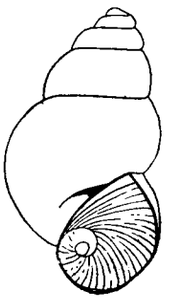

Fig. 14. *Littoridina saracochae* sp.nov. × 11.

13. *Littoridina saracochae* sp.nov. (Fig. 14)

Description of the type. Height 3·5 mm., width 2·3 mm., height of aperture 1·5 mm., width of aperture 1·0 mm. Shell slender, conical, greyish beige coloured, translucent, smooth, narrowly umbilicate. Whorls $5\frac{1}{2}$, swollen with gradually increasing obesity, increasing regularly in size; suture deep, slightly appressed. Apex planorboid; the last whorl almost evenly rounded, a trifle more swollen on the under side. Umbilicus narrow, not even partly covered by the peristome. Aperture small, oblique, pear-shaped, pointed above; peristome simple all round, not thickened, continuous, the parietal margin adnate to the preceding whorl. Operculum terminal, corneous, paucispiral, the nucleus situated at about two-fifths of the height and one-quarter of the width of the aperture, close to the columellar margin; spire of operculum very slightly raised, with the nucleus sunk.

Discussion. The many paratypes reveal a rather distinct range of variation of the height-width relation, the more slender specimens having a narrower, and the stouter ones a wider, umbilical opening. The type is one of the tallest shells.

Distribution. This new species was found only in the two Lagunillas, and most of the samples collected by the expedition come from Lagunilla Saracocha, with one collection

only from Lagunilla Lagunilla and another from the river draining Lagunilla Saracocha. Since the two Lagunillas have a common history and origin, and since their separation seems to be of a relatively very recent date, the occurrence of identical species endemic to both of them, as well as to the river which drains one of them into Lake Titicaca, is not surprising.

Localities: Lagunilla Lagunilla 2–3 m.; Lagunilla Saracocha 0–16 m.; Saracocha River.

14. *Littoridina vestita* sp.nov. (Fig. 15)

Description of the type. Height 4·1 mm., width 1·9 mm., height of aperture 1·6 mm., width of aperture 1·1 mm. Shell broadly turreted, thin, rimate, with a deciduous greyish periostracum, under which the surface is raised into low hair-like perpendicular lamellae. Whorls almost 6, regularly increasing, convex, separated by a distinct but not very deep suture. Apex flat, tip not sunk, very swollen; subsequent whorls less so; last whorl evenly rounded. Umbilicus a narrow chink. Aperture small, ovate, pointed above; peristome continuous, simple, very slightly expanded and thickened at the columellar and parietal margins, the latter shortly adnate to the preceding whorl. Operculum almost terminal, hardly sunk, thin, corneous, paucispiral with flatly raised spire, nucleus one-third from the base and two-fifths from the outer margin.

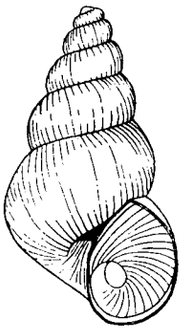

Fig. 15. *Littoridina vestita* sp.nov. ×11.

Discussion. The five paratypes show a certain variability in the degree of obesity of the whorls, which can be greater than in the type. In the specimens with less obese whorls the last one is more swollen basally than it is above.

Comparison. L. vestita shows many parallel features to, and is in fact very much like, *L. profunda* of the greater depths of Lake Titicaca. In each there is a deciduous surface layer to the shell raised into hair-like lamellae, and the whorls of the spire are unusually swollen. These features cannot be due to similar environmental conditions, for *L. vestita* was collected at depths of only 3–5 m. in Lagunilla Saracocha, whereas *L. profunda* was collected between 56 and 82 m. deep in Lake Titicaca.

15. *Littoridina berryi* Pilsbry (Fig. 16)

Littoridina (Heleobia) berryi Pilsbry 1924, p. 52, fig. 2.

This species, which is almost the most abundant one in the entire Titicaca material under study, was well defined by Pilsbry. To the distinguishing characters described by him there can be added one more, namely the outline of the last whorl, which above the periphery is either slightly concave or flat, but never convex as in *L. andecola* (D'Orbigny), the species otherwise most closely related to *L. berryi*.

Pilsbry gave the dimensions of his species as 7·5–8 mm. in height, and as 3·2–4·1 mm. in width. Specimens from Coata Bay, Lake Titicaca, attain a height of 11·5 mm., and a width of 5·1 mm., with the height of aperture 4·0 mm., and its width 2·8 mm. Both dimensions, however, may vary considerably; the width may be visibly smaller, as little as 4·6 mm., while the height may attain 12·1 mm. A similar range of variation is shown in Pilsbry's figures of specimens from Yunguyo, Lake Titicaca, though their maximum dimensions did not exceed 8 mm. in height and 4 mm. in width.

The operculum, unknown to Pilsbry, has been studied in the Coata specimens. It is of the type characteristic of *Littoridina*, retracted about one-third of a whorl, thin, paucispiral with a subbasal nucleus.

L. berryi ranges in depth from the shallowest water to 30 m.; most of the tallest specimens were found in waters deeper than 9 m., but exceptionally these giants occur also in shallower water, for instance near Moho, where they were obtained in 1·7–1·8 m. Average specimens of about the size indicated by Pilsbry occur in shallow water, though here and there they are also found in depths of 10 or 11 m. The species seems to be confined to Lake Titicaca, where it is abundant, having been found at practically all the stations visited.

Localities: Achacache Bay 0·2 m.; Ancoraimes 0·8–24 m.; Paton 2–34 m.; Sucuné 0·6–16 m.; Choccocoya 1·5–4 m.; Japitse 3·5–25 m.; Moho 1–3 m.; Piata 2–3 m.; Capachica 1·7–10 m.; Taman 0·3–30 m.; Chiflon Bay 0·3–1·7 m.; Uruñi Bay 0·5–3·6 m.; Isla Campanaria de Ccotos 0·6–6 m.; Molinopampa 0·5–27 m.; Isla Titicaca 0·6–3·5 m.; Siripata 1–37·5 m.; Coata Bay 0–30 m.; Esteves Island 0·5–1·4 m.; Puno Bay 0·7 m.; Chucuito 1–2·5 m.; Catachaca 1·3–15 m.; Isla Taquiri 2·7–2·8 m.; Isla Suana 0–14·3 m.; Guaqui 2·2–5·4 m.; off mouth of Rio Tiahuanaco 2·1–2·9 m.

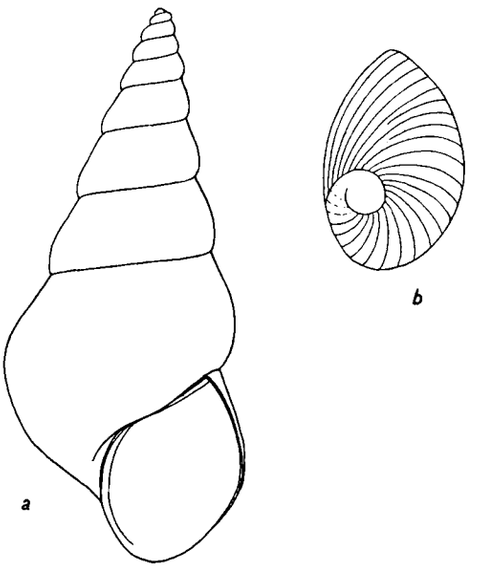

Fig. 16. *Littoridina berryi* Pilsbry. *a*, shell, × 6; *b*, operculum, × 7·5.

16. *Littoridina andecola* (D'Orbigny) (Figs. 17–20)

Paludina andecola D'Orbigny 1835, p. 29.
Paludestrina andecola D'Orbigny 1835–47, p. 385, Pl. 47, fig. 13; Bavay 1904, p. 153, fig. 1*d*; 1906, p. 143, fig. 34*d*; Posnanski 1914, p. 34, Pl. 2, fig. 4, partim.
Hydrobia andecola Frauenfeld 1864, pp. 571, 665.
Littoridina andicola Pilsbry 1911, p. 561; Biese 1944, p. 172.
L. (*Heleobia*) *andecola* Pilsbry 1924, p. 51, fig. 1*a–c*.
Paludestrina culminea D'Orbigny 1835–47, p. 386, Pl. 47, figs. 10-12; Bavay 1904, p. 153, figs. 1*a–c*; 1906, p. 143, fig. 23*a–c*; Posnanski 1914, p. 34, Pl. 2, fig. 4, partim.
Hydrobia culminea Frauenfeld 1864, pp. 595, 666.
Paludestrina (*Heleobia*) *culminea* Stimpson 1865, pp. 46–47.
Littoridina (*Heleobia*) *culminea* Pilsbry 1924, p. 52 (as form of *L.* (*Heleobia*) *andecola*).
L. andicola ecarinate form: *Paludestrina culminea* Pilsbry 1911, p. 561.
L. culminea Biese 1944, p. 172.
Pyrgula neveui Bavay 1904, fig. 6; 1906, p. 145, fig. 28.
Littoridina (*Heleobia*) *neveui* Pilsbry 1924, p. 53.
L. neveui Pilsbry 1911, p. 561; Biese 1944, p. 172.

The forms of *Littoridina* united here under the name of *andecola* represent the most intriguing and difficult group within the genus, and I am well aware that serious objections may be raised to my grouping of three apparently constant forms and good species under one single name. I have been induced to do so by the study of long series of specimens each collected at one and the same locality and at the same depth. Even if one only of these series studied had presented a complete transition by almost imperceptible gradations from the smooth, ecarinate *L. culminea* to the heavily keeled *L. neveui*, it would have suggested that the two species in question might in fact be only one single

species, although intermediate stages linking the two extremes together were apparently absent in most of the localities where the two occur. If, however, such transitional series from *L. culminea* to *L. neveui* were to be found in a number of localities in Lake Titicaca at some distance from one another, then the conchological evidence of their identity would seem established beyond doubt—and that is what really has happened. Such chains of forms linking the typical *L. culminea* with the *Pyrgula*-like *L. neveui* have been found from Molinopampa (5·6–8 m.), Guaqui (1·8 m.), between Guaqui and Taraco (3·3 m.), and between Guaqui and Desaguadero (11 m.) (Fig. 17). Incomplete chains, containing transitions only from *L. culminea* to *L. andecola*, are much more frequent and are found in almost every sample. Some of the best and most convincing come from Molinopampa (3–8 m.), and from Sucuné (5 m.); however, as already stated, specimens intermediate between *L. culminea* and *L. andecola* occur almost everywhere, e.g. specimens of *L. culminea* with the last whorl flattened and slightly angulate, or of *L. andecola*, with flattened whorls, but without a pronounced keel on the last one. Smaller samples contain either both typical *L. culminea* and *L. andecola*, or only one of these species in its typical shape.

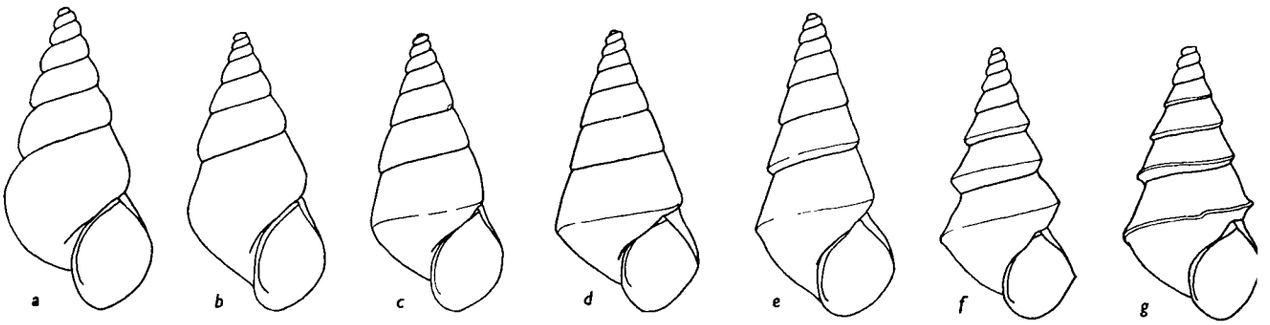

Fig. 17. Chain of forms linking *Littoridina andecola* (D'Orbigny) with the forms *culminea* (D'Orbigny) and *neveui* Bavay. × 6.

The extreme *L. neveui* form, is much more frequent in the southern half of Lake Titicaca and was not collected north of Paton. It is therefore not surprising that the collections showing a complete series of transitional forms between *L. culminea* and *L. neveui* all come from the southern part of the lake. Forms transitional between the intermediate phase, *L. andecola* and the extreme *L. neveui*, are much less frequent than those between *culminea* and *andecola*; thus *L. neveui* appears to be a separate species, unless rather large quantities of shells are studied. Bavay, for example (1904, p. 153; 1906, p. 143) recognized that *L. culminea* and *L. andecola* were inseparably connected by means of intermediate forms, but failed to see—I believe for lack of sufficient material—that his *L. neveui* also belongs to, and is the continuation of, this chain of forms. The shape of this form, so unlike that of *Littoridina* in general, caused him to place it with the European genus *Pyrgula*. Pilsbry (1911, p. 561) correctly grouped *L. neveui* with *Littoridina*, but did not connect it with the chain of forms from *L. culminea* to *L. andecola* which he recognized as Bavay had done. It is thus only now possible to connect the extreme form *L. neveui* with the species *L. andecola*. Fig. 17, showing this transition, illustrates at the same time one of the most remarkable examples of shell variability in a recent species. The material gathered by the Percy Sladen Expedition

in Lake Titicaca invites a thorough statistical study of the thousands of shell-specimens. I am not in a position to devote myself to this important but very lengthy task; I trust that others will perform what I am unable to do. Alcoholic material of all the forms involved is available and will be studied anatomically elsewhere. Anatomical evidence will thus be available in due course to check the conchological evidence presented above.

Unfortunately the earliest name given to this species is *L. andecola* D'Orbigny 1835, which was given to an intermediate form in the chain, and not to its starting-point—the primitive form known as *L. culminea* D'Orbigny 1840. According to the rules of nomenclature, we must adopt the name *L. andecola.*

As stated above, the forms of *L. andecola* seldom live in pure populations; in other words any collection of more than a few specimens from one locality is composed not simply of typical *culminea* or *andecola*-forms of the species but in every case includes specimens which are intermediate between the two extremes. These transitional forms rarely constitute a complete chain linking the *culminea* form with the *andecola* form, but commonly consist of *L. culminea* with rounded whorls, but with a more or less accentuated keel on the last whorl, or of *L. andecola* with flattened whorls and with the carina on the last whorl less accentuated than in the extreme form. Transitions from the *andecola* to the *neveui* form are rarer, and are most frequently represented by specimens of *L. andecola* with a more or less well-defined keel on the penultimate or even on earlier whorls. It is therefore evident that although uninterrupted chains of forms have been found which link *L. culminea* through *L. andecola* with *L. neveui*, the named forms nevertheless represent three fixed points—three pillars of the bridge connecting the extremes—which are less plastic than the intermediate stages and which may be on the way to become distinct species, as the spans connecting them gradually disintegrate. Whether this interpretation is correct or not, it appears worth while to describe the three forms of the complex separately, as if they were so many individual species.

16*a*. f. *culminea* (Fig. 18)

This form is characterized by conspicuously convex whorls, a moderately marginate suture, and by a narrow though distinct umbilical chink. The colour of the rarely preserved periostracum is siena brown, it is wrinkled into closely set narrow low and hair-like folds. The dimensions of average specimens are about $6{\cdot}6 \times 2{\cdot}9$ mm., their number of whorls is $7\frac{1}{2}$; specimens of $10{\cdot}9 \times 4{\cdot}5$ mm. and $9\frac{1}{2}$ whorls however occur, though not very frequently.

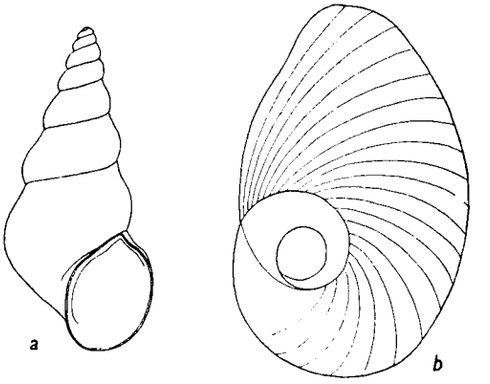

Fig. 18. *Littoridina andecola* f. *culminea* (D'Orbigny). *a*, shell, × 7; *b*, operculum, × 20.

Specimens with a minute angulation on the last half or third of the ultimate whorl are not uncommon; they represent the first step of transition toward the *andecola* form. As a second step the angulation on the last whorl becomes longer and stronger, the last whorl itself becomes less convex than the penultimate, and the umbilical chink becomes narrower and is encircled by a low keel ending at the aperture, which renders the base of the peristome pointed.

16*b*. f. *andecola* (Fig. 19)

Typically, the suture is linear and shallow, the whorls are flat, the last one is peripherally strongly angulate, the underside is narrowly perforated rather than rimate. Average specimens measure 7·8 × 3·6 mm. and have 9 whorls; larger specimens may attain 10 whorls and measure 9·0 × 3·9 mm. The aperture is pointed or angular at the ending of the peripheral keel, the base may be likewise, according to the degree of development of the keel or crest which borders the umbilicus.

Specimens in which the earlier whorls are convex constitute transitions towards the *culminea* form, and those in which the penultimate whorl projects slightly over the ultimate whorl at the suture, making it stand out like a keel, are transitional with the *neveui* form. Included in the *andecola* form are some specimens which differ slightly in dimensions; they are much more slender, almost imperforate, with 9 whorls, and measure 8·9 × 3·3 mm. The keel on the last whorl is the continuation of the suture, exactly as in the *andecola* form, but it is not in these specimens just an angulation but a real, though low, projecting carina. The operculum, which in the *culminea* form is somewhat immersed, is almost apertural in this form, which may represent a side branch of the direct chain linking *L. culminea* through *L. andecola* with *L. neveui*.

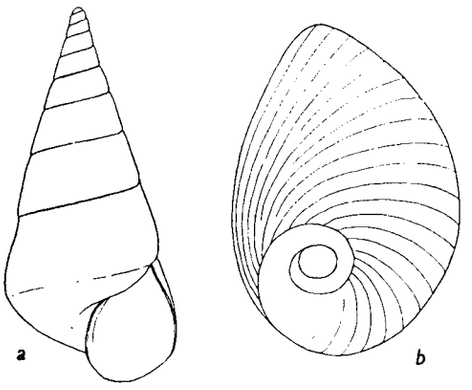

Fig. 19. *Littoridina andecola* f. *andecola* (D'Orbigny). *a*, shell, × 7; *b*, operculum, × 20.

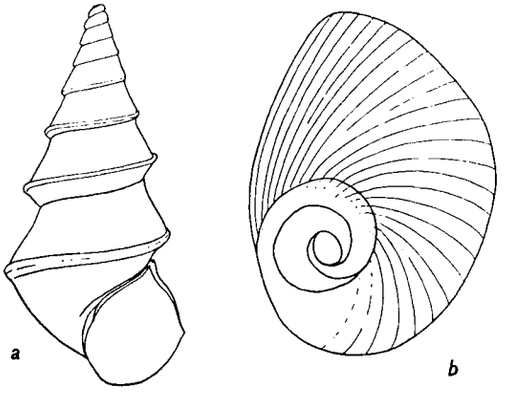

Fig. 20. *Littoridina andecola* f. *neveui* Bavay. *a*, shell, × 7; *b*, operculum, × 20.

16*c*. f. *neveui* (Fig. 20)

Pilsbry (1911) was the first to include this form in the South American hydrobiid genus *Littoridina*, where it was more likely to belong than in the European genus *Pyrgula*. Ultimate confirmation must depend on anatomical studies. Bavay's original figure of *Littoridina neveui* is poor and his description needs additional notes on the range of variation of the shell.

In his diagnosis Bavay mentions only that form of *L. neveui* which has the 2 first whorls rounded, the following 2 angulated, and the last 1½ whorls strongly carinated—the form, in other words, which corresponds to Fig. 17*f*. There are, however, other forms whose features are such that Bavay's type has to be considered intermediate between the following two extremes. In the one extreme (Fig. 17*d*, *e*) the apical whorls are rounded; after the fourth whorl they grow gradually flatter, and an angle, which is in fact the projecting suture, appears on the fifth whorl near its base and continues on the last

1½ whorls; on the last whorl this angle is peripheral and slightly swollen, so that here it can be termed a keel. This extreme is connected by intermediates with the average shape represented by the type. The other extreme (Fig. 17*g*) is characterized by the development of the angle which from its first appearance is high and projects over the periphery of the shell so as to merit description as a keel even on the fourth whorl; this keel gains gradually in height toward the aperture and stands out almost like a lamella. With this gradual gain in height of the keel, the outline of the carinate whorls becomes more and more concave, so that the two last look as if carved out like a cork-screw. This extremely carinate form is also connected with that of the type by imperceptible gradations.

Most of the many hundreds of specimens before me have 7½–8 whorls, not 6½ as indicated by Bavay; the dimensions differ correspondingly, from those in Bavay's original description (5 × 3 mm.). The measurements are set out in Table II.

TABLE II. *Dimensions (mm) of* Littoridina andecola *f.* neveui

Height	Width	Height of aperture	Width of aperture
7·8	3·5	2·0	1·7
7·5	3·2	2·0	1·6
7·2	3·4	2·0	1·8

The greyish green periostracum present in fresh specimens is very deciduous and often destroyed, in part or even completely, in living specimens. Practically all of the shells collected dead have lost it entirely. The operculum is very deeply set in the aperture, in the alcoholic specimens before me from half a whorl to almost an entire whorl deep; it is very thin, horny, paucispiral, with the centre near the angle between the columellar and basal margins and not as central as Bavay's figure indicates.

The bathymetrical range of this form is from very shallow water to 37·5 m., but apparently the specimens from various depths show no more variation than specimens from one and the same habitat.

The *culminea*-form of *L. andecola* is represented from many localities in Lake Titicaca and from one locality (Laguna Arapa) outside this lake; this is the only example of a member of the *andecola* and *berryi* group being found outside Lake Titicaca proper.

Localities:

A. Lake Titicaca:

Ancoraimes 0·8–24 m.; Sucuné 2–16 m.; Choccocoya 2·5–23 m.; Japitse 4·5–25 m.; Moho 20–30 m.; Piata 0–3 m.; off Rio Ramis 6–9 m.; Taman 0·5–82 m.; Uruñi Bay 1·7 m.; Isla Campanaria de Ccotos 3–6 m.; Molinopampa 3·4–27 m.; Isla Titicaca 1 m.; Siripata 2–7·9 m.; Coata Bay 23 m.; Esteves Island 1·9 m.; Puno Bay 0·7 m.; Catachaca 13–15 m.; Isla Taquiri 2·7–2·8 m.; Isla Suana 1–14·6 m.; off Rio Desaguadero 1–4 m.; Guaqui-Taraco 1·8–12·2 m.; off mouth of Rio Tiahuanaco 2·1–8 m.

B. Lagoons in the Titicaca basin:

Laguna Arapa 0·5 m.

The *andecola* form of *L. andecola* is only known from Lake Titicaca proper.

Localities: Sucuné 0·2–16 m.; Choccocoya 11–23 m.; Japitse 3·5–4·5 m.; Moho 20–30 m.; off Rio Ramis 6–9 m.; Taman 0·8–30 m.; Molinopampa 0·5–7·3 m.; Siripata 6–37·5 m.; Chucuito 1–2·5 m.; Isla Taquiri 2·7–2·8 m.; off efflux of Rio Desaguadero 2·6 m.; Guaqui-Taraco 3·5–8·6 m.; off mouth of Rio Tiahuanaco 0·9 m.

The keeled *neveui* form of *L. andecola* is also restricted to Lake Titicaca itself, and from the localities visited by the Percy Sladen Trust Expedition, it is evidently far more frequent at the southern end of the lake; four of the seven localities below are in the Lago Pequeño, and Siripata and Isla Titicaca are at the south end of the Lago Grande. The most northerly locality is Paton.

Localities: Paton 8–11 m.; Isla Titicaca 0·6 m.; Siripata 2·4–37·5 m.; Isla Suana 14·3 m.; off Rio Desaguadero 1–4 m.; Guaqui-Taraco 1·8–5·4 m.; off mouth of Rio Tiahuanaco 2·4–2·5 m.

Complete series grading between the *culminea* and the *andecola* forms of *L. culminea* were found in Lake Titicaca at Sucuné (5 m.) and Molinopampa (3–8 m.) while series connecting the *culminea* form with the *neveui* form were collected at Molinopampa (5·6–8 m.), between mouth of Rio Desaguadero and Guaqui (11 m.), between Guaqui and Taraco (3·3 m.) and Guaqui (1·8 m.).

17. *Littoridina aperta* sp.nov. (Fig. 21)

Description of the type. Height 3·0 mm., width 2·2 mm., height of aperture 1·4 mm., width of aperture 1·2 mm. Shell ovately conical, greyish white, translucent, but not fragile, smooth, openly umbilicate. Whorls about 5, the first ones slightly, the last ones definitely swollen, separated by a clear-cut though not deep suture; apex flat, not rising above the second whorl; last whorl more swollen below than above, with a pervious umbilicus. Aperture ovate, pointed above, peristome continuous, straight, without a lip, the columellar margin only projecting slightly over the umbilicus, the parietal margin adnate to the preceding whorl. Operculum terminal, corneous, paucispiral, with the eccentric nucleus situated close to the left side of the basal margin.

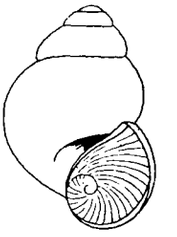

Fig. 21. *Littoridina aperta* sp.nov. × 10.

Locality of type: Molinopampa Bay, Titicaca 0·5 m.

Discussion. This species, which was found only at a few localities listed below and nowhere in great numbers, apparently does not vary to any great degree. All the characteristic features appear clearly in all the samples studied, and it is only the dimensions and the height-width ratio which shows a slight tendency toward variation. Specimens from Isla Titicaca, from 1 m. have the following measurements: height 3·1 mm., width 2·0 mm., height of aperture 1·4 mm., width of aperture 1·2 mm.

Comparisons. The only species with which *L. aperta* can be compared is *Strombopoma ortoni* Pilsbry which is, of all the known Littoridinidae of Lake Titicaca, the only one with an open umbilicus but which, as mentioned above, is much more slender, and much more turriculate than *Littoridina aperta.*

Localities (Lake Titicaca only): Sucuné 2·9 m.; Japitse 3·5–4·5 m.; Molinopampa Bay 0·5 m.; Isla Titicaca 1 m.; Isla Suana 14·3 m.; between Guaqui and Taraco 3·3 m.

Genus *STROMBOPOMA** gen.nov.

A genus of transparent, thin-shelled, slender hydrobiids with a hollow, top-shaped operculum. This operculum is sinistrorse, thin, horny, not at all calcified, with at least as many whorls as the corresponding shell, hollow on its inner side, spirally ornamented with a thin horny lamella projecting from the suture of its whorls and lacerated on its

* στρόμβος spinning top, πῶμα lid.

margins. The base of this operculum is smaller than the aperture of the shell; its position there varies according to the species. The study of the anatomy of this new genus may show whether or not it belongs to the subfamily Hydrobiinae of the Hydrobiidae, and, in particular, to the tribe Littoridineae.

The structure of the operculum of *Strombopoma*, strange and unfamiliar as it may appear, is nevertheless not unique in the Prosobranchiata, since a similar operculum, hollow on the inner face and with a spiral horny lamella on the outer face, is found also in the genus *Spirostoma* Heude in the Cyclophoridae. The similarity of the opercula does not, however, imply any closer relationships between the families Cyclophoridae and Hydrobiidae. The operculum of *Strombopoma* is further discussed at the end of the description of the new genus *Rhamphopoma* which follows that of the two species of *Strombopoma* below, namely *S. ortoni* (Pilsbry) which is selected as the type of the new genus, and *S. gracile* sp.nov. from the Lagunilla Lagunilla.

18. *Strombopoma ortoni* (Pilsbry) (Fig. 22)

Littoridina (Heleobia) ortoni Pilsbry 1924, p. 53, fig. 1*d*.

Pilsbry's original description is founded on a single, imperfect specimen which lacks the most characteristic feature of the new genus *Strombopoma*—the operculum; hence the describer could not possibly foresee that he was dealing with a hydrobiid shell which

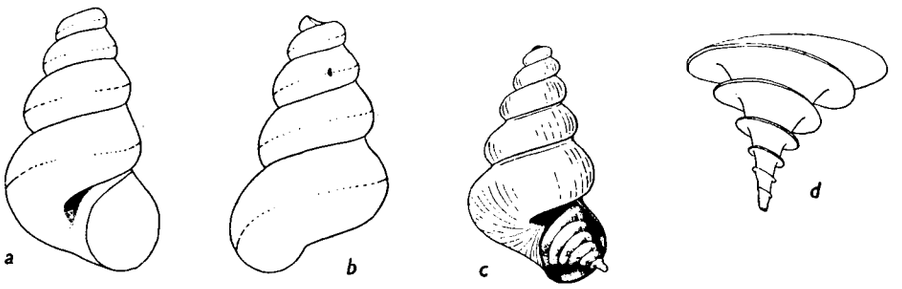

Fig. 22. *Strombopoma ortoni* (Pilsbry) gen.nov. *a*, *b*, type, × 12; *c*, perfect shell, × 10; *d*, operculum, × 22.

was not a *Littoridina*. Only after having seen, through Dr Pilsbry's kindness, the type of *L. ortoni*, did I become aware that this species is a representative of the new genus *Strombopoma* here described on the basis of more plentiful and better preserved material than that which Pilsbry had at his disposal. Since the type, as mentioned before, is an imperfect specimen without the operculum and with the apical whorls broken off, I judge it wise to offer the description below which is based on a perfect specimen. The type is also figured here (Fig. 22*a*, *b*), while Fig. 22*c*, *d* represent one of the entire specimens collected by the Percy Sladen Trust Expedition.

Description of a perfect specimen. Height 3·1 mm., width 1·7 mm., height of aperture 0·9 mm., width of aperture 0·8 mm. Shell thin, whitish, waxy-transparent, elongate-turriform, smooth with distinct traces of sharply cut thin straight growth-marks. Whorls 6½, obese in the middle, flattened toward the suture, which is shallow, appressed and marginate; apical whorl small, smooth; ultimate whorl more obese peripherally than the others, flattened below, imperforate, but with a false umbilical chink formed exclusively by the base of the last whorl. Aperture small, pear-shaped, with continuous and straight peristome, almost as high as wide, shortly pointed above, broadly rounded below. Operculum long, as long or longer than the width of the aperture, its tip touching the palatal margin

or slightly projecting beyond it when *in situ* and so not immersed in the aperture; it has at least 7 whorls, the earliest of them very indistinct, the later ones increasingly distinct on account of the gradual increase in height of the horny sutural lamella.

Discussion. Specimens present some variation both in dimensions and in shape. Thus the height of specimens with $6\frac{1}{2}$ whorls as described above may attain 4·5 mm. and the width 2·1 mm. The shell may be slightly narrower or wider, and in some specimens the ultimate whorls are so obese as to appear almost as a wide, rounded angle on the periphery. The number of whorls of the operculum may be as many as 10.

Localities: Strombopoma ortoni (Pilsbry) is known only from Lake Titicaca. Pilsbry gives no specific locality, and the Percy Sladen Expedition collected it at one station only: in Puno Bay between Chimu and Isla Esteves in 0·7 m.

19. *Strombopoma gracile* sp.nov. (Fig. 23)

Description of the type. Height 5·4 mm., width 2·0 mm., height of aperture 1·4 mm., width of aperture 1·2 mm. Shell thin, slender, subulate, greyish green, smooth, with sparsely set growth-lines which are sometimes more closely set behind the aperture to make this region appear wrinkled. Whorls almost 7, regularly increasing, obese in the middle, flattened toward the suture which is deep, clear-cut and simple. Aperture small, pear-shaped, higher than wide; peristome continuous with sharp margins and completely lipless; columellar margin scarcely appressed, and so bordering an umbilical chink; base otherwise imperforate. Operculum with 7 whorls, comparatively small, not projecting over the palatal wall when *in situ*, but generally directly retracted into the aperture.

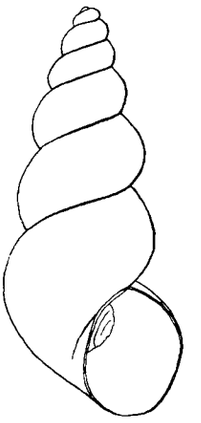

Fig. 23. *Strombopoma gracile* gen. et sp.nov × 10·5.

Discussion. Most of the variation of this species is shown in the obesity of the whorls; the type is an average specimen, and the whorls may be more or less convex. There is some variation in shape, which is usually slender and awl-shaped but in some specimens is somewhat more pyramidal.

Localities: Strombopoma gracile has been found as yet only in Lagunilla Lagunilla at 2–3 m.

Genus *RHAMPHOPOMA** gen.nov.

A genus of slender, pyramidal, whitish, transparent, but rather compact hydrobiid shells, characterized by a thin, uncalcified, horny operculum bearing a hook-like appendage with a slight spiral twist on its outer side near the lower margin (see Fig. 24*b*). This operculum is roughly egg-shaped and pointed at either end; it is thin, horny, translucent and flexible. It consists of a plate on which very weak, eccentric spiral growth marks are discernible, arising from a centre near the left side of the lower margin where a hollow, hook-like appendage arises from the plate. This slightly hooked cone shows a sinistral spiral twist, and the right margin of the plate continues on to the cone as a lamella on what could be called the suture of its spiral coil. The cone-shaped appendage projects somewhat beyond the basal margin of the plate. The view from the inside showing the opening into the hollow cone-shaped appendage and the continuation of the right margin of the plate into the spire of the cone brings to mind the view into a shell of

* *ῥάμφος* beak, *πώμα* lid.

Haliotis. In contrast to the plate of the operculum, which is thin, very translucent, and in alcohol almost colourless, this cone-shaped appendage is considerably more solid and opaque, and is of a light horn colour.

No comparable form of operculum has come to my knowledge; as in the case of the foregoing genus *Strombopoma*, the study of the anatomy has the last word in the task of assigning the correct systematic position to this new genus, which may be no hydrobiid at all or which may constitute a subfamily of its own among the Hydrobiidae. No sufficient explanation can be suggested for the strange opercular formations in these two genera. The cavity of the opercular appendages, no doubt, provides additional space for insertion of the retractor muscle of the operculum; but why should these two genera need a stronger retractive power for their opercula than other hydrobiids with normal opercula living with them under identical circumstances?

The Percy Sladen Expedition to Lake Titicaca brought home two closely related species of the new genus *Rhamphopoma*; *R. magnum* sp.nov., which is here selected as type of the genus, and *R. parvum* sp.nov.

20. *Rhamphopoma magnum* sp.nov. (Fig. 24)

Description of the type. Height 4·8 mm., width 2·6 mm., height of aperture 2·2 mm., width of aperture 1·5 mm. Shell slender, pyramidal, whitish and somewhat translucent but rather solid, smooth, imperforate with a short and narrow umbilical chink. Whorls about 7, regularly increasing, slightly convex, separated by a shallow suture; apex small and smooth; first 5 whorls widest at the periphery, two ultimate whorls widest below the periphery; last whorl about one-half of entire height, straight or almost concave above, definitely swollen at, and flatter below, the periphery. Aperture about one-quarter of the entire height of the shell, oval, but pointed above and below; protracted below so to become slightly effuse, with the columellar margin caved in and somewhat appressed, projecting half way over the umbilical chink; all the other margins of the peristome straight, not reflexed. Operculum as described for the genus.

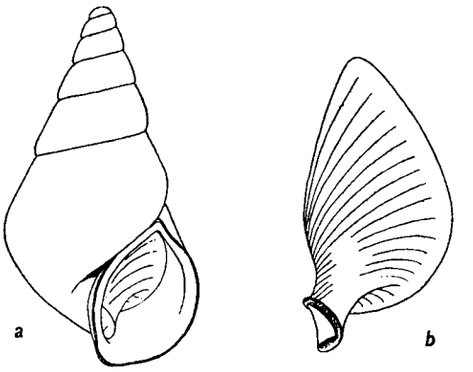

Fig. 24. *Rhamphopoma magnum* gen. et sp.nov. *a*, shell, × 10; *b*, operculum, × 22.

Discussion. The specimen selected as type is an average individual both in measurements and shape, which seem to be the most variable features. An apparently full-grown specimen 5·8 mm. high and 3·2 mm. wide represents the stouter form of this species, and another specimen, 5·4 mm. high and 2·4 mm. wide, belongs to the slimmer form. There is a slight variation in the shape of the base of the aperture which may be more or less effuse. The specimens from Taman Cove belong to the slimmer form. For a comparison with *R. parvum* see under that species below.

Localities: Rhamphopoma magnum was collected in Lake Titicaca at Choccocoya (3·5–4·5 m.) and Taman Cove (0·5–0·7 m.).

21. *Rhamphopoma parvum* sp.nov. (Fig. 25)

Description of the type. Height 3·5 mm., width 1·8 mm., height of aperture 1·4 mm., width of aperture 1·0 mm. Shell shortly pyramidal, whitish, transparent, thin, smooth with occasional low hair-like growth-marks, imperforate, but with an umbilical chink. Whorls about $6\frac{1}{2}$, convex, separated by a deeply cut suture; apex smooth, conspicuous; last whorl somewhat more than one-half of entire height of the shell, equally convex above and below the periphery. Aperture comparatively small, ovate, pointed above and roundedly protracted below, slightly effuse, with a continuous peristome; columellar margin not appressed, all margins straight, not reflexed.

Discussion. The paratypes include slightly larger and stouter individuals as well as smaller and slimmer ones, and the degree of convexity of the whorls is subject to a certain amount of variation; in some specimens the outline of the spire is almost straight and the suture consequently less deep.

Comparisons. This species of *Rhamphopoma* differs from the foregoing by being smaller and stouter, with a more convex outline to the spire. The umbilical chink is wider, the columellar margin of the aperture is not appressed, and the base is less pointed, less protracted and less effuse.

Localities: Rhamphopoma parvum is known only from one station in Lake Titicaca—Molinopampa 5·4–7·3 m.

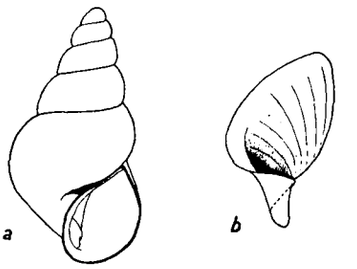

Fig. 25. *Rhamphopoma parvum* gen. et sp.nov. *a*, shell, × 10; *b*, operculum, × 22.

Genus *HELIGMOPOMA** gen.nov.

A genus of whitish, translucent, umbilicate, contracted *Amnicola*-like shells with a rather thick, immersed, corneous, spiral operculum. The number of the whorls of this operculum is about three, the nucleus is situated in about the lower third and close to the columellar margin, the suture of the whorls of this opercular plate being raised as lamellae above the outer surface. A single species, *H. umbilicatum* from Siripata Bay, Lake Titicaca, automatically becomes the type of the genus.

22. *Heligmopoma umbilicatum* sp.nov. (Fig. 26)

Description of the type. Height 3·3 mm., width 2·7 mm., height of aperture 1·9 mm., width of aperture 1·5 mm. Shell globosely conical, whitish, translucent, smooth, narrowly umbilicated; whorls $5\frac{1}{2}$, regularly increasing, separated by a shallow, linear suture, the first 3 flat, the following ones gradually swelling at the periphery; apex small and flat; last whorl flattened, even slightly concave above the middle, tumid at the periphery, less so below and especially in the umbilical area; umbilicus narrow. Aperture comparatively high, pear-shaped, pointed above, protracted below so as to form a broadly pointed projection, and slightly effuse; columellar margin rather concave; peristome continuous, simple on the outer and basal margins, slightly thickened and expanded on the columellar margin which projects somewhat over the umbilicus, adnate on the parietal margin; the border of the peristome shows in places a light brownish colour, particularly so on the columellar lip. Operculum as described in the diagnosis of the genus.

Discussion. The width of the umbilicus varies from fairly open to a very narrow chink, and the height-width proportion varies correspondingly from 3·1 × 2·4 mm. in

* ἑλιγμός twist, πῶμα lid

a widely umbilicate specimen to 4·0 × 2·3 mm. in one with a very narrow umbilical chink. The brownish border line of the peristome may extend into the umbilicus.

Comparisons. The new genus *Heligmopoma* with its single species *H. umbilicatum* appears rather isolated among the South American Littorinidae. The configuration of its operculum as well as the effuse and partly thickened peristome rather suggest a closer relationship with the hydrobiid subfamily Amnicolinae, within which *Heligmopoma* would stand nearest to such genera as *Petterdiana* Brazier from Tasmania.

Localities: a single station only in Lake Titicaca, Siripata Bay 2·4 m.

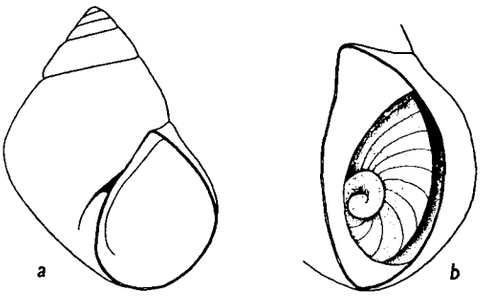

Fig. 26. *Heligmopoma umbilicatum* gen. et sp.nov. *a*, shell, × 12; *b*, aperture with operculum *in situ*, × 15.

Genus *BRACHYPYRGULINA** gen.nov.

This new genus probably belongs to the Hydrobiidae, and is characterized by a short, ovate-conical, strongly bicarinate shell which is narrowly rimate and which possesses an operculum composed of an outer, thin, paucispiral layer and a smaller inner one on which is a raised worm-like, slightly coiled formation. The only species, *Brachypyrgulina carinifera* to be described below, is the type of the genus, which seems to have no close relatives. None of the Littoridineae known has a comparable shell. The heavily keeled species of *Littoridina*, *L. neveui* and *L. compacta* treated above, are more slender and, despite their keels, much more *Littoridina*-like than is *Brachypyrgulina*. Of North American Hydrobiidae, the genus *Pyrgulopsis* Call & Pilsbry, also possesses a carinate rather ovate-conical shell, but there is only a single keel present and the whorls never appear as concave as in the Titicaca shell. Externally the subgenus *Brachypyrgula* Polinski of *Pyrgula* Cristofori & Jan, looks very similar, but has three keels on the last whorl and a narrow, but unmistakable umbilicus. No representatives of the subfamily Pyrgulinae are known from outside Europe, and it would be rash to classify *Brachypyrgulina* with them. I think it wiser to treat it as a hydrobiid, possibly representing a subfamily of its own, until the study of the anatomy allows a final decision.

23. *Brachypyrgulina carinifera* sp.nov. (Fig. 27)

Description of the type. Height 3·9 mm., width 3·1 mm., height of aperture 2·5 mm., width of aperture 2·4 mm. Shell ovate conical, whitish yellow, translucent but rather solid, imperforate, but shortly rimate, smooth, even shining. Whorls about 5½, the first two rather convex, but without a keel, the remaining ones with a strong, blade-like projecting carina, the last with an additional keel below the periphery. The portion of the carinated whorls between the upper suture and the keel is almost flat and horizontal, the portion between the keel and the lower suture almost flat and vertical; thus the spire is stepped with the upper carina projecting horizontally at the head of a right-angle. The lower keel of the last whorl is the continuation of the suture between the penultimate and the ultimate whorl and also projects horizontally; the face between the two carinae is somewhat concave, that below the lower keel is flat, and slightly excavated in the umbilical region. The aperture is large, almost as wide as high and polygonal; it reaches up to the lower keel of the last whorl and it is pointed

* Similar to the European hydrobiid subgenus *Brachypyrgula* Polinski.

where the keels end at the edge, the keels being visible on the inside of the aperture as shallow furrows ending at the edge of the continuous peristome; at the base, the peristome is broadly angled and very slightly effuse. The edges of the peristome are sharp, without any lip, only the somewhat thickened columellar margin bends slightly over the umbilical chink and passes gently into the equally thickened parietal margin. Operculum small, closing the shell at at least half a whorl's distance from the aperture, the outer layer with about $3\frac{1}{2}$ whorls with an eccentric nucleus situated nearer the basal angle, the smaller, inner one with a worm-like, slightly coiled periostracal formation.

Discussion. No noticeable range of variation in size and shape could be observed in the material studied of this species except that the specimens from Sucuné taken at a depth of 7·3 m. are higher (5·1 mm.) and more slender than the type, and have up to $6\frac{1}{2}$ whorls.

Localities: Brachypyrgulina carinifera seems to be confined to Lake Titicaca, and the stations where it was found are both in the Lago Grande—Sucuné 2·2–7·3 m.; Japitse 4·5–25 m.

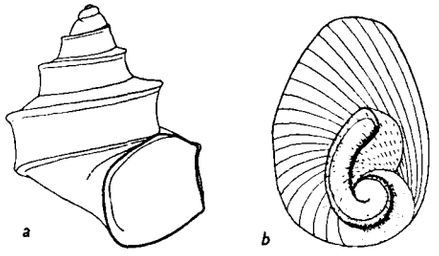

Fig. 27. *Brachypyrgulina carinifera* gen. et sp.nov. *a*, shell, × 9·5; *b*, operculum from inner side, × 20.

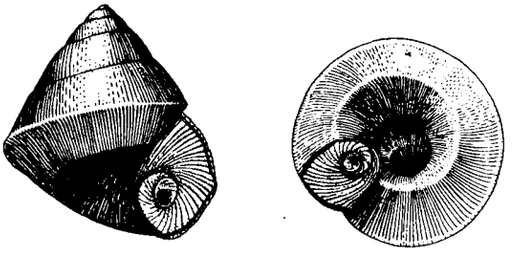

Fig. 28. *Limnothauma crawfordi* gen. et sp.nov. From the side and from below, × 9·5.

Genus *LIMNOTHAUMA** gen.nov.

A new hydrobiid genus, characterized by the elongately trochiform shape of the shell, the presence of two keels (a peripheral and a basal one), the presence of a perforate umbilicus in the centre of the concave base, and a stiff, large operculum projecting over the margin of the aperture. The only known species *Limnothauma crawfordi* to be described below is the type of this new genus.

No comparable forms among living hydrobiids have come to my knowledge, either in general shape or in possessing a perforate umbilicus. There has been described, however, from the pliocene of California, a hydrobiid genus *Brannerillus* (Hannibal 1912, Pilsbry 1935*a*), which is also trochiform, umbilicate and carinate; it differs from *Limnothauma* by its apex which is very flat or even sunk, while in *Limnothauma* it is convex and extant. Hence, no true relationship between the two genera can be assumed.

24. *Limnothauma crawfordi* sp.nov. (Fig. 28)

Description of the type. Height 3·5 mm., width 2·8 mm., height of aperture 1·8 mm., width of aperture 1·2 mm. Shell elongately trochiform, thin, covered with a light-brown periostracum, perforate-umbilicate. Whorls about 5, regularly increasing, the first ones slightly swollen, the later ones flatter, the last one with straight outline above and below the blunt peripheral keel, concavely hollowed almost funnel-shaped and perforated by the pervious umbilicus below the basal keel; apex lighter in colour, depressedly globular, smooth; suture well marked. Surface of the shell almost smooth, showing a weak striation, the thin striae being of a somewhat darker brown than the much wider spaces. Aperture elliptical with slightly broadened margins which show two definite projections,

* λίμνη lake, θαῦμα wonder.

where the peripheral and basal keels end; columellar and palatal margins apparently united by a thin parietal callus. Operculum horny, thin and transparent, rather stiff, large, projecting over the margins and not drawn into the aperture; paucispiral with about $2\frac{1}{2}$ whorls and with a sunken centre.

Remarks. It is by no means impossible that the shell here described, a unique specimen, is not fully grown. Any additional growth, however, could not alter the features listed above, except that the aperture might acquire a somewhat wider or even differently shaped peristome; all the other shell characteristics could not possibly be veiled or changed.

The only specimen of this strange new species contains the soft parts and is kept in alcohol. It was collected in Lake Titicaca at Isla Titicaca, at a depth of 1 m., and is named after Mr G. I. Crawford, a member of the expedition.

SUMMARY

The species listed below have been discussed and described on the foregoing pages. All of them were collected by the Percy Sladen Expedition in the lakes and rivers of the High Andes, most of them in the basin of Lake Titicaca:

PLANORBIDAE

1. *Tropicorbis* (*Lateorbis*) *canonicus* (Cousin)
2. *Taphius montanus* (D'Orbigny), with the forms *andecolus* D'Orbigny and *heteropleurus* Pilsbry & Vanatta, as well as with varieties *concentratus* Pilsbry and *bakeri* var.nov.

ANCYLIDAE

3. *Anisancylus crequii* (Bavay)
4. *A. lagunarum* sp.nov.
5. *Hebetancylus* sp.

HYDROBIIDAE

6. *Littoridina stiphra* sp.nov.
7. *L. cumingii* (D'Orbigny)
8. *L. cuzcoensis* Pilsbry
9. *L. lacustris* sp.nov.
10. *L. languiensis* sp.nov.
11. *L. popoensis* (Bavay)
12. *L. profunda* sp.nov.
13. *L. saracochae* sp.nov.
14. *L. vestita* sp.nov.
15. *L. berryi* Pilsbry
16. *L. andecola* (D'Orbigny), with the forms *culminea* D'Orbigny and *neveui* Bavay
17. *L. aperta* sp.nov.
18. *Strombopoma ortoni* (Pilsbry)
19. *S. gracile* gen. et sp.nov.
20. *Rhamphopoma magnum* gen. et sp.nov.
21. *R. parvum* sp.nov.
22. *Heligmopoma umbilicatum* gen. et sp.nov.
23. *Brachypyrgulina carinifera* gen. et sp.nov.
24. *Limnothauma crawfordi* gen. et sp.nov.

Thus five new genera, fourteen new species, and one new variety were contained in the material collected by the Percy Sladen Expedition. All of the new genera are apparently endemic to the lakes of this area, while the new species of *Anisancylus* and *Littoridina* seem to be endemic species of genera which occur also in rivers and in ponds. The high number of new species in *Littoridina*, seven out of twelve represented in the material, is quite remarkable. Of the other families of fresh-water gastropods, which are known to occur in South America, and which therefore might have been expected to live in the region explored by the Percy Sladen Expedition, the Lymnaeidae and the Physidae among the pulmonates and the Thiaridae among the prosobranchiates are not represented. The local distribution of the twenty-four species listed above is shown in the Appendix.

REFERENCES

BAKER, F. C. 1945. *The Molluscan Family Planorbidae.* Urbana, Ill., 530 pp., 141 pls.

BAVAY, A. 1904. "Mission de Créqui-Montfort et Sénéchal de la Grange en Amérique du Sud. Mollusques terrestres et fluviatiles récoltés par le Dr Neveu-Lemaire." *Bull. Soc. zool. Fr.* XXIX, 152–6, 7 figs.

—— 1906. "Mollusques." In Neveu-Lemaire, *Les lacs des hauts plateaux de l'Amérique du Sud.* Paris, pp. 142–7, figs. 23–29.

BIESE, W. A. 1944. "Revisión de los moluscos terrestres y de agua dulce provistos de concha de Chile." *Bol. Mus. Nac. Chile*, XXII, 169–90, pls. 1–3.

CLESSIN, S. 1841–86. "Die Familie der Limnaeiden enthaltend die Genera *Planorbis*, *Limnaeus*, *Physa* und *Amphipeplea*. In Abbildungen nach der Natur mit Beschreibungen. Begonnen von Dr H. C. Küster und Dr W. Dunker, fortgesetzt und beendet von S. Clessin." Martini-Chemnitz, *Syst. Conch. Cab.* (2), I, 17, pp. 1–35, 35*a*, 35*b*, 36–430, pls. 1–55.

COUSIN, A. 1887. "Faune malacologique de la république de l'Equateur." *Bull. Soc. zool. Fr.* XII, 187–287, pls. 3–4.

D'ORBIGNY, A. 1835. "Synopsis terrestrium et fluviatilium Molluscorum in suo per American meridionalem itinere collectorum." *Mag. Zool.* V, cl. 5, no. 61, 44 pp.

—— 1835–47. *Voyage dans l'Amérique Meridionale (Le Brésil, La République Orientale de l'Uruguay, etc....) exécuté pendant les années 1826, 1827,...et 1835* Paris. (Vol. V. *Mollusques.*)

FRAUENFELD, G. VON. 1864. "Verzeichniss der Namen der fossilen und lebenden Arten der Gattung *Paludina* Lam., nebst jenen der nächststehenden und Einreihung derselben in die verschiedenen neueren Gattungen." *Verh. zool.-bot. Ges. Wien*, XIV, 561–672.

GILSON, H. C. 1939. "The Percy Sladen Trust Expedition to Lake Titicaca in 1937. I. Description of the Expedition." *Trans. Linn. Soc. Lond.* (3), I, 1–20.

HANNIBAL, H. 1912. "A synopsis of the recent and Tertiary fresh-water Mollusca of the Californian province, based upon an autogenetic classification." *Proc. Malacol. Soc. Lond.*, X, 191.

PILSBRY, H. A. 1911. "Non-marine Mollusca of Patagonia." *Rep. Princeton Exped. Patagonia*, III (2, Zool.), pp. 513–653, 38 figs., pls. 38–41, 41A–C, 42–43, 43A, 44–46, 46A, 47.

—— 1924. "South American land and fresh-water mollusks. Notes and descriptions. I. Mollusks of Lake Titicaca." *Proc. Acad. Nat. Sci. Philad.* LXXVI, 49–51, figs. 1–3, pl. 4.

—— 1925. "Lake Titicaca mollusks." *Nautilus*, XXXVIII, 103–4.

—— 1935*a*. "Mollusks of the freshwater Pliocene beds of the Kettleman Hills and neighboring oilfields, California." *Proc. Acad. Nat. Sci. Philad.* LXXXVI, 561–5, pl. 23.

—— 1935*b*. "South American land and fresh-water mollusks. IX. Colombian species." *Proc. Acad. Nat. Sci. Philad.* LXXXVII, 83–8, pl. 6.

PILSBRY, H. A. and VANATTA, E. G. 1896. "New species of fresh water mollusks from South America." *Proc. Acad. Nat. Sci. Philad.* pp. 561–5, pls. 26–27.

POSNANSKI, A. 1914. *Eine prähistorische Metropole in Südamerika.* Berlin. Vol. I, 184 pp., 84 pls.

SOWERBY, G. B. 1878. "Monograph of the genus *Planorbis*." In REEVE, *Conch. Icon.* XX, 14 pls.

STIMPSON, W. 1865. "Researches upon the Hydrobiinae and allied forms; chiefly made upon materials in the Museum of the Smithsonian Institution." *Smithson Misc. Coll.* no. 201, 59 pp., 29 figs.

THIELE, F. 1929. *Handbuch der systematischen Weichtierkunde*, I, 141.

APPENDIX

Distribution of the aquatic gastropods collected by the Expedition

LAKE TITICACA

A. LAGO GRANDE

Achacache Bay

Littoridina berryi Pilsbry; 0·2 m.

Ancoraimes

Taphius montanus montanus (D'Orb.); 0·8 m.
T. m. andecolus (D'Orb.); 0·6–24 m.
T. m. heteropleurus (Pilsb. & Van.); 3·4–24 m.
Anisancylus crequii (Bavay); 5·5–14 m.
Littoridina berryi Pilsbry; 0·8–24 m.
L. andecola culminea (D'Orb.); 0·8–24 m.

Paton

Taphius montanus montanus (D'Orb.); 4·0–5·5 m.
T. m. andecolus (D'Orb.); 2–11 m.
T. m. heteropleurus (Pilsb. & Van.); 25–34 m.
Anisancylus crequii (Bavay); 8–11 m.
Littoridina lacustris Haas; 2 m.
L. berryi Pilsbry; 2–34 m.
L. andecola neveui (Bavay); 8–11 m.

Sucuné

Taphius montanus montanus (D'Orb.); 1·2 m.
T. m. andecolus (D'Orb.); 2·4–16 m.
Anisancylus crequii (Bavay); 1·2–16 m.
Littoridina lacustris Haas; 0·6–16 m.
L. berryi Pilsbry; 0·6–16 m.
L. andecola culminea (D'Orb.); 2–16 m.
L. a. andecola (D'Orb); 0·2–16 m.
L. aperta Haas; 2·9 m.
Brachypyrgulina carinifera Haas; 2·2–7·3 m.

Japitse

Taphius montanus montanus (D'Orb.); depth ?
T. m. andecolus (D'Orb.); 3·5–15 m.
Anisancylus crequii (Bavay); 4·5 m.
Littoridina berryi Pilsbry; 3·5–25 m.
L. andecola culminea (D'Orb.); 4·5–25 m.
L. a. andecola (D'Orb.); 3·5–4·5 m.
L. aperta Haas; 3·5–4·5 m.
Brachypyrgulina carinifera Haas; 4·5–25 m.

Choccocoya

Taphius montanus andecolus (D'Orb.); 1·5–4·5 m.
T. m. heteropleurus (Pilsb. & Van.); 11–23 m.
Anisancylus crequii (Bavay); 1·5 m.
Littoridina berryi Pilsbry; 1·5–4 m.
L. andecola culminea (D'Orb.); 2·5–23 m.
L. a. andecola (D'Orb.); 11–23 m.
Rhamphopoma magnum Haas; 3·5–4·5 m.

Near Moho

Taphius montanus andecolus (D'Orb.); 1·7–30 m.
T. m. bakeri Haas; 1–3 m.
T. m. heteropleurus (Pilsb. & Van.); 20–30 m.
Littoridina berryi Pilsbry; 1–3 m.
L. andecola culminea (D'Orb.); 20–30 m.

Jonsaní

Taphius montanus andecolus (D'Orb.); 15–20 m.
T. m. heteropleurus (Pilsb. & Van.); 15–20 m.
Littoridina berryi Pilsbry; 15–20 m.

Piata

Taphius montanus andecolus (D'Orb.); 2–9 m.
Anisancylus crequii (Bavay); 2–3 m.
Littoridina berryi Pilsbry; 2–3 m.
L. andecola culminea (D'Orb.); 0–3 m.

Off Rio Ramis

Taphius montanus andecolus (D'Orb.); 6 m.
T. m. bakeri Haas; 6 m.
Littoridina andecola culminea (D'Orb.); 6–9 m.
L. a. andecola (D'Orb.); 6–9 m.

Capachica

Taphius montanus montanus (D'Orb.); 0·2–0·7 m.
T. m. andecolus (D'Orb.); 0·5–6 m.
T. m. bakeri Haas; 1–3 m.
Anisancylus crequii (Bavay); 1·7–6 m.
Littoridina berryi Pilsbry; 1·7–10 m.
L. andecola culminea (D'Orb.); 1·7–6 m.

TAMAN

Taphius montanus andecolus (D'Orb.); 0·5–30 m.
T. m. heteropleurus (Pilsb. & Van.); 15–82 m.
Anisancylus crequii (Bavay); 0·4–30 m.
Littoridina lacustris Haas; 0·5–66 m.
L. profunda Haas; 66–82 m.
L. berryi Pilsbry; 0·3–30 m.
L. andecola culminea (D'Orb.); 0·5–82 m.
L. a. andecola (D'Orb.); 0·8–30 m.
L. aperta Haas; 0·5–0·7 m.
Rhamphopoma magnum Haas; 0·5–0·7 m.

CHIFLON BAY

Anisancylus crequii (Bavay); 0·3–0·6 m.
Littoridina lacustris Haas; 0·3–0·6 m.
L. berryi Pilsbry; 0·3–1·7 m.

URUÑI BAY

Taphius montanus montanus (D'Orb.); 0·9 m.
T. m. andecolus (D'Orb.); 0·5–11·3 m.
Anisancylus crequii (Bavay); 0·9–3·6 m.
Littoridina berryi Pilsbry; 0·5–3·6 m.
L. andecola culminea (D'Orb.); 1·7 m.

ISLA CAMPANARIA DE CCOTOS

Taphius montanus montanus (D'Orb.); 0·2–0·6 m.
T. m. andecolus (D'Orb.); 1–20 m.
Littoridina berryi Pilsbry; 0·6–6 m.
L. andecola culminea (D'Orb.); 3–6 m.

MOLINOPAMPA

Taphius montanus montanus (D'Orb.); 10–25 m.
T. m. andecolus (D'Orb.); 3·4–27 m.
T. m. heteropleurus (Pilsb. & Van.); 10–27 m.
Anisancylus crequii (Bavay); 3–27 m.
Littoridina stiphra Haas; 3 m.
L. berryi Pilsbry; 0·5–27 m.
L. andecola culminea (D'Orb.); 3·4–27 m.
L. a. andecola (D'Orb.); 0·5–27 m.
L. aperta Haas; 0·5 m.
Rhamphopoma parvum Haas; 5·4–7·3 m.

ISLA TITICACA

Taphius montanus montanus (D'Orb.); 2·5–7·8 m.
T. m. andecolus (D'Orb); 0·5–3 m.
Anisancylus crequii (Bavay); 1 m.
Littoridina berryi Pilsbry; 0·6–3·5 m.
L. andecola culminea (D'Orb.); 1 m.
L. a. andecola (D'Orb.); 7·8 m.
L. a. neveui (Bavay); 0·6 m.
L. aperta Haas; 1 m.
L. lacustris Haas; 0·2–0·3 m.
Limnothauma crawfordi Haas; 1 m.

SIRIPATA

Taphius montanus andecolus (D'Orb.); 6–16 m.
Anisancylus crequii (Bavay); 16 m.
Littoridina berryi Pilsbry; 1–37·5 m.
L. andecola culminea (D'Orb.); 2–7·9 m.
L. a. andecola (D'Orb); 6–37·5 m.
L. a. neveui (Bavay); 2·4–37·5 m.
Heligmopoma umbilicatum Haas; 2·4 m.

B. PUNO BAY

COATA BAY

Taphius montanus montanus (D'Orb.); 1 m.
T. m. heteropleurus (Pilsb. & Van.); 12–30 m.
Littoridina berryi Pilsbry; 0–30 m.
L. andecola culminea (D'Orb.); 23 m.

ESTEVES ISLAND

Taphius montanus montanus (D'Orb.); 1·4 m.
T. m. andecolus (D'Orb.); 0·5 m.
Anisancylus crequii (Bavay); 0·5–4 m.
Littoridina berryi Pilsbry; 0·5–1·4 m.
L. andecola culminea (D'Orb.); 1·9 m.

PUNO BAY (between Chimu and Esteves Island)

Taphius montanus montanus (D'Orb.); 0·7 m.
Littoridina berryi Pilsbry; 0·7 m.
L. andecola culminea (D'Orb.); 0·7 m.
L. a. andecola (D'Orb.); 0·7 m.
Strombopoma ortoni (Pilsbry); 0·7 m.

Off CHUCUITO

Taphius montanus andecolus (D'Orb.); 1–2·5 m.
Anisancylus crequii (Bavay);1 m.
Littoridina berryi Pilsbry; 1–2·5 m.
L. andecola andecola (D'Orb.); 1–2·5 m.

Off CATACHACA

Taphius montanus montanus (D'Orb.); 3 m.
T. m. andecolus (D'Orb.); 13–15 m.
T. m. concentratus Pilsbry; 13–15 m.
T. m. heteropleurus (Pilsb. & Van.); 13–15 m.
Anisancylus crequii (Bavay); 1·3 m.
Littoridina berryi Pilsbry; 1·3–15 m.
L. andecola culminea (D'Orb.); 13–15 m.

C. LAGO PEQUEÑO

ISLA TAQUIRI

Taphius montanus montanus (D'Orb.); 2·7–2·8 m.
T. m. concentratus Pilsbry; 2·7–2·8 m.
Littoridina berryi Pilsbry; 2·7–2·8 m.
L. andecola culminea (D'Orb.); 2·7–2·8 m.
L. a. andecola (D'Orb.); 2·7–2·8 m.
L. a. neveui (Bavay); 2·7–2·8 m.

ISLA SUANA

Taphius montanus montanus (D'Orb.); 3–14·7 m.
T. m. andecolus (D'Orb.); 0–14·3 m.
T. m. heteropleurus (Pilsb. & Van.); 14·2–14·6 m.
Anisancylus crequii (Bavay); 14·2–14·6 m.
Littoridina berryi Pilsbry; 0–14·3 m.
L. andecola culminea (D'Orb.); 1–14·6 m.
L. a. neveui (Bavay); 14·3 m.
L. aperta Haas; 14·3 m.

OFF RIO DESAGUADERO

Tropicorbis (*Lateorbis*) *canonicus* (Cousin); 1–2·6 m.
Taphius montanus montanus (D'Orb.); 1 m.
Littoridina andecola culminea (D'Orb.); 1–4 m.
L. a. andecola (D'Orb.); 2·6 m.
L. a. neveui (Bavay); 1–4 m.

BETWEEN GUAQUI AND TARACO

Taphius montanus andecolus (D'Orb.); 1·8–3·3 m.
Anisancylus crequii (Bavay); 1–8 m.
Littoridina berryi Pilsbry; 2·2–5·4 m.
L. andecola culminea (D'Orb.); 1·8–12·2 m.
L. a. andecola (D'Orb.); 3·5–8·6 m.
L. a. neveui (Bavay); 1·8–5·4 m.
L. aperta Haas; 3·3 m.
L. lacustris Haas; 3·3 m.

OFF MOUTH OF RIO TIAHUANACO

Taphius montanus montanus (D'Orb.); 0·9–2·9 m.
T. m. andecolus (D'Orb.); 2·3–2·7 m.
Littoridina berryi Pilsbry; 2·1–2·9 m.
L. andecola culminea (D'Orb.); 2·1–8 m.
L. a. andecola (D'Orb.); 0·9 m.
L. a. neveui (Bavay); 2·4–2·5 m.

LAKES, LAGOONS AND RIVERS IN THE TITICACA BASIN

RIO RAMIS at PUENTE RAMIS

Littoridina cumingi (D'Orb.); 0·3 m.

RIO RAMIS at AYAVIRI

Tropicorbis (*Lateorbis*) *canonicus* (Cousin); 1 m.

LAGUNA SUNUCO

Taphius montanus andecolus (D'Orb.)
Anisancylus crequii (Bavay)

LAGUNA TEJANE near PIATA

Taphius montanus andecolus (D'Orb.); 0–0·5 m.
Anisancylus lagunarum Haas; 0–0·5 m.
Littoridina cumingi (D'Orb.); 0 m.

LAGUNA YAPUPAMPA

Tropicorbis (*Lateorbis*) *canonicus* (Cousin); 0–0·5 m.

LAGUNA ARAPA

Tropicorbis (*Lateorbis*) *canonicus* (Cousin); 0·3–0·7 m.
Taphius montanus montanus (D'Orb.); 0·3 m.
T. m. andecolus (D'Orb.); 0·1–0·7 m.
Littoridina cumingii (D'Orb.); 0·1–0·7 m.
L. andecola culminea (D'Orb.); 0·5 m.

STREAM near CAPACHICA

Tropicorbis (*Lateorbis*) *canonicus* (Cousin)

HACIENDA YLPA (outflow of LAGO UMAYO)

Tropicorbis (*Lateorbis*) *canonicus* (Cousin)

LAGO UMAYO

Taphius montanus concentratus Pilsbry; 0–1 m.
Littoridina cumingii (D'Orb.); 0–1 m.

LAGUNILLA LAGUNILLA

Tropicorbis (*Lateorbis*) *canonicus* (Cousin); 0·4–25 m.
Anisancylus lagunarum Haas; 0·3–9·9 m.
Littoridina cumingii (D'Orb.); 0·1–24·5 m.
L. saracochae Haas; 2–3 m.
Strombopoma gracile Haas; 2–3 m.

OUTFLOW OF LAGUNILLA LAGUNILLA

Tropicorbis (*Lateorbis*) *canonicus* (Cousin)
Anisancylus lagunarum Haas; in Rio Lagunillas
Littoridina cumingii (D'Orb.)

LAGUNILLA SARACOCHA

Tropicorbis (*Lateorbis*) *canonicus* (Cousin); 0–16 m.
Taphius montanus andecolus (D'Orb.); 0–18 m.
Anisancylus lagunarum Haas; 0–16 m.
Littoridina cumingii (D'Orb.); 0–16 m.
L. saracochae Haas; 0–16 m.
L. vestita Haas; 3–5 m.

OUTFLOW of LAGUNILLA SARACOCHA

Tropicorbis (*Lateorbis*) *canonicus* (Cousin)
Anisancylus crequii (Bavay)
Littoridina saracochae Haas

LAGO POOPÓ

Tropicorbis (*Lateorbis*) *canonicus* (Cousin)
Littoridina popoensis (Bavay); 0–1·8 m.

AMAZON SYSTEM

LA RAYA

Tropicorbis (*Lateorbis*) *canonicus* (Cousin)

LAGO LANGUI

Tropicorbis (*Lateorbis*) *canonicus* (Cousin); 0–27 m.
Hebetancylus sp.; 0–0·6 m.
Littoridina languiensis Haas; 3–7 m.
Anisancylus crequii (Bavay); 0·6–27 m.

RIO LANGUI (outflow of the lake)

Tropicorbis (*Lateorbis*) *canonicus* (Cousin)
Littoridina cumingii (D'Orb.)
L. languiensis Haas

LAYO (streams entering LAGO LANGUI)

Tropicorbis (*Lateorbis*) *canonicus* (Cousin)

RIO URUBAMBA at PACHAR STATION

Littoridina cumingii (D'Orb.)

POND near RIO HUATANAY
(5 miles below CUZCO)

Tropicorbis (*Lateorbis*) *canonicus* (Cousin)
Littoridina cuzcoensis Pilsbry