VI.4e. The Mollusca

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As they take up little room and are easy to transport, the terrestrial and freshwater molluscs were frequently collected during expeditions by the great explorers of the last century and in the case of Lake Titicaca they are probably the organisms that occur most frequently in museum collections. Despite this, with the exception of species lists, the malacalogical fauna of this large lake remains poorly known. Subjects such as their biology and ecology have been little or not studied, although these organisms certainly play a very important role in production and in decomposition of organic matter in shallow water areas, particularly in the Huiñaimarca.

History of past studies

Many of the first collections were of a casual nature, taken from near the shore or in shallow water and leading to the first species descriptions. The works of D'Orbigny (1835, 1835–47), Pilsbry and Vanatta (1896), Bavay (1906) and Pilsbry (1924) come into this category. It was not before the works resulting from the Percy Sladen Trust Expedition in 1937 (Gilson, 1939) that more systematic studies were carried out, giving rise to the works of Haas (1955, 1957) in which five new genera and nine new species were described. A few years later Blume (1958) published a supplementary study of the genera *Littoridina* and *Strombopoma*, based on collections made by workers from the Munich Natural History Museum.

After this period, there was then a gap before new data on the molluscs of Lake Titicaca were provided by the studies of Medina (1983 a and b) on the benthos of Puno Bay, and the collections made by Hinz during an expedition to the Andes (Kuiper and Hinz, 1983) and our own works (Dejoux, 1988 and in press) on the benthic fauna of the Huiñaimarca and the Bolivian part of the Lago Grande.

C. Dejoux and A. Iltis (eds.), Lake Titicaca, 311–336.

Taxonomy, endemism and polymorphism

As with other groups of animals (Ostracoda, Amphipoda, Amphibia, etc.), the molluscs of Lake Titicaca show a great variability of form depending on the sampling site, a variability which led the first taxonomists to divide the fauna into multiple species, which later workers have attempted to merge; the most important effort in this field has been carried out by Haas (1955). A list of known species is given below, but for reasons of brevity, synonyms are not given for each species. For these the reader should refer to Haas (*op. cit.*)

GASTROPODA

PLANORBIDAE
- *Tropicorbis* (*Lateorbis*) *canonicus* Cousin, 1887
- *Taphius montanus* D'Orbigny, 1835

ANCYLIDAE
- *Anisancylus crequii* Bavay, 1904

HYDROBIIDAE
- *Littoridina stiphra* Haas, 1955
- *Littoridina lacustris* Haas, 1955
- *Littoridina profunda* Haas, 1955
- *Littoridina berryi* Pilsbry, 1924
- *Littoridina andecola* D'Orbigny, 1835
  - *L. a.* spp. *neveui*
  - *L. a.* ssp. *andecola*
  - *L. a.* ssp. *culminea*
- *Littoridina aperta* Haas, 1955
- *Littoridina forsteri* Blume, 1958
- *Strombopoma ortoni* Pilsbry, 1924
  - *S. o.* ssp *ortoni* Blume, 1958
  - *S. o.* ssp *schindleri* Blume, 1958
- *Rhamphopoma magnum* Haas, 1955
- *Rhamphopoma parvum* Haas, 1955
- *Heligmopoma umbilicatum* Haas, 1955
- *Brachypyrgulina carinifera* Haas, 1955
- *Limnothauma crawfordi* Haas, 1955
- *Ecpomastrum mirum* Haas, 1957

LAMELLIBRANCHIATA
- *Sphaerium titicacense* Pilsbry, 1924
- *Sphaerium forbesi* Philippi, 1869
- *Sphaerium lauricochae* Philippi, 1869
- *Pisidium meierbrooki* Kuiper and Hinz, 1983

To this list of species already recorded in the literature, must be added two others found in our samples and differing in morphological characters from the species given above. One, belonging to the genus *Rhamphopoma*, has been collected sporadically from various sites in the Bolivian part of the lake and the other, probably belonging to the genus *Littoridina*, is for the moment only known from the littoral zone of Sun Island.

The degree of endemism is high for all the species recorded from Lake Titicaca. Some of them, such as *Ecpomastrum mirum*, *Brachypyrgulina carinifera* and *Limnothauma crawfordi*, have never been collected other than in this water body; others such as *Taphius montanus* are only known from a few other aquatic biotopes close to the lake.

For at least two genera, *Taphius* and *Littoridina*, there is very pronounced polymorphism, whose causes are still far from understood. The most complex case of polymorphism is certainly that presented by the genus *Taphius*. The systematics of this group was not clarified until the works of Haas (1955), and in our opinion the final solution of this problem is yet to be found. Haas proposed an evolutionary morphological phylogeny in two branches starting from an ancestral form *Taphius montanus* D'Orbigny, the least specialised form.

Figure 1 has been drawn up from the explanations of this author, using his drawings in diagrammatical form. One of the branches of the evolutionary line leads directly to the form *T. montanus heteropleurus* Pilsbry and Vanatta, almost given it the status of a subspecies. The other branch, leading to the form *T. montanus andecolus*, has several intermediary varieties including one (*Planorbis titicacensis* Clessin, 1884) which is simply mentioned without a drawing, as from the evidence it represents a simple transition form between two extreme forms.

The form *concentratus* has a very compact and angular shell, with a very deep umbilicus, and another variety (*T. montanus concentratus* var.*bakeri*) shows these characters in an exaggerated manner (Plate 1, Figs 3 and 4), an adaptation to living in shallow water under wave influence according to Haas (*op. cit.*). We will discuss this hypothesis later. At the other extreme, the branch leading to the form *heteropleurus* ends in a rather unspecialised planorbid, restricted to deep water zones.

Polymorphism is also very pronounced in *Littoridina* spp., but the relationship between the two extreme forms is more obviously linear; all the intermediates and extreme forms can be present in the same sampling location.

In the genus *Littoridina* the variation also involves the formation of a more or less pronounced keel on the median part of the whorls, compared to an original form with broad round smooth whorls. Three subspecies have been distinguished: *L. andecola culminea* which is considered as the ancestral smooth form, an intermediate subspecies called *L. andecola andecola* and at the other extreme a form *L. andecola neveui* with a very pronounced keel (Fig. 2).

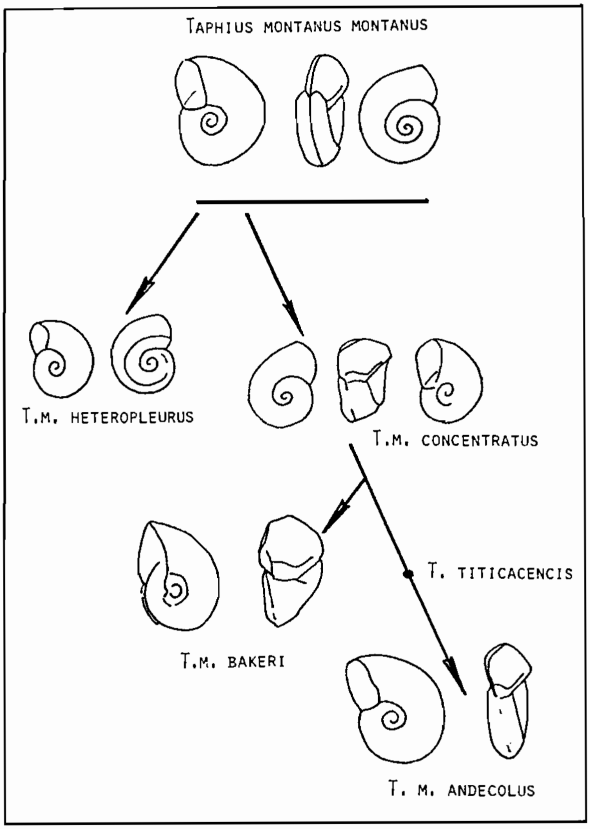

Figure 1. The polymorphism of *Taphius montanus* in Lake Titicaca, relationhips between the forms (from Haas, 1955).

Brief description of the species, distribution and ecological notes

GASTROPODA

PLANORBIDAE

Tropicorbis (*Lateorbis*) *canonicus* Cousin, 1887

This species, first described from Ecuador and also recorded from Colombia and Peru, occurs in the rivers and lakes of the Altiplano both on the Atlantic and Pacific slopes (Plate 1, Fig. 5). There is only one record from Lake Titicaca, but this was collected at the mouth of a small stream near Capachica (Haas, 1955; Fig. 3A), making it likely that this species was carried down to the lake in the drift. This species has never been recorded in our own

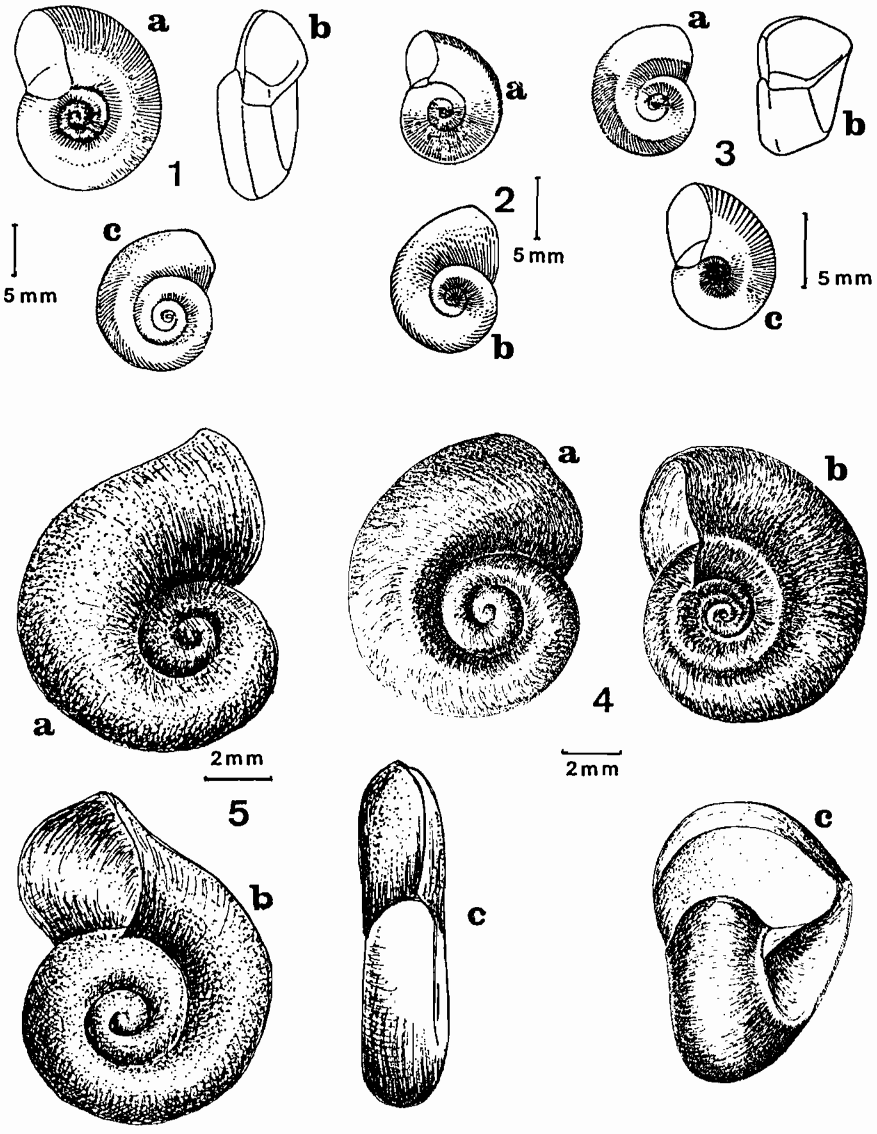

Plate 1. Fig. 1a, 1b, 1c: ventral lateral and dorsal views of *Taphius montanus montanus*. Fig. 2a and 2b: ventral and dorsal views of *Taphius montanus* var. *heteropleurus*. Fig. 3a, 3b, 3c and 4a, 4b and 4c: dorsal lateral and ventral views of *Taphius montanus* var. *bakeri*. Fig. 5: *Tropicornis canonicus*.

samples, and it is not sure that Lake Titicaca is a favourable habitat for its survival. On the other hand it is recorded from Lake Poopo, so that a relatively high salinity would not appear to be a limiting factor for its occurrence.

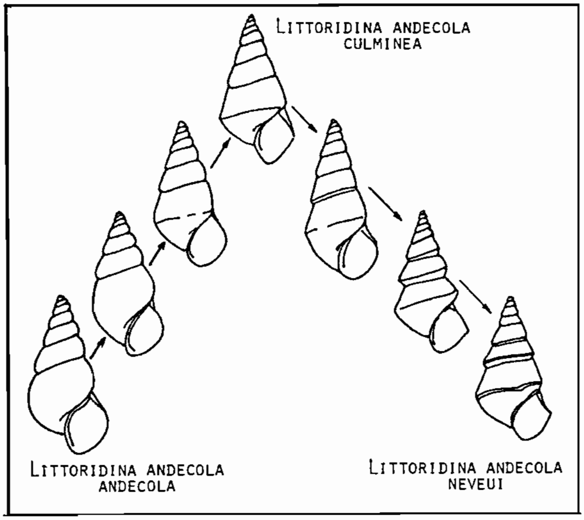

Figure 2. Relationships between the various forms of *Littoridina andecola* in Lake Titicaca (from Haas, 1955).

Taphius montanus D'Orbigny, 1835

This species of Planorbidae is endemic to the Lake Titicaca basin and has been recorded in numerous lakes and running waters on the Altiplano (Plate 1, Figs 1–4). It is a large species, with largest specimens reaching 22 mm in diameter and nearly 10 mm high, the shell being wound in $4\frac{1}{2}$ whorls. The distribution of the various described forms within the lake would appear to be less simple than the impression gained from reading Haas (*op. cit.*). This author stated that *T. montanus heteropleurus* was characteristic of deep water (10 to 82 metres depth), but that it could also occur in depths of 3 to 5 metres. In our samples coming from the entire Bolivian part of the lake, this form was found at practically all depths from 2 to 54 metres, but was dominant at a depth of about ten metres (Fig. 3B).

In contrast, it is certain that the subspecies *T. montanus andecolus* and its two related forms (*concentratus* and *bakeri*) are much more abundant at about 3 to 4 metres depth than at 15 to 20 metres depth, where they occur frequently but at low densities. Living specimens have been found down to 30 metres depth.

An extensive and detailed study would be needed to determine the depth preferenda of each form of the genus *Taphius*, but it is not certain that this is the most important factor in determining the distribution of this mollusc. From the available data it is possible however to draw up the following table showing the possible overlaps in the depth distributions.

	Extreme depths	Most frequent recorded depths
T. montanus montanus	0.20 to 25 m	0.50 to 3 m
T. montanus andecolus	0.10 to 30 m	0.50 to 4 m
T. montanus concentratus	2.70 to 15 m	3 to 6 m
T. montanus bakeri	1 to 6 m	1 to 3 m
T. montanus heteropleurus	3.40 to 82 m	15 to 35 m

The distribution of the various forms of *T. montanus* shown in Fig. 3B, drawn up from data in the literature and from our own sampling, shows that the varieties *montanus* and *andecolus* are by far the most widely distributed in the lake. In contrast the variety *bakeri* is frequent in the Huiñaimarca, but only occurs in isolated spots in the Lago Grande.

ANCYLIDAE

Anisancylus crequii Bavay, 1904

This relatively easy to identify small species has an apex set off to one side and a frequently concave lower margin (Plate 2. Fig. 1a and b). The usual shape of the base of the shell is oval, with a more or less pronounced lateral flattening. Morphological variability in this species involves the shape of the apex and that of the base of the shell which can be almost flat and also broadly oval. Haas (1955) suggested that *A. crequii* could be just an extreme form of *Anisancylus lagunarum*, described from samples found in small lakes near Lake Titicaca (Laguna Tejane, Lagunilla Lagunilla and Lagunilla Saracocha). As we have found some shells in Lake Titicaca very close in shape to typical specimens of *A. lagunarum*, it seems likely that the two forms occur in both the lake itself and in high altitude lakes in the Cordillera, but it is still impossible to say whether these are really two different species.

A. crequii occurs in almost all areas of the lake where the water is shallow or of medium depth. The localities in which it has been recorded are shown in Fig. 3C. Its depth distribution extends as far as the eulittoral where it can be found under stones in only a few centimetres depth to the 5 to 8 metres depth zone, where it reaches it maximum abundance. As some individuals have been collected from a depth of 30 metres its area of distribution can be considered as going beyond that of the strictly littoral zone. This species is also frequent in the aquatic vegetation, among stems of Characeae or on the leaves of *Potamogeton*.

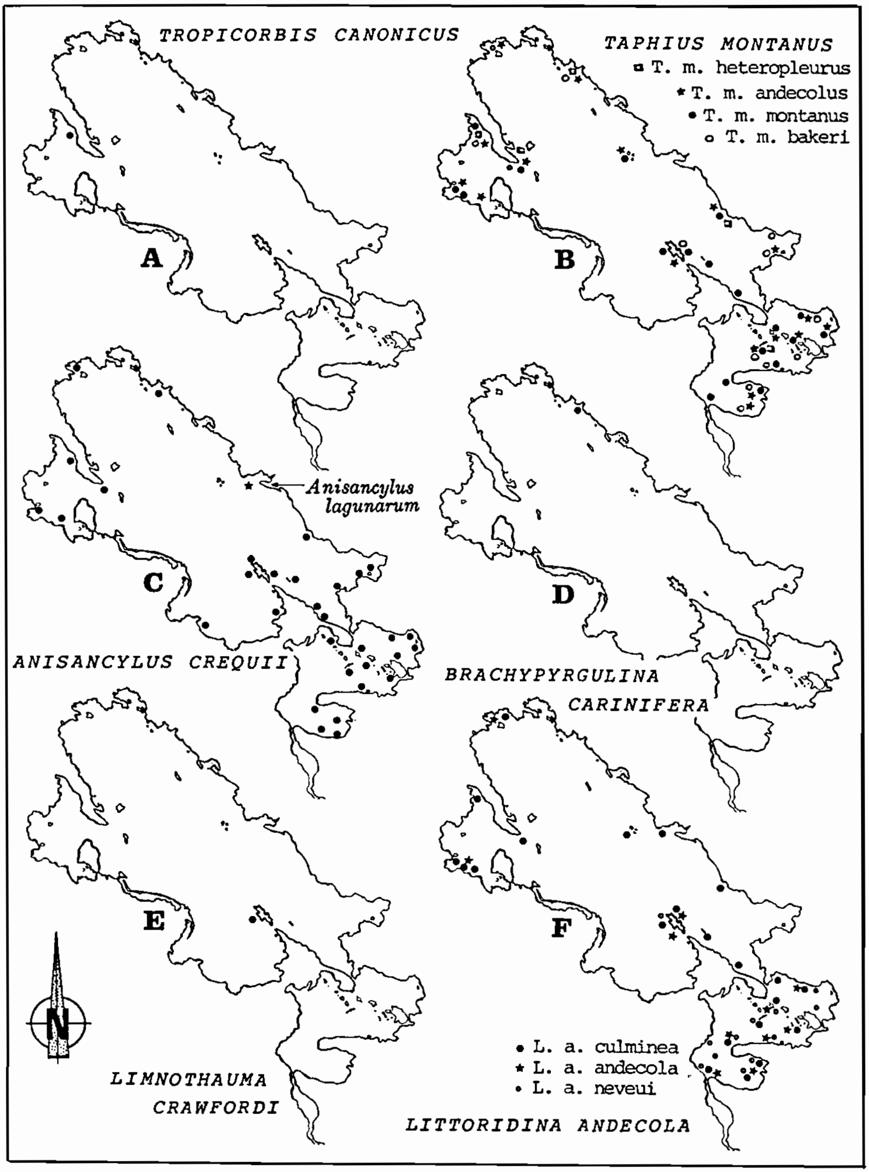

Figure 3. Distribution of various species of mollusc in Lake Titicaca.

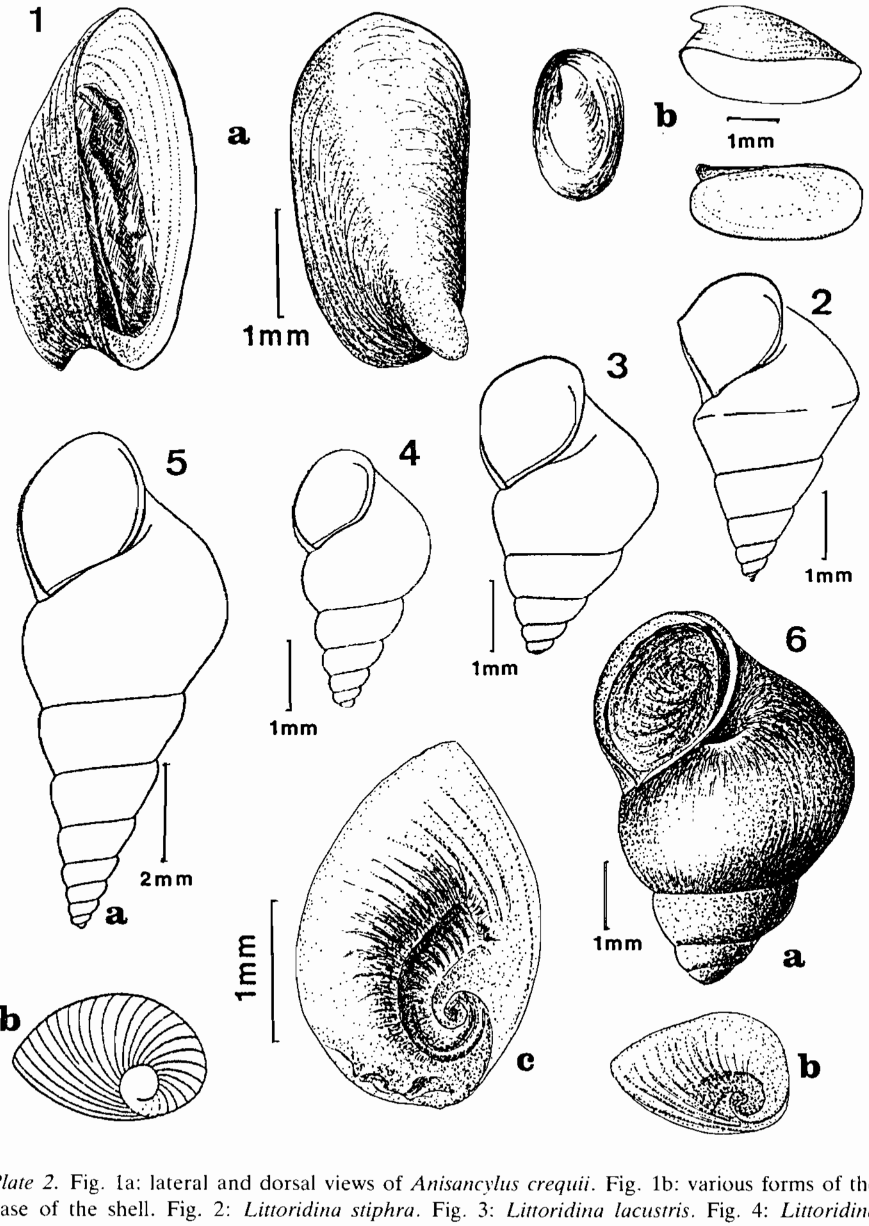

Plate 2. Fig. 1a: lateral and dorsal views of *Anisancylus crequii*. Fig. 1b: various forms of the base of the shell. Fig. 2: *Littoridina stiphra*. Fig. 3: *Littoridina lacustris*. Fig. 4: *Littoridina profunda*. Fig. 5a: *Littoridina berryi*; 5b: operculum. Fig. 6a: *Littoridina aperta*; 6b: outer surface of the operculum; 6c: inner surface of the operculum showing the presence of a horny spiral thickening. (Figs 2, 3, 4 and 5 from Haas, 1955).

HYDROBIIDAE

Littoridina stiphra Haas, 1955

The measurements of the type specimen are as follows: height 4.2 mm, breadth 2.8 mm, aperture 1.4 × 1.1 mm. It is therefore a small, thin, transparent species with a conical shell having $6\frac{1}{2}$ whorls. The upper four whorls are convex, whereas the lower whorls are flattened, the last whorl even being concave towards the aperture (Plate 2, Fig. 2). The operculum is deeply set, thin and horny. Variations in shape affecting this species mainly involve the degree of prominence of the keel. Except for its size, which is relatively smaller, this species is rather similar to certain specimens of *Littoridina andecola neveui*. We have not been able to identify this species in our own samples and for the moment we consider it is a rare species, known only from Molinopampa (Haas, 1955), living at a depth of 3 metres (Fig. 4A).

Littoridina lacustris Haas, 1955

This is also a small species scarcely exceeding 4 mm in height and 3 mm in breadth. Its general shape is therefore strongly conical, the shell being translucent grey, but of solid appearance (Plate 2, Fig. 3). A thin horny operculum closes the shell at a distance about 1/3 of a whorl from the aperture. The number of whorls is reduced to 5–6 at the maximum, a character which distinguishes this species from another of a similar shape: *L. berryi*, but which is much larger and has at least 7 whorls.

From the characteristics of the sampling locations, it seems that *L. lacustris* occurs from the margins to depths of up to 66 metres. Its present known distribution is given in Figure 4B.

Littoridina profunda Haas, 1955

Haas described this species in 1955 from only 7 specimens, collected near Taman at between 56 and 82 metres depth. It is not abundant in our material although it was found regularly in samples taken at depths of between 4.5 and 10 metres in the Huiñaimarca and at 40 m in the Lago Grande off Moon Island. The type specimen, described from a dead shell, is of small size (height 3.5 mm; breadth 2.3 mm; aperture 1.5 × 1 mm), whereas our largest specimen reaches almost 6 mm, but also has a shell with $6\frac{1}{2}$ whorls. Certain individuals which have dimensions close to those of the type specimen also have $6\frac{1}{2}$ whorls. The main character of the species is that it has a rugous dirty grey periostracum. Another species of *Littoridina* (*L. vestida*) has a similar periostracum but it is smooth and white and this species probably only occurs in the Lagunilla Soracocha and not in Lake Titicaca.

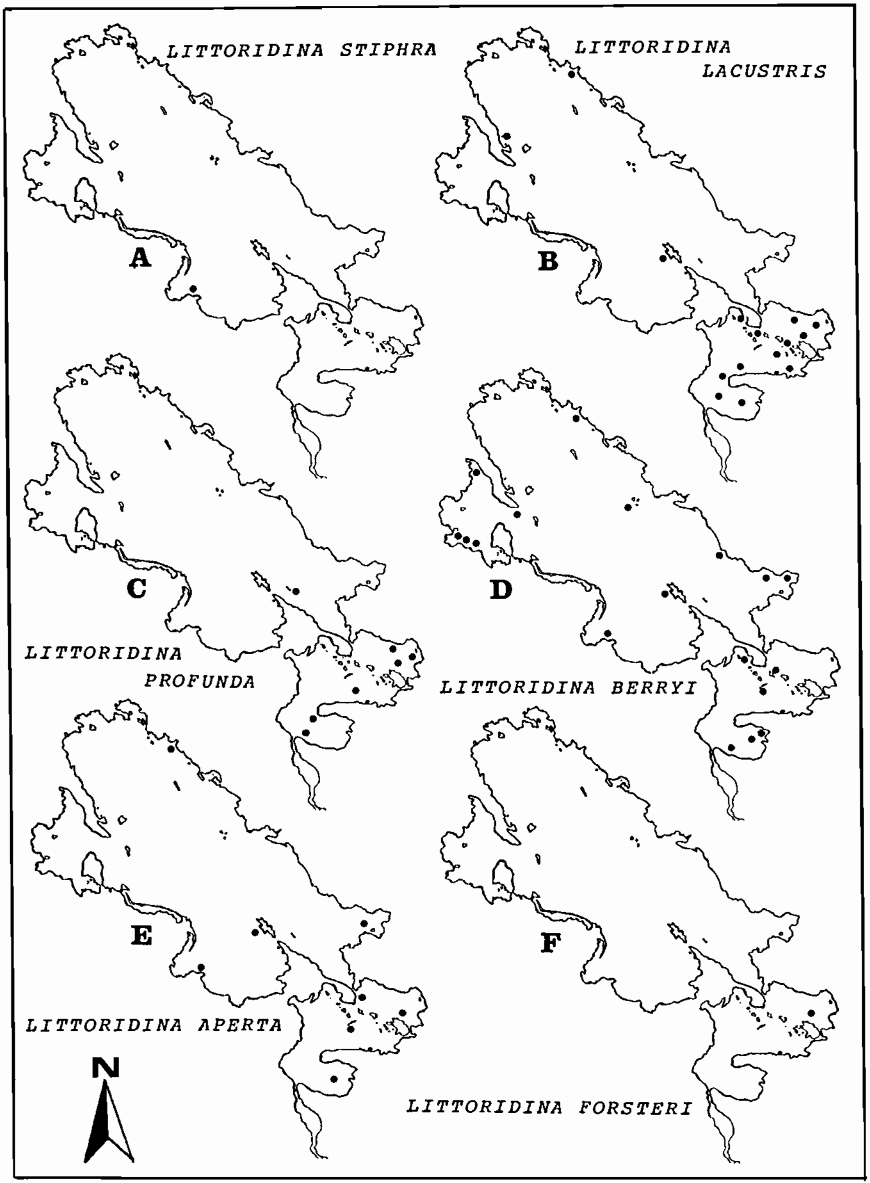

Figure 4. Distribution of various species of mollusc in Lake Titicaca (continued).

Littoridina berryi Pilsbry, 1924

Although recorded as the most frequent species in Lake Titicaca and also the largest (Haas, 1955), this species shows such size variations that distinguishing it from *Littoridina andecola culminea* does not always seem very evident to us. Pilsbry in his description of the species describes a shell height varying from 7.5 to 8 mm for adult individuals, with a breadth varying between 3.2 and 4.1 mm (Plate II, Fig. 5). In contrast, Haas (1955) records specimens exceeding 12 mm in height and 5.1 mm in breadth and having 9 to $9\frac{1}{2}$ whorls. In view of the fact that *L. a. culminea* can also have $9\frac{1}{2}$ whorls and measure 10.9×4.5 mm, the only character remaining to distinguish the two species is that the last whorl of *L. berryi* is slightly concave or at most flat at the extremity of the aperture, and never convex as in *L. andecola*: character which is not very evident in our view! As, in addition, the opercula of these two species are practically identical, the correct identification of these species in samples where they occur together would appear to be a matter of chance.

At the start of the century, *L. berryi* was considered as having a very wide distribution throughout the lake (Fig. 4D), living at depths ranging from 20 cm to more than 30 metres. In our samples we have only identified with certainty 15 individuals belonging to this species, whereas the various forms of *L. andecola* occur almost everywhere. This leads us to think that the relative proportions of certain organisms living in Lake Titicaca have changed greatly, a fact that is also encountered with the Hydracarina.

Littoridina aperta Haas, 1955

This small species (type specimen: height = 3 mm, breadth = 2.2 mm, aperture = 1.4×1.2 mm) was collected by the Percy Sladen Expedition in small numbers at a few locations in the lake at depths ranging from 0.5 to 14.3 metres. The shell has a translucent but solid appearance, with up to 5 whorls, the operculum is terminal and horny, the umbilicus is very open and the general colour is greyish white (Plate 2, Fig. 6). Our sampling in the Bolivian part of the lake provides details of the distribution of this species (Fig. 4E) which is rather infrequent in the study area as a whole, but can be abundant in areas where it lives, reaching densities of more than 6000 individuals per square metre (Sun Island, 22 February 1987, depth 30 metres). The depth at which this sample was taken makes it likely that this species occurs over a wide depth range.

Littoridina forsteri Blume, 1957

This small species, described by Blume (1957), is close in general form to *L. aperta* and *L. lacustris*. It differs from the latter by the presence of an umbilicus and from the former by the less globular shape and different dimensions, all of these characters not being very obvious to recognize, taking into account the morphological variability of most of the species occurring in the lake (Plate 3, Fig. 1).

The shell is robust, almost non-transparent and greyish white in colour. There are $5\frac{1}{2}$ whorls with well-defined sutures. The umbilical aperture is deep and also well pronounced. The surface of the shell has a pitted appearance and the last few whorls have growth striae along the sutures, clearly visible under a binocular microscope. If the pitted appearance of the shell isn't an artefact (erosion ?), it is certainly the most obvious character for distinguishing this species from the two mentioned above. It is however strange that we have never found this species of *Littoridina* in the abundant material that we have collected in the area of the Huiñaimarca from where the type specimen comes (between Huatajata and Patapatani. Fig. 4F). The drawing that we show of this species is very similar to that of *Littoridina aperta* and if we accept the possibility that some special form of erosion occurred to a series of shells at a particular time, it is not impossible that these are in fact the same species.

Littoridina andecola D'Orbigny, 1835

The extreme morphological variability of this species has already been mentioned so only brief descriptions of two of the extreme forms and of the most frequent intermediate form will be given below.

Littoridina andecola culminea
The mean size of this form is 6.5 mm high with a width of about 3 mm; the shell has between 7 and 8 whorls which are slightly convex (Plate 3, Fig. 3a). This is certainly the most frequent form at present, at least in the Huiñaimarca (Fig. 3F).

Littoridina andecola andecola
This form has linear very shallow sutures, the whorls being almost flat, except the last which can be angled at its margin, announcing the transition towards the form *neveui* (Plate 3, Fig. 4a). The operculum is apertural, whereas it is always much deeper in the form *culminea*. The mean size is also different, Haas (1955) giving the following values: H = 7.8 mm; B = 3.6 mm, for a snail with 9 whorls.

Littoridina andecola neveui
This form, which is more abundant than the previous form but less so than the first, is certainly the easiest to identify (Plate 3, Fig. 5). Its general appearance, typified by the presence of a keel which can be very pronounced, resembles the European genus *Pyrgula*. This form has 7.5 to 8 whorls and has mean dimensions of the same order of magnitude as those of *L. a. andecola*.

We have frequently encountered all three forms in the same sample and

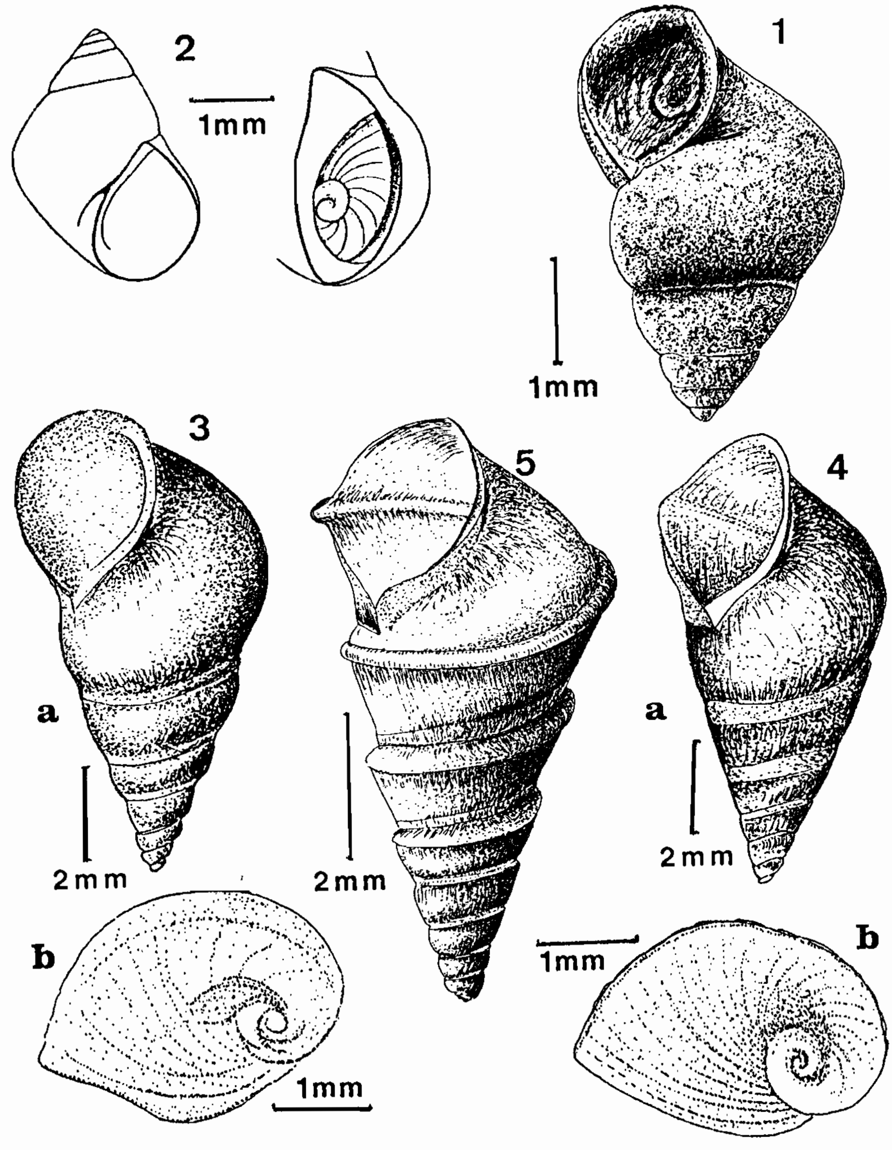

Plate 3. Fig. 1: *Littoridina forsteri*. Fig. 2: *Heligmopoma umbilicatum*. Fig. 3a and 3b: *Littoridina andecola andecola* and its operculum. Fig. 4a and 4b: *Littoridina andecola culminea* and its operculum. Fig. 5: *Littoridina andecola neveui*. (Fig. 1 from Blume, 1958; Fig. 2 from Haas, 1955).

the analysis of their distribution in the Bolivian part of the lake, the only part we have surveyed, indicates a very wide distribution (Fig. 3F).

Littoridina (?) sp.

A brief description is given here of three empty shells of a mollusc that we place with uncertainty in the genus *Littoridina*.

One of the three specimens examined still had remains of soft parts inside but no operculum. It is therefore a form still living at present in the lake, but certainly rare or very local, judging by the small number of individuals found.

The shells are transparent, but of a rather robust consistency; the well-marked columella is very distinctive. The measurements of the three available examples are as follows (in mm):

	Number of whorls	Length	Width at the last whorl	Dimensions of the aperture
1	9.5	4.4	1.3	0.8 × 1.1
2	9	3.6	1.1	0.7 × 1.0
3	8.5	3.7	1.0	0.6 × 0.8

It is therefore a small very elongate species, with a characteristic aperture in which the two outside angles are slightly greater than right angles, the angle along the mid-line of the last whorl is particularly well-marked, giving the impression that the shell is keeled on this whorl. The umbilicus is open but not very well-marked from the exterior, the sutures are linear and the peristome lacks distinctive features. A lamellar periostracum seems to cover the shell (Plate 5, Fig. 4).

Strombopoma ortoni Pilsbry, 1924

This species was originally described under the name *Littoridina* (*Heleobia*) *ortoni* by Pilsbry (1924), from an example without an operculum, but was placed in the genus *Strombopoma* created by Haas (1955), largely on the basis of the description of the operculum alone. Haas himself seemed however to be rather uncertain of the exact systematic position of this genus. Anatomical studies, which to our knowledge have never been carried out, could confirm whether it really belongs to the tribe of the Littoridinae within the sub-family Hydrobiinae, family Hydrobiidae!

S. ortoni is a very small mollusc (height of the type specimen: 3.1 mm; breadth 1.7 mm; aperture: 0.9 × 0.8 mm), with a thin, whitish, translucent shell, one of the characteristics of the genus. Growth striae are clearly visible and the whorls ($6\frac{1}{2}$) are convex in the centre and flat near the sutures, which

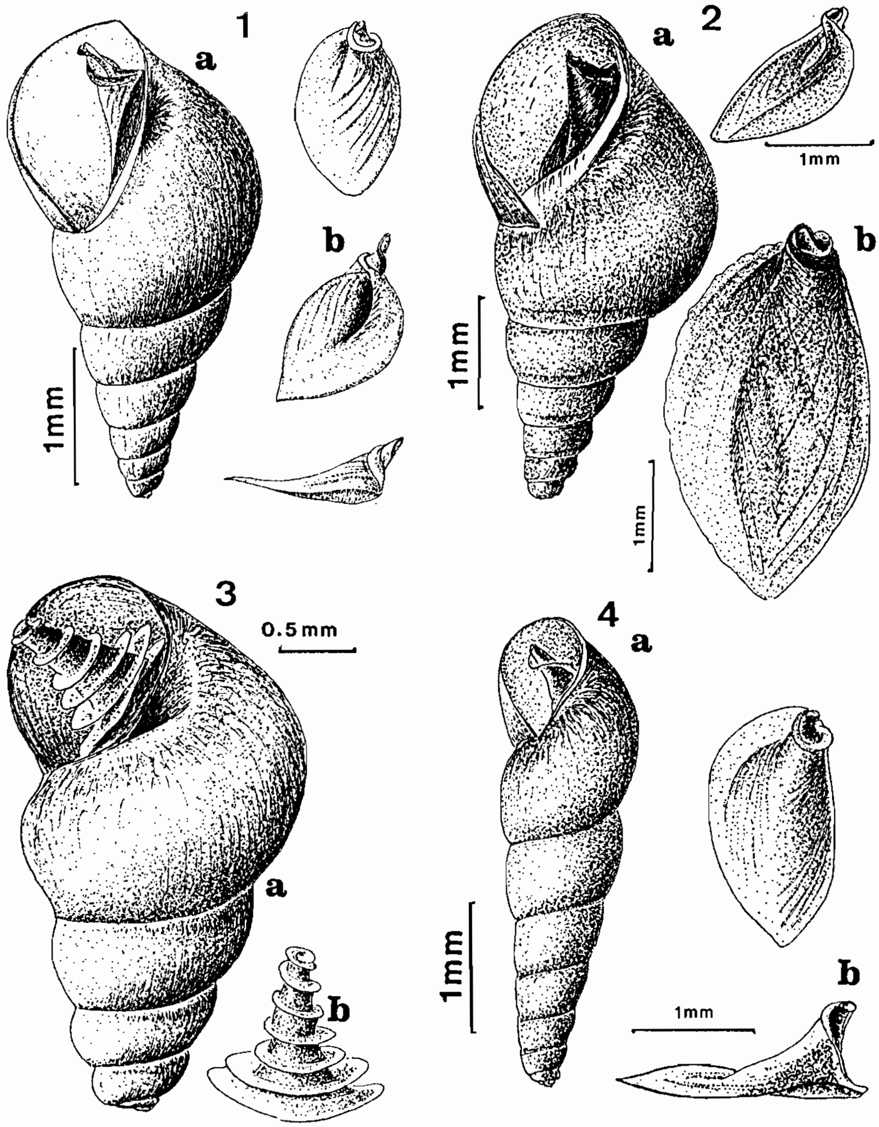

Plate 4. Fig. 1a: *Rhamphopoma magnum*; 1b: various views of the operculum. Fig. 2a: *Rhamphopoma parvum*; 2b: various views of the operculum. Fig. 3a: *Strombopoma ortoni*; 3b: operculum. Fig. 4a: *Rhamphopoma* sp.; 4b: lateral and outer views of operculum.

are rather shallow (Plate 4, Fig. 3a). The shell is imperforate, but the last whorl is somewhat detached at its base forming an aperture resembling an umbilicus. The peristome is straight and continuous, the aperture being pear-shaped.

The operculum is characteristic (Plate 4, Fig. 3b) and has at least as many whorls as the shell. It is horny, hollow on its internal face and ornamented with a sinistral spiral lamella having up to 10 whorls. The diameter at the base is less than that of the shell.

The shell is subject to rather great variability in shape and dimensions, reaching 4.5 mm in height and being more or less straight and elongated. This last character led Blume (1958) to propose a division into two subspecies: *S. ortoni ortoni*, the form closest to the type and corresponding to the more elongated individuals, and the subspecies *S. ortoni schindleri*, more robust, globular and with the aperture more detached from the rest of the shell.

Without discussing the validity of such a subdivision, especially as ecological data concerning one or other of these taxa are not available, it is nevertheless worth noting that the same evolutionary tendency will be seen below concerning *Ecpomastrum mirum*. Such variations are perhaps evidence of a particular evolution specific to certain molluscs in Lake Titicaca.

Generally *Strombopoma ortoni* seems to be a rare component of the malacological fauna of the lake. Its present known distribution is restricted to two localities in the Lago Grande (Puno and Ascoma Cove at the mouth of the Rio Suchez) and a few stations in the Huiñaimarca, at between 5 and 13 metres depth, amongst aquatic vegetation (Fig. 5C).

Rhamphopoma magnum Haas, 1955

This moderate-sized species (4.5 to 5.4 mm high), with a relatively translucent shell in young animals becoming whitish opaque in older individuals, is pyramidical in shape, with about 7 whorls, the first five being broader at the margin. The aperture (2.2 × 1.5 mm) is oval, but often pointed at the anterior and posterior ends. The border of the columella is hollow and projects slightly over the umbilical slit (Plate 4, Fig. 1a).

The operculum is oblong and has a horny opaque excresence, rolled into a spiral anteriorly and projecting above the opercular plate (Plate 4, Fig. 1b). The spiral is sinistral, the invaginated twisting being particularly clear in young individuals.

Haas (1955) recorded the existence of two forms, one being more elongated and thinner, corresponding to the type. After collecting a rather large amount of material we now think that a full range of intermediate forms exist. The genus *Rhamphopoma* was created by Haas (*op. cit.*) to include two species apparently endemic to Lake Titicaca, since this is the only locality from which they have been recorded up till now. Some uncertainty still exists however as to whether this new genus really belongs to the family Hydrobiidae or at least to its own sub-family, because of the absence of precise anatomical studies.

The present known distribution of this species (Fig. 5A) is restricted to two stations in the Lago Grande and one in the Huiñaimarca, the samples coming from depths of between 0.5 and 11 metres.

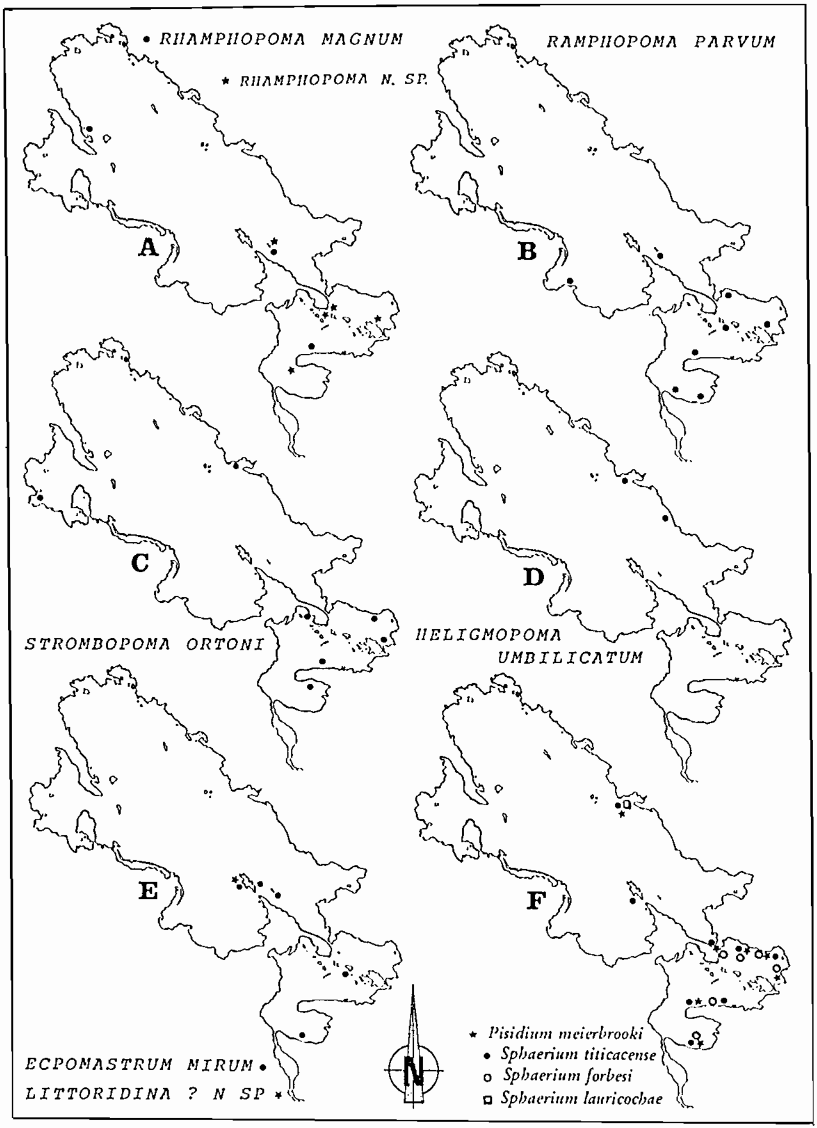

Figure 5. Distribution of various species of mollusc in Lake Titicaca (continued).

Rhamphopoma parvum Haas, 1955

This second species, collected by the Percy Sladen Expedition, is smaller than the previous one and is more robust looking (type specimen: height = 3.5 mm; breadth = 1.8 mm; aperture = 1.4 × 1.0 mm). The shell is whitish and has a non-perforated umbilicus. The whorls are convex, number $6\frac{1}{2}$ and have a strongly marked suture. The peristome is continuous and the border of the columnella is neither hollow, neither does it project over the umbilicus.

Haas (1955) recorded individual variations in this species which can vary in robustness, width and height. The distinction from the previous species is therefore far from evident, the differences listed making much use of terms such as "less flattened, less pointed and less projected" when talking of the collumellar border – an essential character – which in our view makes precise identification very difficult! The transparency of the shell, especially in large individuals, seems to be a more reliable differentiating character.

This species was only collected by the Percy Sladen Expedition at Molinopampa at depths of between 5.4 and 7.3 m. Our much more abundant samples lead us to think that it has a much wider distribution, especially in the Huiñaimarca (Fig. 5B). It occurs in samples either as a few individuals or in contrast in hundreds and so has a much more clumped distribution than the previous species.

Rhamphopoma sp.

The form of the operculum (Plate 4, Fig. 4b) leaves no doubt that the two series of molluscs that we collected in the Huiñaimarca in February 1987 belong to the genus *Rhamphopoma*. It is even possible that they represent a form of variation of *R. magnum*, although when the two species are put side by side they are very different. A brief description is all that will be given here.

The shell is very elongated, slightly transparent but with a resistant appearance. The largest individuals have $7\frac{1}{2}$ whorls, more or less obtuse in the centre, the last bearing distinct growth striae. The umbilicus is only slightly or not at all evident, the peristome is strong, becoming slightly detached at the base of the aperture. The example chosen as type specimen is 3.7 mm high and 1 mm wide; the largest individual found in our samples (1 empty shell) measures 3.9 mm high and has 8 whorls. The aperture is oval and very pointed at the top, measures 0.9 mm high and 0.6 mm wide. The operculum is identical in shape to that of *R. parvum*.

Heligmopoma umbilicatum Haas, 1955

This is a small species (height of the type specimen 3.3 mm; breadth 2.7 mm, aperture 1.9 × 1.5 mm), with a strongly conical, whitish translucent shell. The suture separating the $5\frac{1}{2}$ spires is linear, the umbilicus is usually narrow, but can be widely open in some individuals. The peristome is simple, rather broad and is brown coloured in places. The operculum is thick, horny and usually sunken into the shell. It has three and a half whorls extending in the form of lamellae from the external surface.

The genus comprising a single species was created by Haas (1955) from material coming from a single station (Siripata, Fig. 5D). We have only found this mollusc twice in the Lago Grande, off the mouth of the Rio Suchez, at a depth of 6 metres and further south at a depth of 78 metres.

Limnothauma crawfordi Haas, 1955

A single specimen of the mollusc was collected by the Percy Sladen Expedition, at a depth of one metre, on the shore of Titicaca Island (= Sun Island), but with no further details. It was an animal which had not yet reached full size, but whose very characteristic shape led to it being described as a new genus and species at the time. We have only once found two individuals belonging to this species, despite taking numerous samples in the same region, which confirms its rarity.

It is a small mollusc (height 3.5 mm; breadth 2.8 mm, aperture: 1.8 × 1.2 mm), with a broadly conical shape. The shell, covered with a brown periostracum has about 5 whorls, marked with two keels. The umbilicus is widely open and invaginated, the aperture is closed by a thin transparent horny operculum, projecting beyond the margin (Plate 5, Figs 2a and b).

Brachypyrgulina carinifera Haas, 1955

This seems to be another rarity, only collected from two stations in the Lago Grande by the Percy Sladen Expedition (Fig. 3D) and that Haas placed in the Hydrobiidae with uncertainty. Again, we have never found this species but we have never had the opportunity of sampling in localities where it was first collected. The very characteristic shaped shell, with two very pronounced keels is somewhat like a compressed form of *Littoridina a. neveui* (Plate 5, Figs 3a and b). Measuring scarcely 4 mm high, with a width of 3.1 mm and an aperture of 2.5 × 2.4 mm, it has a conical shape, closed umbilicus and is translucent whitish yellow. The operculum is very deeply set in and has a horny structure similar to that of *Littoridina aperta*. This species was collected at depths ranging from between 2.2 and 25 metres.

Ecpomastrum mirum Haas, 1957

This species, with its very characteristic completely unrolled shell, is another endemic species with a very restricted distribution (Fig. 5E). Described from a single empty shell by Haas (1957), we have found numerous living examples living in two regions of the lake, in the area of Sun and Moon islands in the northern basin and at two sites in the Huiñaimarca (Dejoux and Mourguiart, in prep.). The largest living individuals collected scarcely exceed 3.5 mm in height and 1.4 mm in breadth, the shell having $5\frac{1}{2}$ whorls. The type specimen measures 4.9 mm high and has 6 whorls; it must therefore be concluded that our specimens were of as yet not fully grown individuals or that the type specimen was particularly large. The operculum is very deeply inset into the shell (on preserved specimens) and is typical of a *Strombopoma* operculum in being conical, chitinised and with a membranous lateral extension wound in a sinistral spiral, with the same number of whorls as the shell (Plate 5, Figs 1 a to e). The problem remains as to whether this mollusc really belongs to the new genus *Ecpomastrum* created for it, or whether it belongs to the genus *Strombopoma*.

LAMELLIBRANCHIATA

For a long time only one species of *Pisidium* was known from Lake Titicaca: *P. titicacense* Pilsbry, 1924, described from a single valve collected from Yunguyo Bay! Two other species had also been recorded (*Pisidium forbesi* Philippi, 1869 and *Pisidium chilense* D'Orbigny, 1835, recorded by Bavay in 1904), but their occurrence remained doubtful and it was only after the study of Kuiper and Hinz (1983) that the situation concerning the lamellibranch fauna of Lake Titicaca became clearer. It seems that a single species of *Pisidium* (*P. meierbrooki*) and three of *Sphaerium* (*S. forbesi*, *S. lauricochae* and *S. titicacense*) are present in this water body.

Pisidium meierbrooki Kuiper and Hinz, 1983 (Plate 6, Fig. 2a to e).

P. meierbrooki has an elongate oval, but bulbous form and is distinguished from the other Sphaeriidae in the lake by its very convex, solid, shiny, non-transparent shell with irregular concentric growth rings and a dark line in the centre. The ligament, also dark coloured, is clearly visible from the outside.

The dimensions of the holotype are as follows: L = 4.1 mm, H = 3.3 mm, D = 2.8 mm. The largest individuals rarely exceed 5 mm in length.

According to Kuiper and Hinz (1983), *P. meierbrooki* is more a running water species, living in deep calm waters, but which is also found in Lake Titicaca at depths of down to 20 metres. We have frequently collected it and give its present known distribution in Fig. 5C. This species is frequently associated with *S. forbesi*, and also occurs with *S. lauricochae* and *S. titicacense*.

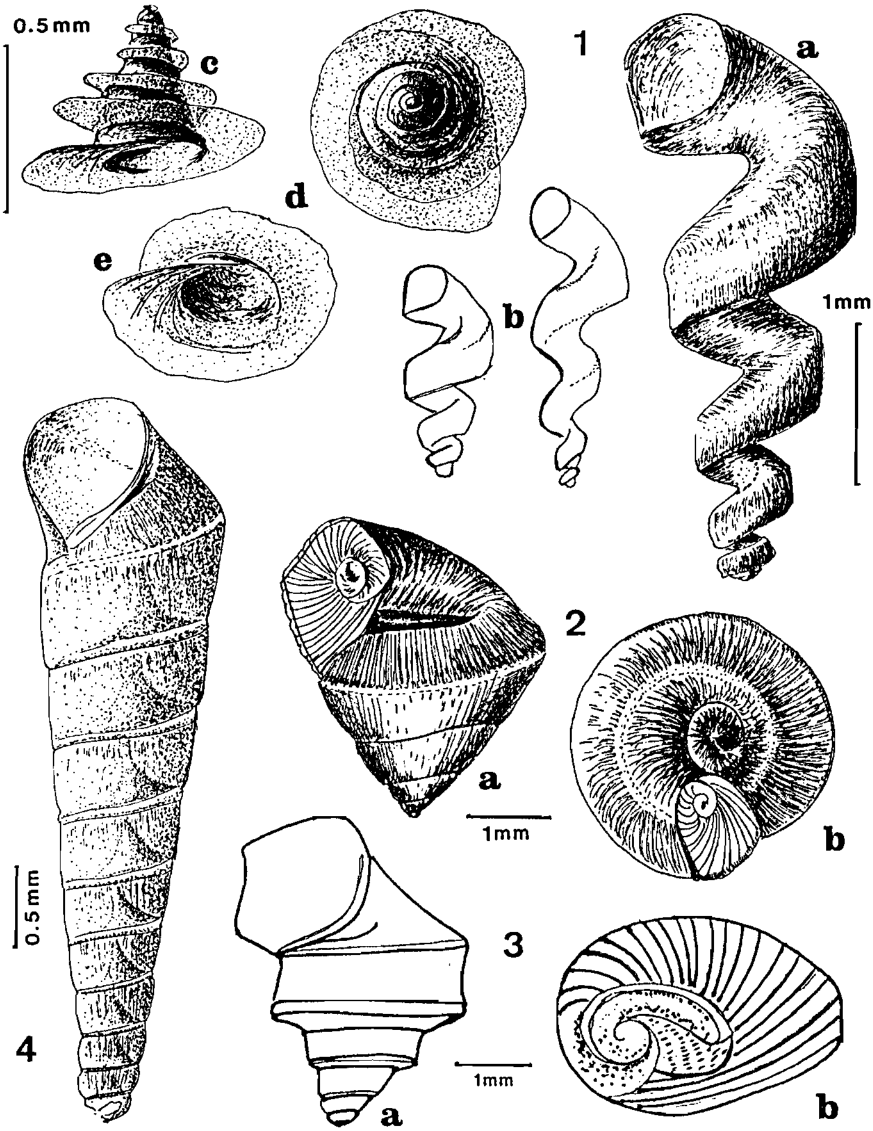

Plate 5. Fig. 1a: *Ecpomastrum mirum*; 1b: various views of the shell winding; 1c, 1d, and 1 e.: operculum from various angles. Fig. 2a and 2b: *Limnothauma crawfordi*, lateral and ventral views. Fig. 3a: *Brachypyrgulina carinifera*; 3b: operculum. Fig. 4. *Littoridina* (?) sp.

Shaerium forbesi Philippi, 1869 (Plate 6, Fig. 3a to e)

This species which lives at altitudes of between 3200 and 4700 metres frequently occurs in the lakes of the northern Altiplano and the Cordillera, and is also very common in Lake Titicaca (Fig. 5F). The shape of the shell in

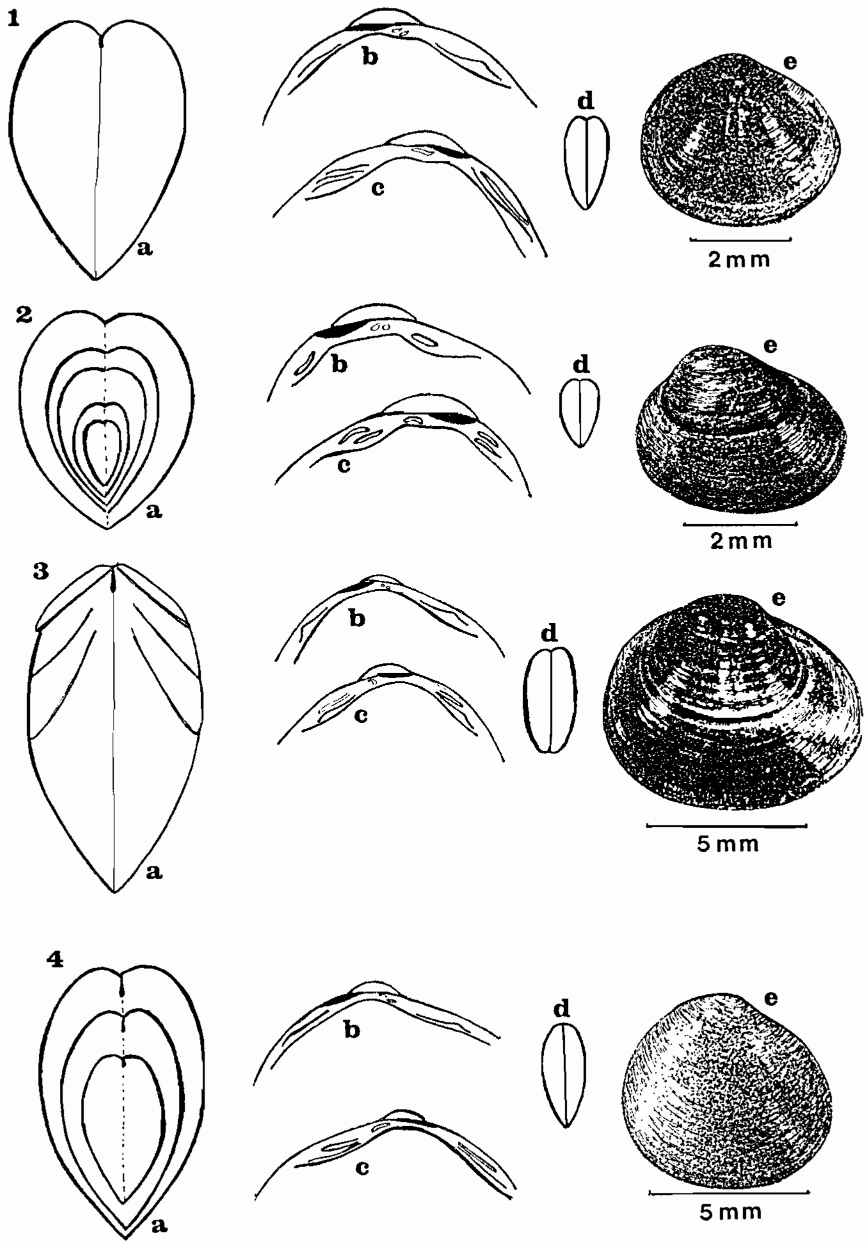

Plate 6. Fig. 1: *Sphaerium titicacense*; 1a: lateral view; 1b hinge of left valve; 1c: hinge of right valve; 1d: outline of juvenile; 1e: adult. Fig. 2: *Pisidium meierbrooki*; 2a: lateral view at various stages of growth; 2b hinge of left valve; 2c: hinge of right valve; 2d: outline of juvenile; 2e: adult. Fig. 3: *Sphaerium forbesi*; 3a: lateral view; 3b hinge of left valve; 3c: hinge of right valve; 3d: outline of juvenile; 3e: adult. Fig. 4: *Sphaerium lauricochae*; 4a: lateral views at various stages of growth; 4b hinge of left valve; 4c: hinge of right valve; 4d: outline of juvenile; 4e: adult.

young individuals is characteristic with very rounded margins in profile. In adults, which can exceed a centimetre in length and have a generally globular shape, the first stage of shell growth is clearly distinguishable at the hinge of each valve and separated by a more or less well pronounced ridge, in some cases having the appearance of a cap on each side of the hinge. This extreme form is known as *excessiva*. The general colour of *S. forbesi* is brownish-yellow, the area near the hinge sometimes being bluish-grey.

Sphaerium lauricochae Philippi, 1869 (Plate 6, Fig. 4 a to e)

Kuiper and Hinz (*op. cit.*) did not record this species from Lake Titicaca, but in its near neighbourhood. We give a brief description because we have collected it in the lake itself from the mouth of the river Suchez (Fig. 5F). It is possible however that the individuals found in this locality had been brought down as larvae in the drift of the river (where this species is recorded) and had continued their development in this part of the Lago Grande. The material collected by Philippi seems to have been lost, so a new description of the neotype was given by Kuiper and Hinz, from which we derive the following main characters:
- shell thin, subtransparent and relatively flat,
- periostracum greyish,
- no visible growth rings,
- brownish ligament visible from the exterior,
- hinge long (about 2/3rds of the circumference),
- cardinal tooth small and short, lateral tooth long and straight.

S. lauricochae seems to be a form morphologically intermediate between *S. forbesi* and *S. titicacense* and its status as a separate species is not at all certain; it could just be a variety of *S. forbesi*. The differences in morphology and structure between the two taxa seems to be clearer marked in young individuals, *S. forbesi* being flat and with a rounded lower profile, whereas *S. lauricochae* is more globular and pointed in its lower part.

Sphaerium titicacense Pilsbry, 1924 (Plate 6, Fig. 1 a to e)

Originally described from a young individual as belonging to the genus *Pisidium*, it is in fact a *Sphaerium* (Kuiper and Hinz, 1983) and has been rediscovered as abundant in Puno Bay at a depth of 25 metres.

This species resembles *S. lauricochae* but has a thick non-transparent shell. It is also usually a smaller species, which is probably endemic to Lake Titicaca. The ligament is scarcely visible from the exterior and can only be distinguished on large individuals. Kuiper and Hinz (*op. cit.*) recorded a relationship between shell diameter and depth, the maximum size increasing

Table 1.

Species	Abundance Sampled number	Percentage
Anysancylus cf. *lagunarum*	6	0.02
A. crequil	469	1.94
Taphius montanus	2 219	9.17
Sphaerium titicacense	156	0.64
S. lauricochae	41	0.17
S. forbesi	245	1.01
Pisidium meierbrooki	27	0.11
Littoridina andecola culminea	1 337	5.52
L. andecola andecola	7 004	28.96
L. andecola neveul	2 829	11.70
L. berryi	15	0.06
L. lacustris	4 579	18.93
L. aperta	1 845	7.63
L. profunda	1 334	5.51
L. n. sp.	3	0.01
Rhamphopoma magnum	381	1.57
R. parvum	1 223	5.05
R. n. sp.	153	0.63
Strombopoma ortoni	183	0.75
Limnothauma crawfordi	2	0.008
Heligmopoma umbilicatum	21	0.08
Ecpomastrum mirum	111	0.46
Total :	24 183	

from only 5 mm at 40 metres, to 6 mm at 20 metres and 8 mm at 10/11 metres.

Conclusions

The mollusc fauna of Lake Titicaca would appear to be very diversified and rich in species, with nearly thirty described taxa. Their individual numerical importance is however highly variable, as can be judged from the percentages derived from a study of their distribution in the Bolivian part of the lake, a study during which certain taxa previously recorded from this habitat could not be refound (Table 1).

An almost constant component of the littoral benthic fauna, the molluscs also inhabit the entire area of the Huiñaimarca covered with macrophytes and particularly the carpets of Characeae. The sometimes very high densities of Hydrobiidae, reaching 8000 to 10 000 individuals per square metre, makes them of the highest importance in the primary decomposition of plant material. Practically nothing is known of their biology or their ecology and we have only just started to define their distribution and their prefered biotopes. Although it is known that they are sometimes consumed by fish (see chapters on the fish), their real importance in this respect is not known. It is on the other hand evident that they are "indicators" of ancient lake conditions, but this aspect has been little studied. It is however known that they appear in dense layers at certain levels in sediment cores taken in the Huiñaimarca. This phenomenon could result from massive mortalities occurring for example at periods of sudden rises in lake level, leading to rapid anoxia in depths of 7 to 10 metres, due to decomposition of aquatic vegetation deprived of light. Such a situation has been observed within Guaqui Bay after the major rise in water level in the years 1985/86.

It therefore seems essential that detailed studics of all aspects of this component of the fauna of Lake Titicaca be carried out; even the taxonomy of the species present is not satisfactory. On this subject, in addition to the much needed study of internal anatomical structure, particular attention should be paid to the morphological variations and their causes, as the results are likely to call into question the classification presented in the present inventory.

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