VI.4f. The Ostracoda

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The study of the ostracod fauna living in Lake Titicaca began with the work of Faxon (1876) and of Moniez (1889), but about a century then went by before a new species was described (Lerner-Segeev, 1971) and more information was provided by Vargas' thesis (1982). In 1939, Beauchamp simply wrote of the material collected by the Percy Sladen Trust Expedition (he studied its Rotifera and Turbellaria): "the Protozoa, Cladocera and Ostracoda always predominate", but without any other details.

The only work providing a small amount of information on the systematics and morphology of Andean Ostracoda is that of Delachaux (1928) which deals with the Entomostraca of Lake Huaron in the Huancavelica region of Peru, a long way from Lake Titicaca. Unfortunately, the descriptions of carapace details are not sufficiently precise and because of this, the taxonomy used in this chapter is intentionally left vague so as not to uselessly increase the number of synonyms already very frequent in the literature.

The present fauna

Most of the samples collected in the Lake Titicaca basin reveal at first sight a remarkable number and diversity of species, which is comparable however with other huge ancient lake systems such as Lake Tanganyika.

The majority of species found in Lake Titicaca belong to cosmopolitan genera such as:
Herpetocypris (Family Cyprididae; Baird, 1845),
Cyprinotus,
Cypridopsis,
Potamocypris,
Candonopsis (Family Candonidae; Kaufmann, 1900),
Ilyocypris (Family Ilyocyprididae; Kaufmann, 1900),
Darwinula (Family Darwinulidae; Brady and Norman, 1889),
Limnocythere (Family Limnocytheridae; Sars, 1925),
Cyprideis (Family Cytherideidae; Sars, 1925).

C. Dejoux and A. Iltis (eds.), Lake Titicaca, 337–345.

Endemic South American genera also present are rare, only the following occur:
Chlamydotheca (Family Cyprididae; Baird, 1845),
Amphicypris.

On the other hand, it seems that Lake Titicaca fauna is over 50% endemic at the species level, particularly if one looks at the genus *Limnocythere* (Plate 2). There are however certain convergences with species described by Delachaux from Peru (1928). For example, the species *Neolimnocythere hexaceros* is very close to the species we have called *Limnocythere* sp. A3 and sp. B3, differing only in the angle of the "posterior spine."

The principal species living in Lake Titicaca are shown in Plate 1.

The distribution of communities

In the following section there follows a study of the communities of Ostracoda in relation to the major biotopes found in the lake (Table 1). Nine zones have thus been categorized, each characterized by the density (Table 2), the diversity of the fauna and relative density of each species in the association.

a. The epilittoral zone (ecozone a)

This comprises the streams and rivers that flow into the lake and whose fauna is mainly composed of the genera *Herpetocypris* and *Ilyocypris*, found only in sheltered areas where stands of *Myriophyllum* and/or *Elodea* are usually present. The total density never exceeds 100 individuals per square metre.

b. The supralittoral zone (ecozone b)

This is land liable to flooding where puddles or pools form after the waters have subsided. They harbour an abundant fauna, of up to several hundreds of thousands of individuals. Two very distinct types of populations have been noted:
Type 1 with *Chlamydotheca* and *Herpetocypris* dominant, associated with *Cypridopsis* and *Ilyocypris*.
Type 2 with a more diversified population of *Limnocythere* (2 or 3 species including *L. bradburyi*), *Ilyocypris*, *Cypridopsis*, *Potamocypris* and very large species of *Amphicypris* ($>$ 4 mm).

During periods of flooding, these animals (eggs, larval stages, juveniles

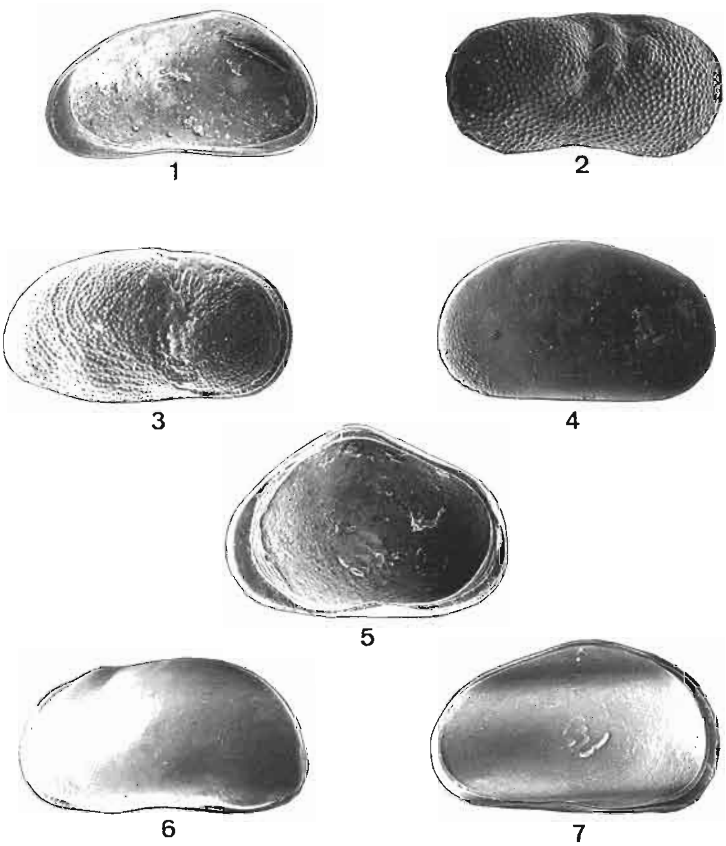


Plate 1. 1 *Candonopsis* sp. (×150); 2 *Ilyocypris* sp. (×150); 3 *Cyprideis* sp. (×93); 4 *Cyprinotus* sp. (×93); 5 *Cypridopsis* sp. (×143); *Amphicypris* sp. (×31.4); 7 *Chlamydotheca incisa* (×52.3)

and adults) can be swept into the lake and influence the shoreline community patterns.

c. The eulittoral zone (ecozone c; 0–1.10 m)

This is a transitional lacustrine zone, its faunal composition being influenced by the presence of species from the epilittoral or supralittoral zones, and/or by typically lacustrine species. The commonest association is that of *Chlamydotheca* and *Herpetocypris*, but *Darwinula*, *Limnocythere* (2 species), *Can-*

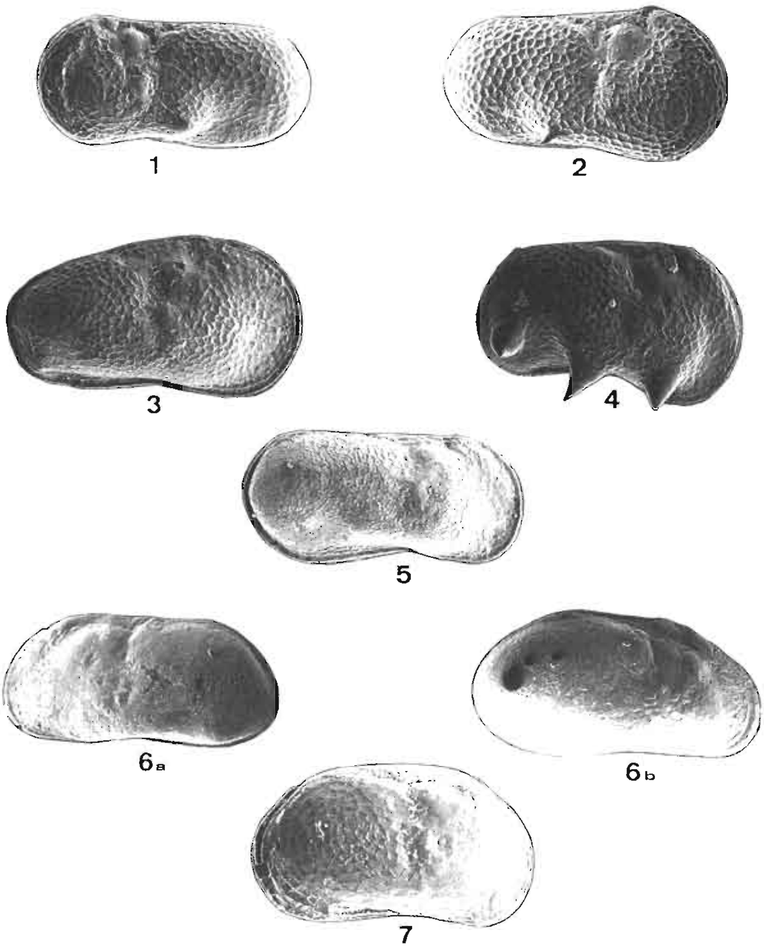


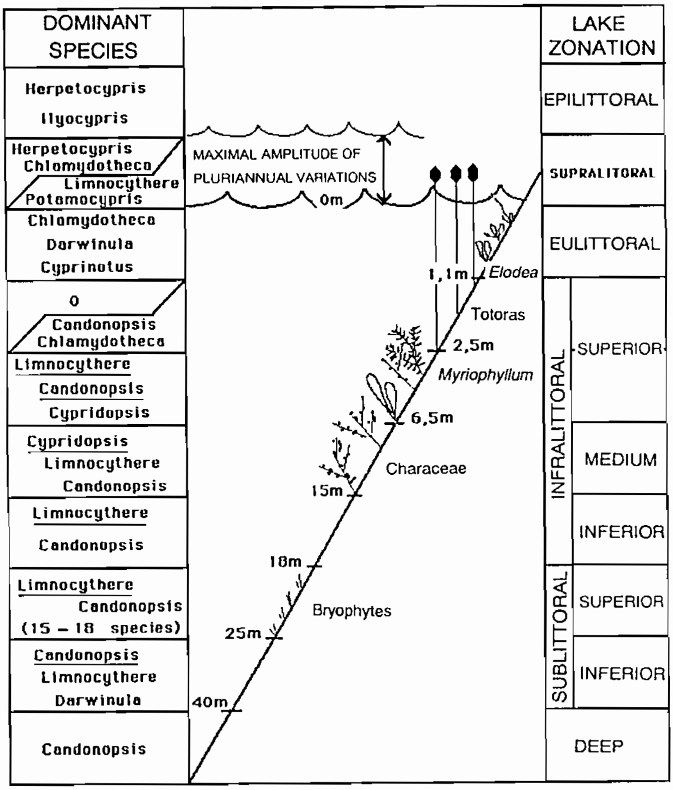
Plate 2. Genus *Limnocythere*.
1 *L.* sp. A1; 2 *L.* sp. A2; 3 *L.* sp. B1; 4 *L.* sp. B3; 5 *L.* sp. B4; 6 *L. titicaca* (×100); 7 *L.* sp. T2 (×136); 8 *L. bradburyi* (×157)

donopsis (2 species), *Ilyocypris*, *Cyprinotus* and *Amphicypris* also occur. The densities remain low (< 1000 carapaces /m^2) because of the generally coarse substrates.

d. The upper infralittoral zone (ecozone d; 1.10–6.50 m)

Totora occupies the shallower areas (1.10–2.50 m). The populations are as a general rule scanty and of low diversity. Common species are *Limnocythere*

Table 1. Distribution of the ostracod communities in Copacabana Bay (1989)



(several species), *Darwinula* and *Candonopsis*, but *Chlamydotheca* and *Herpetocypris* are also present.

In deeper water (2.50 to 6.50 m) the more or less dense macrophyte stands composed of Characeae, *Myriophyllum* and *Elodea* are inhabited by *Limnocythere* (several species), *Candonopsis*, *Darwinula* and *Cypridopsis* living amongst fragments of decaying totora (< 1000 ind. m^{-2}).

e. The middle infralittoral zone (ecozone e; 6.50–15 m)

Cypridopsis is always dominant within the stands of Characeae (over 90% of the population), often found in association with *Candonopsis*, *Darwinula* and *Limnocythere* (sp. B4 and *titicaca*). They are all characterized by the fine ornamentation on their shells.

Table 2. Ostracod density and biomass estimates in relation to habitat type. Macrophytes absent (−); sparse (− +); dense (+); very dense (+ +).

ECOZONES	MACROPHYTES DENSITY	TYPE OF SUBSTRATE	DENSITY g m^{-2}	MEAN WEIGHT µg	BIOMASS g m^{-2}
a	-	Coarse	0		0
	+	Fine	10^{2}	100	10^{-2}
b	+	F	10^{3}–10^{5}	100	0.1–10
	− +	F	10^{4}–10^{6}	40	0.4–40
c	+	G	0–10	50	0.5–10^{-4}
	+ +	F	10^{2}–10^{3}	75	75.10^{-4}–75.10^{-3}
d	+	F	0		0
	+ +	F	10^{2}–5.10^{3}	50	5.10^{-3}–0.25
e	+ +	F	10^{2}–3.10^{4}	25	25.10^{-4}–75.10^{-2}
f	-	F	10^{4}–5.10^{4}	50	0.5–2.5
g	- (bryophytes)	F	10^{5}–10^{6}	50	5–50
h	-	F	10^{2}–10^{3}	40	4.10^{-3}–10^{-1}
I	-	F	0–10^{2}	30	0–3.10^{-3}

f. The lower infralittoral zone (ecozone f; 15–18 m)

This is situated at the limit of macrophyte growth. The fauna is diversified and relatively abundant (often > 10,000 ind. m^{-2}), composed mainly of *Limnocythere* (several species accounting for 50 to 75% of the population) and *Candonopsis* (20 to 40%), but also of a few *Cyprinotus*, *Cypridopsis* and *Chlamydotheca*, rather typical of shallower waters.

g. The upper sublittoral zone (ecozone g; 18–25 m)

Bryophytes are the only plants that grow here. The Entomostraca fauna is very rich (100,000 to 1000,000 individuals per square metre) and very diverse (15 to 18 species) with a majority of *Limnocythere* group A (75 to 90%) and *Candonopsis* (5 to 20%). On the other hand, genera like *Cypridopsis* and *Chlamydotheca* have altogether disappeared.

Table 3. Comparison of the depth zonation of ecozones in the Lago Grande and Lago Pequeño (1989).

ECOZONES	LAGO MAYOR	LAGO MENOR
a		
b	0 m	0 m
c	1.1 m	0.8 m
d	2.5 m	2.5 m
e	6.5 m	3.5 m
f	15 m	7.5 m
g	18 m	?
h	25 m	9 m
i	40 m	14 m

h. The lower sublittoral zone (ecozone h; 25–40 m)

This extends down to around 40 m depth. Ostracoda are still numerous but the species diversity has declined. *Limnocythere* gr. A (40 to 60%), *Candonopsis* (30 to 50%), *Darwinula* and *Amphicypris* are found here.

i. The profundal zone (ecozone i; beyond 40 m)

Only *Candonopsis* survives here (< 100 ind. m^{-2}) but a few empty shells of *Limnocythere* gp. A and *Darwinula* are present in the sediment, suggesting that these two species can live at this depth during certain seasons or that they arrived there after death.

Ecology

The description of the distribution of Ostracoda communities that has just been described reflects the situation as found in the Lago Grande (Copacabana Bay) during 1989.

It is applicable however to most of the lake, with the exception of gently sloping bays such as Achacachi and almost all of Lago Huiñaimarca. In the latter environments the associations are much the same but their depth zonation is different and ecozones e, f, g, h and i (Table 3) are compressed.

There are however numerous exceptions to the model, resulting from local environmental conditions and from the ecology of these entomostracans. To survive and reproduce they require particular substrate conditions, the presence of shelter, good oxygenation, food and a particular chemical composition of the water – factors that vary spatially over the lake and in time.

The density of these microcrustaceans is related to the presence or absence of vegetation and even its density. For ostracods the proximity of plants means shelter and also food (plant detritus and associated periphyton). Photosynthetic activity by submerged macrophytes also provides conditions of oxygenation in the water ideally suited to secondary consumers. On the other hand, bacterial decomposition of the abundant plant and animal remains leads to an under-saturation of dissolved oxygen at the sediment-water interface and tendency for the pH to become acid, factors unfavourable for benthic life.

As a consequence several types of habitat need to be distinguished to explain the spatial distribution of ostracods:
- very dense macrophyte stands
- open macrophyte stands
- bare sediments.

In the midst of a very dense stand of vegetation, benthic life *sensu stricto* is limited by the lack of oxygen and only a few undemanding species can live. These are mainly *Limnocythere* (sp. A1, sp. B4 and *titicaca*) and *Candonopsis*, with occasional *Darwinula*. On the other hand, free-swimming species not dependent on the substrate are very abundant. In the Characeae these are *Cypridopsis* and in the *Myriophyllum* and *Elodea*, *Chlamydotheca* and *Herpetocypris*.

In a sparse stand of vegetation, life is possible at all levels and benthic and swimming ostracods are fully represented:
- the benthic forms by *Limnocythere*, *Candonopsis*, *Darwinula* and *Ilyocypris*,
- the swimming forms by *Chlamydotheca* and *Herpetocypris*. *Amphicypris* is also present in this environment as a predator.

Only benthic forms live on bare substrates. This type of environment is found either in the supralittoral zone (temporary pools) or in the "profundal" zone (below 25 m in Lago Grande and 9 m in Lago Huiñaimarca). In the first case, *Ilyocypris* dominates the community; in the second, species such as *Limnocythere* (sp. A1) and *Candonopsis* not requiring high oxygen concentrations.

At first sight it seems that many species occupy the same biotope, but in reality interspecific competition is avoided as much as possible. For example, two periods of maximum biomass have been observed for the swimming forms: December-January and July-August, but with a delay of 2–3 weeks for *Chlamydotheca*. This latter prefers to inhabit the tops of plants whilst *Herpetocypris* stations itself on the lower parts. Of the benthic forms, *Limnocythere* lives in the top few centimetres of liquid sediment whilst *Ilyocypris* moves over the substrate surface. It is also likely that various species, of *Limnocythere* for example, do not seek the same prey, by selecting particular types and sizes of the particles.

The density of microcrustacea is also related to the trophic status of the lake and the annual range of variation in water level. In the supralittoral zone these fluctuations result in changes in chemical composition of the water. The water is oligohaline in periods of high water level, but becomes progressively more concentrated as the water subsides. Genera such as *Chla-*

mydotheca, *Herpetocypris* and *Ilyocypris* are the first to colonise temporarily-flooded habitats. These are then replaced by *Potamocypris*, *Cypridopsis* or *Amphicypris* when the total salinity exceeds 1.5 g l^{-1}, and then finally by a single species (*Limnocythere bradburyi*), the only one capable of reproducing in waters where the salinity can exceed 30 g l^{-1}.

Changes in lake level also have repercussions on the entire benthos down to the deepest areas. A period of high water level, by favouring water and detritus circulation leads to a proliferation of benthic organisms, particularly in ecozones f and g. A period of declining lake level would have the opposite effect. This distinction between high and low water levels occurs at the seasonal scale: for example the growth of ostracod populations in ecozones h and i is directly correlated with two factors, firstly the supply of fresh organic material coming from shallower zones, and secondly the dissolved oxygen concentration, factors related to the lake's metabolic cycle and induced by the alternance of wet and dry seasons.

As a general rule, the development of ostracod populations appears to be very dependent on the cycle of plant growth in the macrophyte stands, itself related to hydrological changes in the lake under the influence of meteorological factors. The influence of these abiotic factors is more pronounced in the littoral and supralittoral ecozones, but is still felt in the the profundal zones of the lake ecosystem. An increase in lake volume results in a beneficial effect on the benthic fauna of ecozones f, g, h and even i, whereas falling water level brings about a rapid decrease in the density and diversity of the entomostracan fauna.

Conclusions

The numerous observations made between 1977 and 1989 have provided information on the depth distribution of ostracods, related partly to that of the macrophytes and also to the relationships between these organisms and the hydrological cycles existing in Lake Titicaca at two distinct time scales: annual and long-term. The present day data serve as a reference for a palaeoecological interpretation (see Chapter III.1) providing a reconstitution of changes in lake level in Lake Titicaca over the last 7500 years. This information will also serve as the basis for a statistical analysis (transfer functions between Ostracods/Water Depth and Ostracods/Water Chemistry) which will provide a quantitative assessment of the physico-chemical evolution of the lake in terms of water level and total salinity over the Holocene.

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