Historical Changes in the Environment of Lake Titicaca: Evidence from Ostracod Ecology and Evolution

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I. SUMMARY

Lake Titicaca is a high-altitude, nearly closed, basin lake in the tropical belt of South America. The lake is subjected to the influence of the intertropical convergence zone (ITCZ) during the summer months, and is characterized by a flora and fauna that, while not as diverse as that of many other ancient lakes, nevertheless has groups such as molluscs and ostracods which show a fascinating ecological and morphological variability (polymorphism). For these and other groups, Lake Titicaca is an ideal natural laboratory for studies of evolution.

This chapter demonstrates how, by applying transfer functions to quantitative information on the response of extant ostracod communities to habitat heterogeneity and environmental variability, past environments of Lake Titicaca can be reconstructed. Results show the recent history of Titicaca (since 8000 ^{14}C years bp) to have been characterized by major lake-level fluctuations which separated the basin into three palaeolakes at various intervals of geological time, and which have possibly influenced population

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dynamics in the lake for groups such as fishes, molluscs and ostracods. The high-amplitude palaeoenvironmental variations indicated by the transfer function also seem to have had important effects on the dynamics of ostracod populations.

Special attention is given to the formation of habitats and evolution of the lake ecosystem during the past 10 000 years, with particular emphasis on the ostracod crustaceans within the subfamily Limnocytherinae, a key ostracod group in the central Andes, and their highly variable carapace morphology. It is possible to distinguish among several morphs (or subspecies?) within this group, but the overlap is significant and individuals are sometimes difficult to classify. Accordingly, while taxonomic identifications remain based on external carapace morphology only, it is impossible to propose a definitive hypothesis for phylogenetic relations in the Andean limnocytherinid flock and its taxonomic structure. Even so, preliminary surveys of this group beyond the Lake Titicaca basin and adjacent areas suggest that the actual Titicaca fauna is not an isolated lineage, but part of extensive radiations which span the entire Andes. The observed differences between extant ostracod communities of Lake Titicaca and lakes Huaron and Junín can be explained by differential effects of the ITCZ, which produced distinct climatic regimes during the Holocene and resulted in different evolutionary pathways for the respective faunas of these lakes. This evolution appears to be more uniform in the case of Lake Junín, probably because of its closer proximity to the equator (and hence a lower exposure to the influence of the ITCZ) than Lake Titicaca.

II. INTRODUCTION

Lake Titicaca is located on the Andean high plateau (Figure 1), and is the largest and oldest of a series of high mountain lakes and temporary lakelets scattered from north to south along the Andean Cordilleras. These lacustrine environments are home to abundant and diverse ostracod populations, whose wide geographical distribution and subtle ecological requirements make them ideal ecological indicator organisms. Accordingly, the ostracods are a favoured group used by biologists in the reconstruction of palaeoenvironments, and are especially useful in the reconstruction of the water chemistry, temperature and trophic dynamics of lakes. The first goal of this chapter is to demonstrate how information from transfer functions applied to extant lacustrine ostracod assemblages can be used to infer past limnological changes in Lake Titicaca. The second goal is to demonstrate and examine the ecophenotypic variability of carapace characters within the Limnocytherinae, one of the most abundant ostracod groups in South American inland waters (Martens and Behen, 1994), in relation to environmental changes.

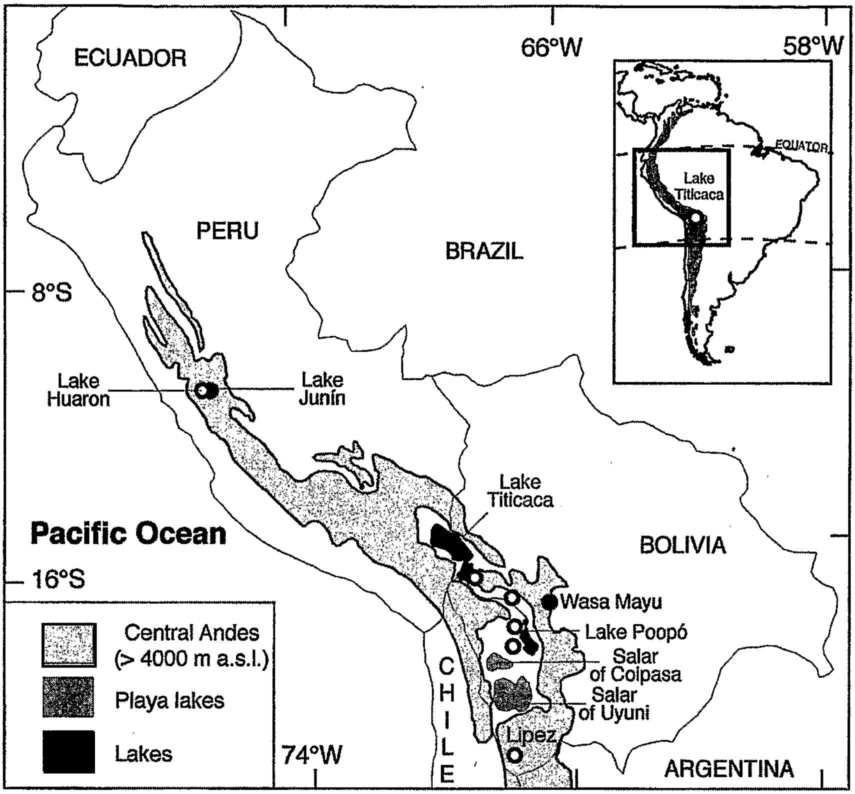

Fig. 1. Map of the central Andes showing localities of ostracod samples referred to in this study. Modern samples (open circles): Lake Huaron, Peru, Lake Titicaca and surroundings, Lake Poopó and adjacent lacustrine systems, South Lipez lakes; and fossil samples (closed circles): Lake Junín, Peru, and Wasa Mayu, Bolivia.

III. LAKE TITICACA: GEOLOGICAL SETTING, REGIONAL CLIMATE AND LIMNOLOGICAL CHARACTERISTICS

Lake Titicaca is a large (*c.* 8000 km^2), warm, monomictic lake (Lazzaro, 1981) that extends between 16°15′ S and 17°30′ S latitude and 68°30′ W and 70° W longitude, at an altitude of *c.* 3809 m. It is located in the northern part of the Altiplano, a 200 000 km^2 intermontane endorheic basin which formed during the Pliocene and Early Pleistocene, some 3–2 Mya, in the central Andes of Peru, Bolivia and Argentina (Lavenu, 1992). The Pleistocene was marked by periodic advances and retreats of glaciers, and these resulted in high-amplitude fluctuations of lacustrine basins (Servant and Fontes, 1978; Lavenu *et al.*, 1984; Mourguiart *et al.*, 1997). The present-day altiplanean climate is dominated by typical tropical wet–dry seasons and local orographic effects, induced by the seasonal latitudinal movements of the intertropical convergence zone (ITCZ).

From November to April, the ITCZ envelops the central Andes. During this period, the warm, moist Amazonian air penetrates the eastern Cordillera from the north-east, bringing stormy rains and causing a steep rainfall gradient between the north and the south (Roche *et al.*, 1992).

The lake drains to the south via the Río Desaguadero to Lake Poopó, a saline lake at an altitude of *c.* 3686 m (Figure 1), and is divided into three main basins (Figure 2). The northern basin, Lake Chucuito, has a maximum depth of *c.* 285 m and is separated from the two southern basins, which combine to form Lake Huiñaimarca, by the Tiquina Strait (Figure 2). The total dissolved salt concentration varies from 0.9 g l^{-1} in Lake Chucuito to 1.2 g l^{-1} in Lake Huiñaimarca. The waters are dominated by chloride, sulphate and sodium ions, with mean pH values around 8.5 (Carmouze *et al.*, 1981, 1992). Water clarities are greater in Lake Chucuito (Secchi disc mean values between 11.3 m and 14.6 m) than in Lake Huiñaimarca (mean values from 3.2 m to 5.6 m) (Iltis *et al.*, 1992).

Lake Titicaca is characterized by some flat shallow areas (Puno and Achacachi bays in Lake Chucuito, and Lake Huiñaimarca), steep escarpment margins (flanks of Lake Chucuito) and flat profundal areas (central part of Lake Chucuito). These different habitat types support different macrophyte communities. A depth-related zonation of macrophytes is also present, and this creates well-defined habitats for benthic communities. According to Collot *et al.* (1983), in Lake Huiñaimarca, at depths from 0.2 m to 2.5 m the emergent *Lilaeopsis* and *Hydrocotyle* growth along the beach shore is replaced by an aquatic macrophyte assemblage of *Myriophyllum, Elodea, Ruppia* and *Potamogeton.* From 2.5 m to *c.* 4.5 m depth *Schoenoplectus tatora* (an emergent sedge of the family Cyperaceae) dominates, and from this depth down to *c.* 7.5 m, dense mats of Characeae species occur. Beyond this there is a zone of *Potamogeton* settlement extending down to 9 m, which is the limit of the photic zone. These macrophyte belts extend all around Lake Titicaca, but some bathymetric differences between basins are known, related mainly to bottom sediment characteristics and light penetration (Iltis and Mourguiart, 1992).

The macrophyte belts provide food and refugia for a variety of invertebrates, which themselves provide potential food for fishes. In turn, the distribution and depth zonation of aquatic macrophytes influence the distribution of associated invertebrate animals. This is illustrated for one group, the ostracods, in Figure 3. Unfortunately, very few ecological studies have been conducted in this remarkable ecosystem, the sum of which has been compiled by Dejoux and Iltis (1992). Rudimentary taxonomic studies have been carried out for several invertebrate groups (e.g. Amphipoda, Cladocera, Copepoda, Mollusca and Ostracoda), among which molluscs and amphipods are the most abundant (Dejoux, 1992), but many taxa remain poorly known or undescribed.

The native fish fauna in the lake is well documented and comprises 26 species, contained within only two genera, *Orestias* and *Trichomycterus* (Lauzanne, 1982, 1992; Parenti, 1984). In the 1940s and the 1950s, two alien species were introduced into the lake as food fish; the rainbow trout

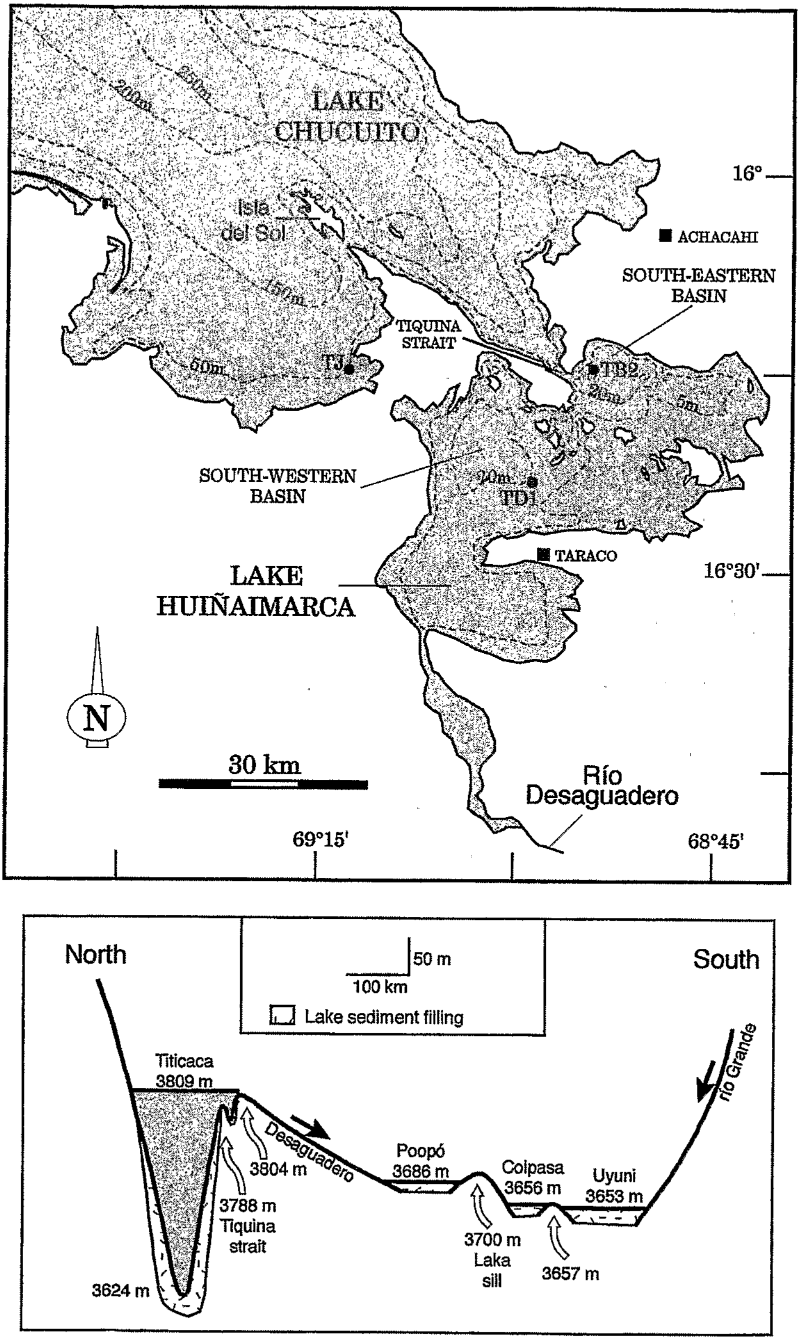

Fig. 2. Bathymetric map of present-day Lake Titicaca, with the three main basins. The lower figure indicates the main communication between basins along the Altiplano.

Oncorhynchus mykiss from North America and the pejerrey *Basilichthys bonariensis* from Argentina. The establishment of these two non-native species has drastically affected the composition and diversity of the natural fish communities. Several endemic species of the genus *Orestias* are now considered endangered or extinct (Lauzanne, 1992), but much more work is needed to determine fully the impact of these introductions on the functioning of Titicaca's ecological communities and ecosystem.

IV. THE OSTRACODA

A. The Ostracod Communities

Ostracods are small, bivalved crustaceans that are abundant in both benthic and periphytic habitats within Lake Titicaca. Their calcified carapaces have an average length of about 1 mm and completely envelop the soft parts. Their carapace valves fossilize readily and constitute common microfossils in cores from lake sediments. Most species are easily identifiable from their carapace and this, combined with the fact that most species are strongly stenotopic, makes the group useful as proxies to reconstruct past environments. In the Altiplano, the large number of aquatic environments, distributed over a hydrologically and climatically diverse area, provides ideal circumstances for comparative studies of ostracod ecology and evolution.

B. Ostracod Distribution Patterns

Field surveys have revealed that modern Lake Titicaca is home to about 50 species of ostracods (Lerner-Seggev, 1973; Mourguiart, 1987, 1992; Carbonel *et al.*, 1990; Mourguiart and Roux, 1990; Mourguiart and Carbonel, 1994), and that the abundance and species composition of extant ostracod assemblages changes from the shallow littoral habitats to the deeper environments (Figure 3). This change is due to both abiotic and biotic factors, such as hydraulic energy level (which acts on the nature of the substrate), oxygen levels at the water–sediment interface, macrophyte cover and food supply. At the landward edge and in the shallower waters of Lake Titicaca (less than 2 m water depth), the ostracod community is dominated by species adapted to unstable conditions. This zone is characterized by maximum physical disturbance (wave action), seasonal water-level fluctuation and wide temperature variation, and here periphytic genera such as *Chlamydotheca* and *Herpetocypris* are always dominant. Within the dense mats of *Schoenoplectus*, which occur at *c.* 2.5–4.5 m water depth, conditions at the water–sediment interface are generally anoxic and this prevents colonization by benthic ostracod species; periphytic species, however, are present on the *Schoenoplectus* stems. In less dense mats, one can occasionally find species well-adapted to poorly oxygenated waters (e.g.

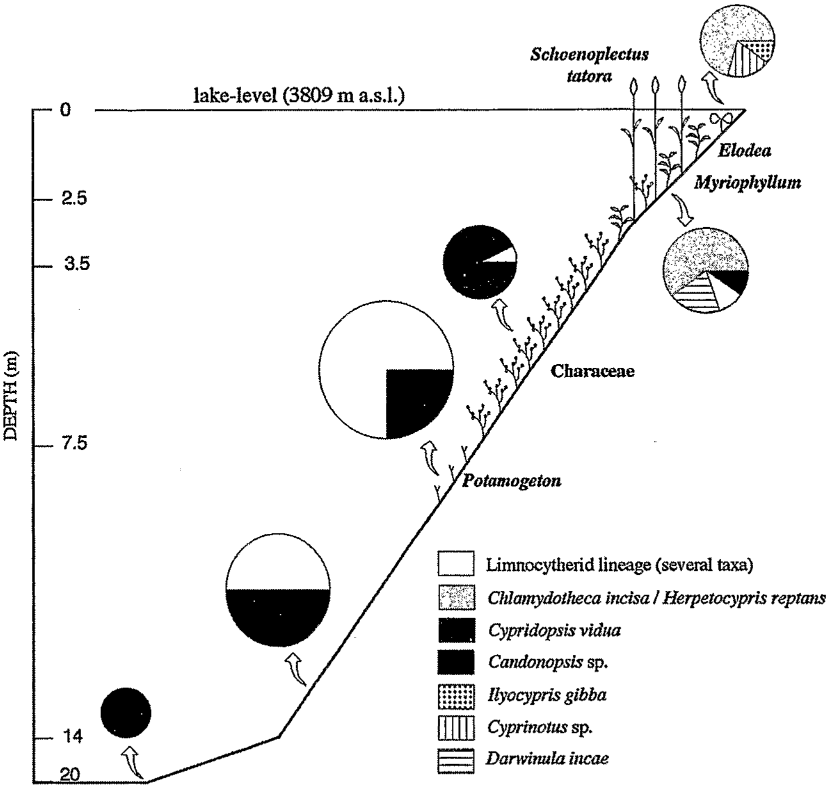

Fig. 3. Ostracod assemblages in relation to macrophyte distribution in Lake Huiñaimarca. The size of the circles is proportional to the density of ostracods. The dominant macrophyte community is indicated in bold type. Modified from Wirrmann and Mourguiart (1995).

Candonopsis sp. and *Limnocythere* sp. A1). At 4.5–7.5 m the ostracod community of Lake Titicaca is poorly diversified: this is in stark contrast to the situation in most lacustrine systems where this bathymetric zone is characterized by high species richness and density. The ostracod assemblages found on and in sediment substrates are dominated by *Candonopsis* sp., *Limnocythere titicaca* and *Darwinula incae*, whereas *Cypridopsis vidua* occasionally occurs at high densities on plant stems. This relatively low species richness is explicable in terms of the low habitat diversity provided by the dense Characeae mats which dominate this depth zone, and the low ambient oxygen concentrations at the water–sediment interface. Just below this zone, species richness and abundance of ostracods increase dramatically down to approximately 10 m. This limit is a function of water clarity and so varies between Lake Chucuito (up to 25–30 m) and Lake Huiñaimarca (*c.* 10 m) (Mourguiart, 1992). Thereafter, at progressively greater depths the diversity and abundance of ostracods decrease slowly, until dropping sharply at the limit of the thermocline, where only low oxygen-tolerant species are present (e.g. *Candonopsis* sp., *Limnocythere* sp. A1 and *L.* sp. A2).

To the south, the effects of the ITCZ are reduced and the lakes become progressively more saline. This is because solute residence time increases as precipitation declines and evaporation increases. In these more saline lakes the most common benthic species are *Cyprideis salebrosa* and *Limnocythere bradburyi* (Mourguiart and Carbonel, 1994; Mourguiart and Corrège, 1998).

This brief section has summarized the extent of the present level of knowledge about this fascinating example of ecological zonation in Lake Titicaca. Clearly, further extensive fieldwork in this and other altiplanean lacustrine ecosystems is merited.

C. Intraspecific Variation

The benthic ostracod community of Lake Titicaca is endemic, whereas periphytic species found there are widespread, occurring also in marshes, springs, or permanent and temporary lakes. Among the species present, the members of the subfamily Limnocytherinae are of particular interest because they exhibit an impressive plasticity in external valve morphology, which is believed to be at least partly environmentally induced (e.g. Mourguiart, 1987; Peypouquet *et al.*, 1987; Carbonel *et al.*, 1990). Furthermore, most of the other species not in this subfamily appear to be more widespread (e.g. *Candonopsis* and *Amphicypris*): in South America, four genera (*Limnocythere, Neolimnocythere, Pampacythere* and *Paracythereis*) and 19 species are presently recognized (Martens and Behen, 1994; Mourguiart and Corrège, 1998).

Because ostracods are very sensitive to strong short-term fluctuations within habitats, they can be used to reconstruct the past limnological conditions of Lake Titicaca during the Holocene epoch (the past 10 000 years). The present-day Titicacan limnocytherinid lineage includes at least four different species, divided into perhaps two distinct genera, and occurring always in discrete microhabitats. The polymorphism displayed by this fauna can be related to ecophenotypic variations under the control of environmental factors such as depth or salinity, and well-defined forms, differing in their carapace shape and ornamentation, are here regarded as "entities". Thus, ecophenotypic morphs, subspecies or species are all considered as entities in the transfer function database, under the criterion that each entity occurs only in a discrete and well-defined habitat type.

D. Methods

Since the pioneering work of Imbrie and Kipp (1971), many attempts to quantify the relationships between biological data and the environment have been made. Researchers have used data on such varied organisms as pollen, beetles, diatoms and molluscs to reconstruct past environments (e.g. Gasse, 1994; Guiot, 1994). Most modern approaches towards reconstructing palaeoenvironments utilize transfer functions, a method whereby values of an environmental variable can be expressed as a function of species data (ter Braak, 1995). In the present study, transfer functions are applied to extant ostracod communities in order to infer past lake levels and climatic changes in Lake Titicaca. Lake-level fluctuations are also reconstructed by subjecting this data to factor analysis of correspondence (FAC).

Fourteen cores were sampled in Lake Titicaca using a Mackereth corer (Barton and Burden, 1979). Radiocarbon dates on carbonated deposits were obtained on six of these cores, either conventionally or by accelerator mass spectrometry. However, three of these cores (TD1, TB2 and TJ) provided records extending back to *c.* 25 000 years bp (Wirrmann and Mourguiart, 1995) and this chapter will henceforth focus on findings and interpretations from these cores only (Figure 4). The lowest section of the lake sediment cores contains no ostracods; in most cores the faunas do not begin to appear until after about 8000 years bp. The absence of ostracods during isotope stage 2 (the last glacial maximum, LGM) has been interpreted in terms of ambient physicochemical conditions having been unfavourable to calcified organisms: the climate was much colder and water pH was low (Mourguiart *et al.*, 1995). In general, ostracod density was between 100 and 50 000 individuals cm^3 of core sample. Ostracod relative abundances and assemblages, defined by examining at least 300 adult specimens per sample, indicated that members of the Limnocytherinae comprised *c.* 50%, 20% and 80%, respectively, of the ostracod assemblages in the three most complete cores (Mourguiart, 1987; Carbonel *et al.*, 1990; Mourguiart *et al.*, 1998). It should be noted, however, that most periphytic ostracod species have such thin shells that normally they do not fossilize. A complete listing of all the ostracod species recovered and their ecological requirements is given in Mourguiart and Roux (1990) and Mourguiart and Carbonel (1994). Because the present study considers only the species preserved in sediments, among the 115 modern samples available, only 28 taxa from nine genera are subjected to statistical analysis.

Seventeen "environmental" categories were determined according to the results of a first FAC by combining (i) five ranges of water depth, (ii) four ranges for the total dissolved salts, and (iii) four ranges for the Mg:Ca ratio in the water. A second FAC was then run by incorporating two matrices, which corresponded to the 115 modern samples and the fossil samples for a given core, respectively (Mourguiart and Roux, 1990; Mourguiart *et al.*, 1998). The product of these three matrices was then subjected to reciprocal averaging and a multiple linear regression (MLR) was then run for the three environmental parameters. The MLR produces a mathematical formula linking the environmental parameters to the relative abundances of ostracod species. Results validating the transfer function are discussed in detail elsewhere

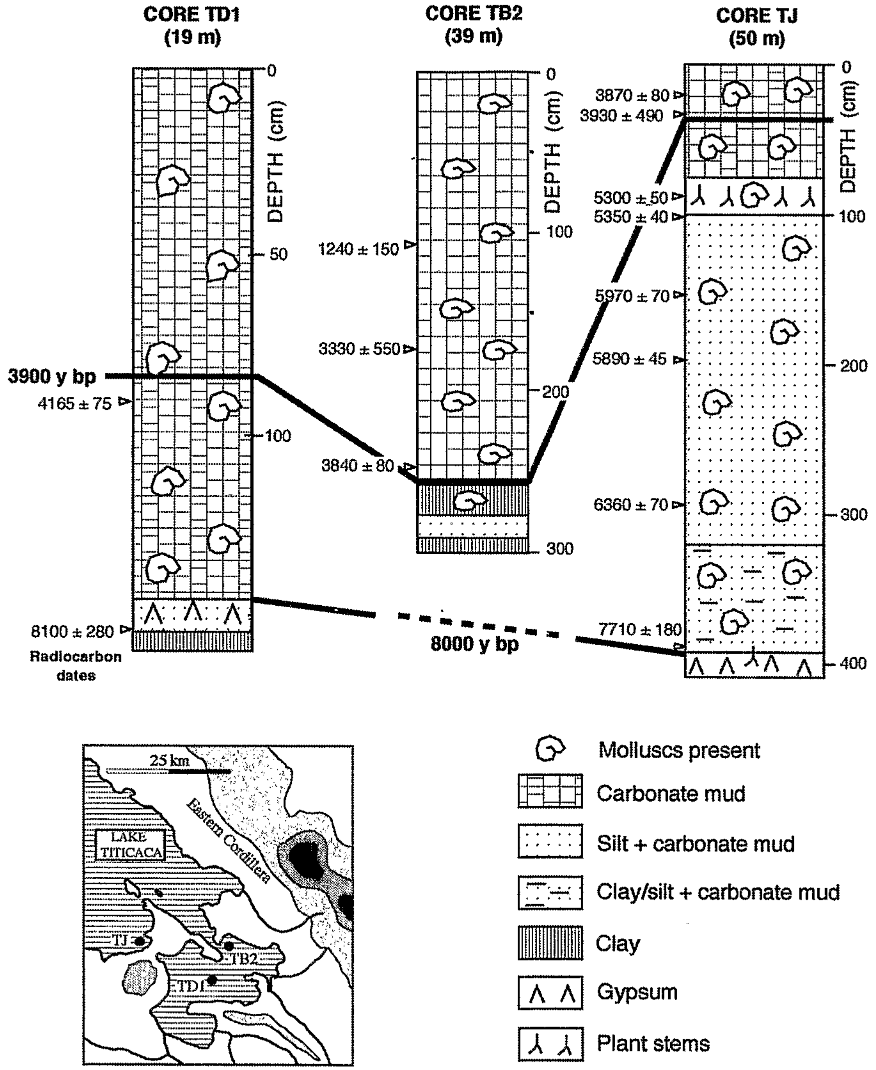

Fig. 4. Principal correlations between cores TD1, TB2 and TJ, based on lithological stratigrahy and radiocarbon dates. Inset map shows the location of the coring sites in the present Lake Titicaca.

(Mourguiart and Roux, 1990; Mourguiart and Carbonel, 1994; Mourguiart *et al.*, 1992, 1997, 1998) and only a summary of the most important findings is presented here (Figure 5).

According to the two first factors, which represent more than 40% of total information or variance (Figure 5b), four separate groups, corresponding to different environment types, can be distinguished (Figure 5a). Plots of residuals given by the MLR results show that the estimates are within ± 0.82 m of the water depths measured in the field, with a corresponding correlation coefficient of 0.98 (Figure 5c). Further, it is important to emphasize that there is good correspondence between the modern samples and the fossil ones. This high

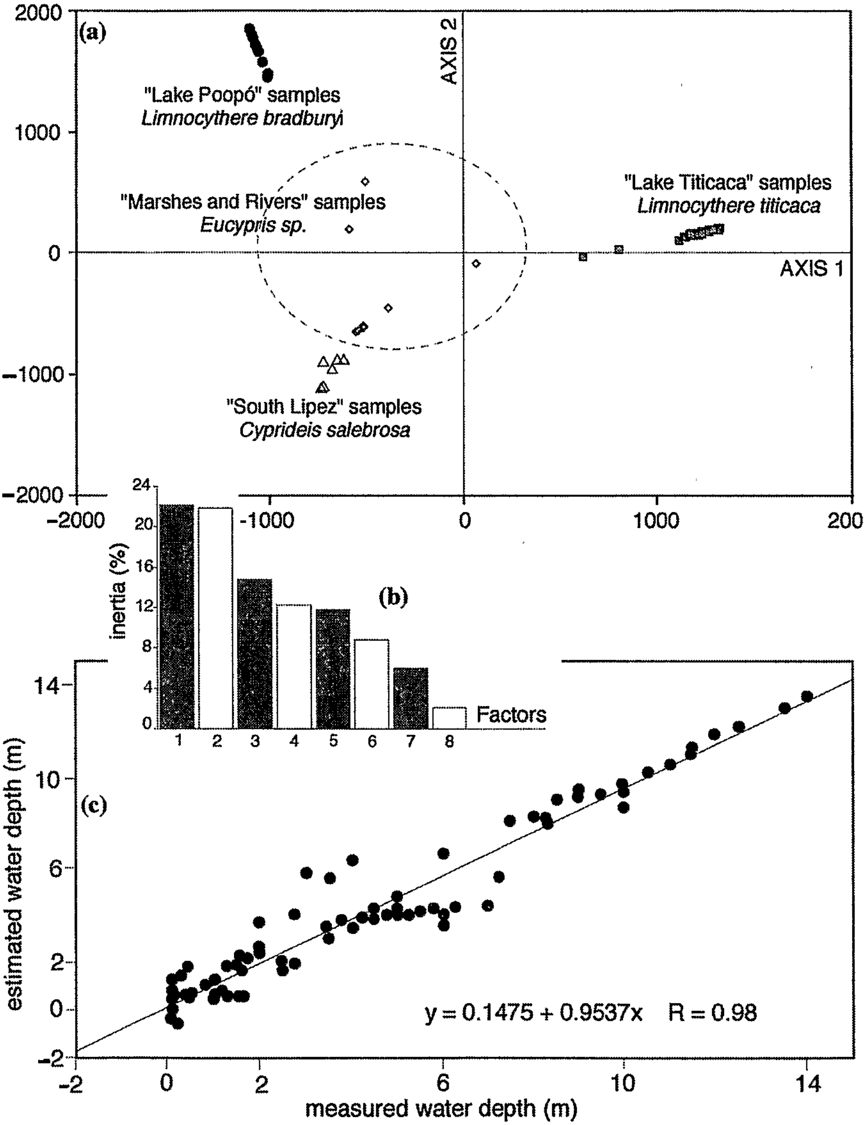

Fig. 5. Main results of the transfer function. (a) Correspondence analysis of modern data as passive elements. For each group, a representative species is given. (b) Factor weightings. (c) Estimated versus measured water depth for the 115 modern samples. Modified from Mourguiart and Carbonel (1994).

reliability of these data means that by applying transfer functions to extant ostracod assemblages at least three ecological variables can be quantitatively reconstructed: (i) depth, (ii) salinity, and (iii) Mg:Ca ratio of water.

The aim here is to advocate, through example, the usefulness of the above approach in reconstructing palaeoenvironments in Lake Titicaca, and perhaps also in other ancient lakes. Therefore, for the purpose of simplicity and clarity, only one factor, water depth, is considered, because it appears to be the most reliable parameter and the easiest one to correlate from core to core. Details and analyses of other factors are given in Mourguiart *et al.* (1998).

V. RESULTS

Transfer function results from three cores retrieved from the three main basins of Lake Titicaca are presented in Figure 6. Palaeolake levels indicate a complex evolution of the three basins, showing in particular the occasional isolation of separate basins (Figures 6 and 7). Some major phases are also evident. From about 8000 to 3900 ^{14}C years bp, the lake levels fluctuated around a mean position of about 3765 m for Lake Chucuito and about 3790 m for the south-western basin (data obtained from cores TJ and TD1). During this period, in the south-eastern basin (Lake Huiñaimarca, core TB2) there are no ostracod fossils in the sediments, except in one level which contains species such as *Potamocypris, Strandesia* and *Cypridopsis*. This association is found today only in pond habitats, and indicates that between 8000 and 3900 ^{14}C years bp, this part of Lake Huiñaimarca corresponded to a very shallow lacustrine environment (Figure 7). At 3900 ^{14}C years bp, the water levels of the three lakes rose drastically. However, evidence suggests that the present-day lake level was not reached until after 680 ^{14}C years bp (Mourguiart *et al.*, 1998).

Detailed analysis of relative abundance of the subfamily Limnocytherinae from the three primary cores (Figures 8–10) reveals different patterns within each of the three basins. These patterns are not fully explicable in terms of water-depth or water-quality differences, and suggest that the three basins should be considered as having been discrete entities throughout most of the Holocene. The Limnocytherinae recovered from core TJ (Figure 8) are more highly diversified than those found in cores TB2 and TD1 (Figures 9 and 10). Separation of the two lineages of the most common species (*Limnocythere* groups A and B)* is based on carapace shape morphology: *Limnocythere* group

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*These closely related pairs of species are similar to males (*L.* sp. B1) and females (*L.* sp. A1) of *L. grafi*, a species from a palaeolake in the Cochabamba region of Bolivia, described by Purper and Pinto (1980). The confusion of these latest authors is probably due to the poor quality of the preserved material in the sediments that they examined. It is evident that for further clarification of the presently confused systematics of *Limnocythere*, a new synthesis of data from different analytical methods and sources (e.g. soft parts) is necessary.

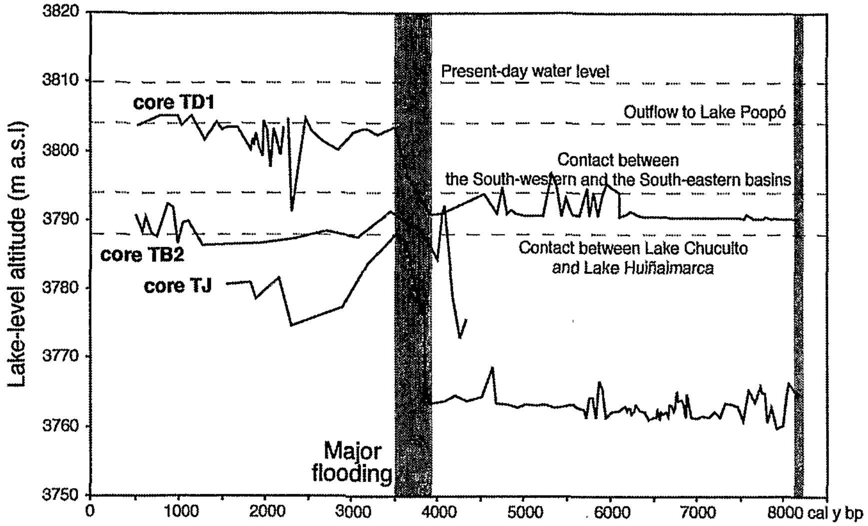

Fig. 6. Lake-level evolutions for the three basins reconstructed from multiple linear regression on the ostracod faunas. All radiocarbon dates were calibrated using the Calib 3.0 program (Stuiver and Reimer, 1993). Between two dated horizons, the ages were calculated by linear interpolation, with the exception of the lowermost and uppermost layers where ages were extrapolated from adjacent intervals. The horizontal broken lines indicate altitudes at which connection was possible between basins. The vertical shaded areas indicate major changes in the evaporation:precipitation ratio. Modified from Martin *et al.* (1997).

B have a more developed flat anterior margin and in dorsal view they appear narrower than do *L.* group A individuals (Carbonel *et al.*, 1990). Both sexes are always present. In Lake Titicaca, these two lineages show an extraordinary morphological variability, and often more than one type or morph is present in a sample. Previous studies (Mourguiart, 1987; Carbonel *et al.*, 1990) have referred to them as "polymorphic" populations, and the same terminology is used here (Figure 11). Sixteen morphs are present in core TJ (four for group A and 12 for group B), whereas only three morphs are present in cores from Lake Huiñaimarca (two for group A and one for group B).

An important aspect of polymorphism concerns the external morphology of the carapace. The observed polymorphism is manifest in differences in reticulation, nodation, spinosity, microconation and size. However, the most spectacular morphological variability seen in this group is in the development of spines. Four morphs belonging to *Limnocythere* "group B" are characterized by having no, two, six or eight spines (Figure 11). The spiny morphs are not found in present-day altiplanean lacustrine environments and can be considered as extinct. In modern Titicaca, another morph belonging to the same lineage (perhaps the same species) is very similar to the six-spined morph,

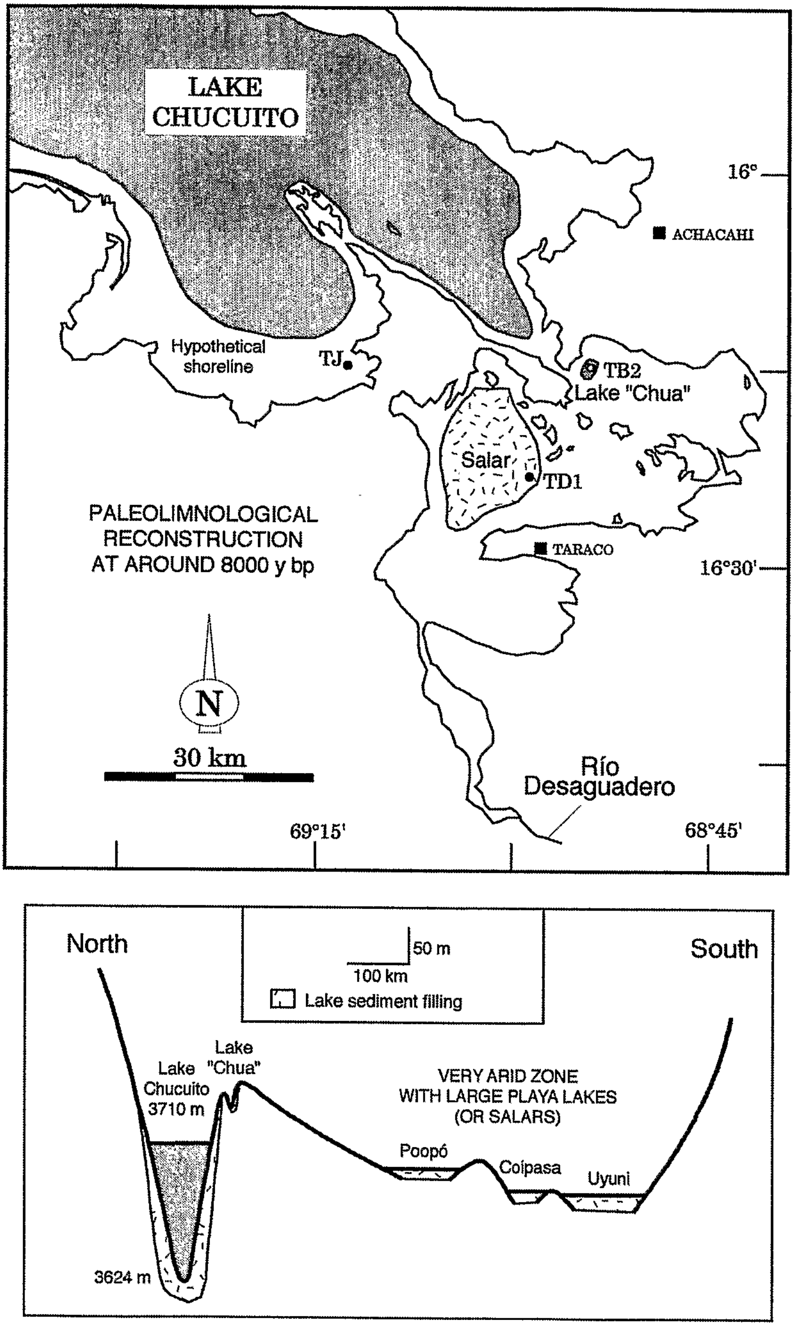

Fig. 7. (Upper) Hypothetical reconstruction of the three basins at 8000 years bp and (lower) corresponding transect along the Altiplano.

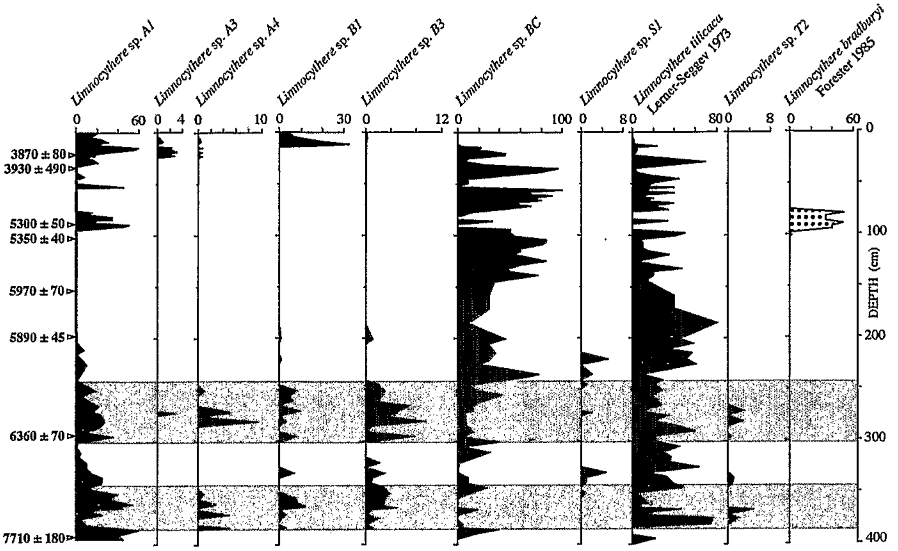

Fig. 8. Distribution of the different Limnocytherinae morphs and species for core TJ. The shaded zones highlight periods of major development of polymorphism. In the figure, the presence of brackish to saline species is indicated by stippled shading.

but displays an atrophy and a different shape of spine (Figure 11). Another very similar species, *Neolimnocythere hexaceros*, has been described from Lake Huaron, Peru (Delachaux, 1928), and in Holocene sediments from Lake Junín (Peru) (De Deckker, 1987; Mourguiart, unpubl.), but this form shows relatively large differences in the length, shape and direction of the spines (cf. Figure 11). These similarities lend support to the hypothesized close phylogenetic affinity between the limnocytherinid species of Lake Titicaca and those of Lakes Huaron and Junín.

VI. DISCUSSION

It is widely accepted that the contemporary biodiversity of South American tropical rainforest has been affected by climatic events during the Pleistocene. In particular, during the LGM, some 20 000–18 000 years bp, the Amazon Basin was believed to have contained widely separated "islands" of forest, which served as refugia for plants and animals (Prance, 1982). The high diversity of the South American rainforest was thus explained by the presence of these numerous perennial refugia. However, recent studies (Ledru *et al.*, 1998) have shown that the Amazon Basin was actually very arid during the LGM and have refuted the refugia hypothesis. In addition, several workers

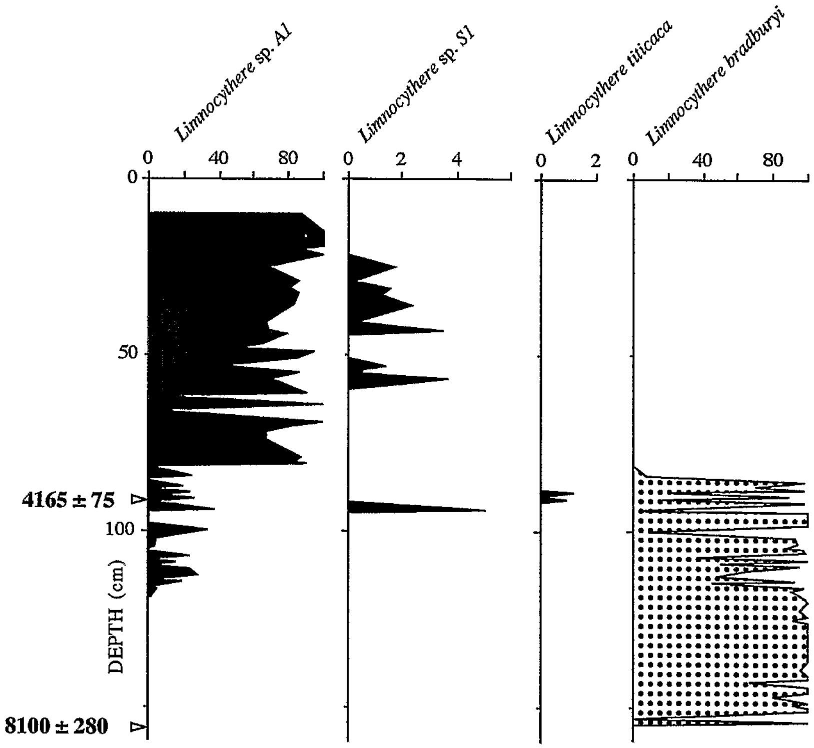

Fig. 9. Distribution of the different limnocytherinid morphs and species for core TB2. Stippled shading denotes the presence of brackish to saline species.

have identified short-term dry events during the Holocene (e.g. Turcq *et al.*, 1998). An alternative hypothesis to explain the high biodiversity of this area is needed. Evidence from reconstruction of ancient ostracod communities offers one such scenario, and shows how the effects of the ITCZ and lake-level fluctuations might have provided a template for speciation within this group.

Analysis of sedimentary archives from Lake Titicaca reveals that ostracod communities in this ancient lake are not rigid entities. Instead, these communities show drastic and relatively short-term (centuries) changes in faunal composition, with certain species disappearing completely (Figure 8). Such species either reappear at later stages of the lake's history, indicating them to have found refugia in other parts of the lake itself or in adjacent water bodies (small marginal lakes or headwaters of rivers) during their absence from the lake, or are not recorded again, indicating their extinction. The highest population densities and degrees of polymorphism occurred during the mid-Holocene epoch (*c.* 7500–6000 years bp; Figure 8). Palaeodata (microcharcoal

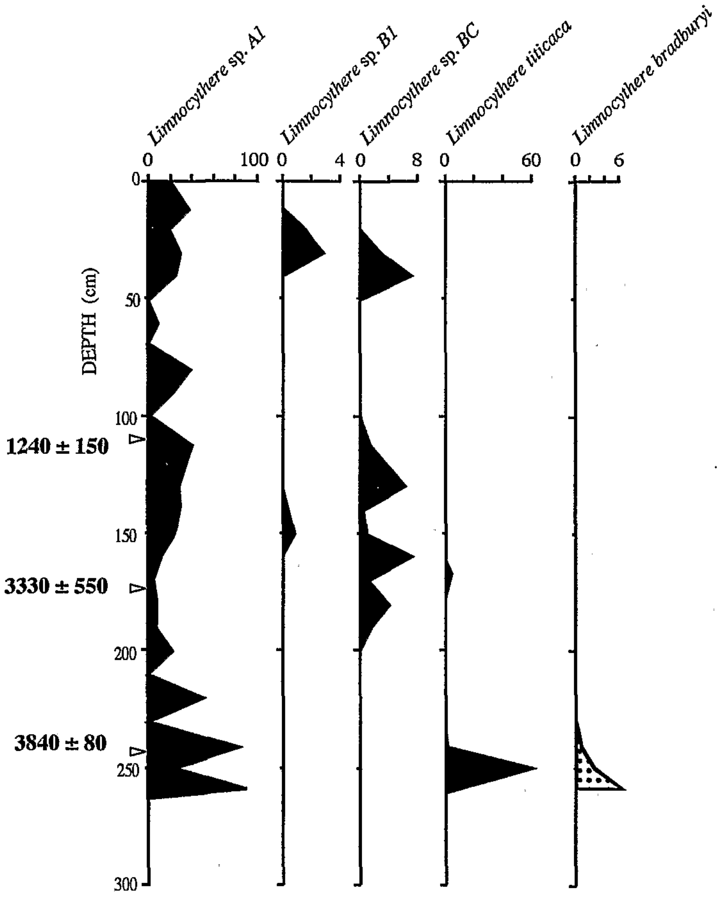

Fig. 10. Distribution of the different limnocytherinid morphs and species for core TD1. Stippled shading denotes the presence of brackish to saline species.

remains in lacustrine sediments) from Amazonian rainforest have shown that short dry-climate episodes frequently occurred during this time (Turcq *et al.*, 1998). When one considers the different ostracod communities in the three basins, it is possible to conclude that the high morphological diversification of the Limnocytherinae in Lake Chucuito (core TJ) is a result of the high habitat diversity and the highly stable environment of the system, which was subject to the effects of the ITCZ. In comparison, in the two cores from Lake Huiñaimarca (cores TB2 and TD1) the ostracod faunas display low morphological and species diversity: in the southern lake basins the effects of the ITCZ were minimal, and data show that during the mid-Holocene these water bodies were temporary and sometimes dried out completely (Hansen *et al.*, 1984; Mourguiart *et al.*, 1997).

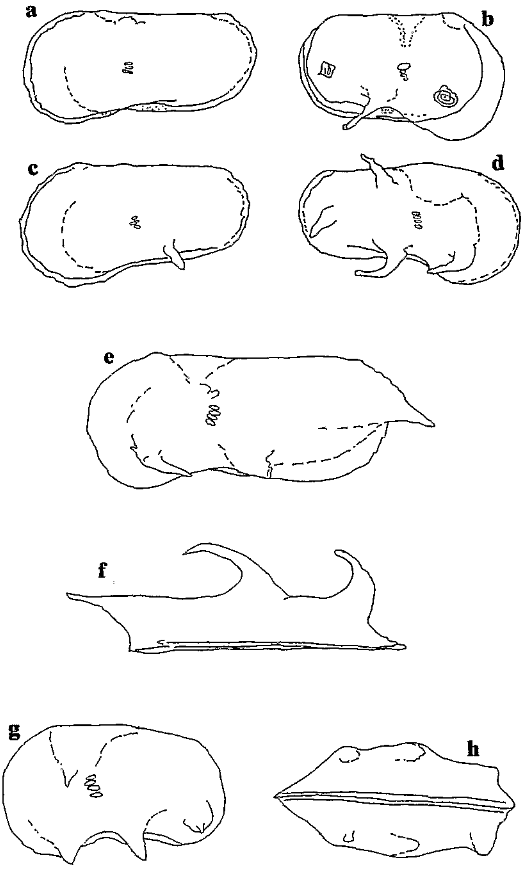

Fig. 11. Examples of morphological variability in ostracods of the subfamily Limnocytherinae. The first four illustrations (a–d) represent morphs from core TJ (Lake Chucuito, sample TJ-295) during the mid-Holocene, respectively characterized by the complete absence of, or the presence of two, six or eight spines on the carapace. The "spiny" morphs are considered as extinct. (a) Smooth morph: *Limnocythere* sp. B1 Mourguiart, 1987; female, lateral view of left valve [length (L) = 0.95 mm]; (b) "biceros" morph: *Limnocythere* sp. B2 Mourguiart, 1987; female, lateral view of left valve (L = 0.91 mm); (c) "hexaceros" morph: *Limnocythere* sp. B4b Mourguiart, 1987, female, lateral view of right valve (L = 0.91 mm); (d) "octaceros" morph: *Limnocythere* sp. B4c Mourguiart, 1987; female, lateral view of right valve (L = 0.95 mm). Parts e and f represent *Neolimnocythere hexaceros* Delachaux, 1928, an ostracod from the Holocene sediments of Lake Junín. (e, f) *Neolimnocythere hexaceros*; male, (e) lateral and (f) ventral views of right valve (L = 1 mm). The final two illustrations show modern morphs found in Lake Chucuito (Isla del Sol). (g, h) "hexaceros" morph: *Limnocythere* sp. B4a Mourguiart, 1987; female, lateral view of left valve (g) and ventral view of carapace (h) (L = 0.85 mm). Differences in spine lengths and shapes are particularly evident between morphs.

Although the effects of climate on the evolutionary history of Titicaca's aquatic fauna are only now beginning to be unravelled, it is apparent that factors outside the lake basin need to be considered (Argollo and Mourguiart, 2000; Lendru and Mourguiart, 2000; Lendru *et al.*, 2000). The humid air carried by the ITCZ to the Altiplano originates from the Amazon Basin, and future studies on the hydrology and limnology of Lake Titicaca should consider the effects of large-scale climate changes within that area.

A. Sympatric and Allopatric Speciation: Climatic and Habitat Effects

The fact that different morphs are found in present-day Lake Titicaca environments, and also in other isolated small lakes (Lakes Huaron and Junín) some hundreds of kilometers north of Lake Titicaca, is particularly significant. It is as yet unclear whether all of these species have a single ancestor or not, but two different evolutionary scenarios can be forwarded: (i) the morphs are different species of allopatric origin, and have evolved in different refuges since the last deglaciation in the Andes, some 12 000 years bp; or (ii) the morphs have a sympatric origin, and developed within each lake system through selection and micropartitioning of diverse stable niches.

The importance of geographical barriers as factors promoting allopatric divergence of species is well recognized. In the high Andean plateau, Pleistocene glaciations could have promoted divergence into closely related pairs of species in different lacustrine systems, such as those found in Lake Titicaca in the south, and Lakes Junín and Huaron in the north, respectively. During glaciations, each unconnected lake basin could thus have provided a refuge, within which species evolved allopatrically. However, the history of these environments is one of drastic climate changes and high-amplitude water-level variations, extending even to complete desiccation in most cases (Hansen *et al.*, 1984; Mourguiart *et al.*, 1997). This begs the question: at times of severe environmental stress or desiccation, where did ostracod communities find conditions favourable to their survival? Possibly, lakes at lower elevations served during Ice Ages as refugia for some lacustrine ostracod taxa. Tentative support for this theory is provided by Wasa Mayu, a lake located at a lower elevation in the Valle Alto near Cochabamba, Bolivia, and where at least three limnocytherinid species lived between *c.* 35 000 and 15 000 years bp (Purper and Pinto, 1980; Strahl, 1998).

In the author's opinion, the differences in the diversities of Titicacan ostracods can be partly explained by the unusual regional climate, characterized by high-amplitude interannual variations in pluviometry owing to the effects of the ITCZ, especially at its southernmost portion. A combination of environmental stability and habitat diversity seems to have promoted species diversity. The highest species richness occurred during the mid-Holocene, a period characterized by frequent disturbances (wet–dry episodes) and high lacustrine productivity, as evidenced by the very high sedimentation rates of biological remains seen in core TJ (Figures 3, 8). At that time, hydrological conditions in Lake Huiñaimarca (cores TB2 and TD1) were too severe to allow colonization by diverse ostracod communities (Figures 9, 10). A contrasting situation is observed in the north, where the high species diversity in Lake Chucuito (core TJ) is a result of the highly diverse habitat and the relatively stable environment. Lastly, in Lakes Huaron and Junín, climate and habitats (mainly Characeae mats) were more uniform throughout the Holocene (Hansen *et al.*, 1984; Mourguiart *et al.*, 1997), and only a small number of limnocytherinid species colonized these lakes. The low habitat diversity there would not have promoted speciation through partitioning of spatial niches.

B. The Need for a Sound Taxonomy

The fundamental difference between ostracod populations from Lake Titicaca and those from Lake Junín concerns the degree of diversification. The Titicaca "morphs" are examples of an incredible ecophenotypic variation under the control of environmental factors (e.g. water depth), which is quasicontinuous (Mourguiart, 1987). Within the same population (living or fossilized), it is generally possible to observe a series of forms intermediate between smooth and highly spinous morphs. In contrast, in Holocene and present-day environments, *Neolimnocythere hexaceros* from Lakes Huaron and Junín shows no morphological variation. However, it is difficult to make meaningful comparison between the fauna of Lake Titicaca and these two lakes. This is because of the disparity in the present level of taxonomic knowledge of the respective ostracod faunas of these lakes. The limnocytherinid taxa found in Lakes Huaron and Junín have been identified based on both external morphology of the carapace and descriptions of soft parts, e.g. *Limnocythere elongata, Neolimnocythere erinacea* and *Paracythereis impudica* (Delachaux, 1928). The identification and separation of different species is thus much more accurate. For example, using characters of external morphology only, it is difficult to differentiate between *Limnocythere titicaca* of Lake Titicaca and *L. elongata*, or even *P. impudica*, of Lake Huaron, yet these species are easily separated on the basis of soft-part anatomy (Lerner-Seggev, 1971). Clearly, whether the different morphs in Lake Titicaca are indeed different species or subspecies, and their relationship to species in other Andean lakes, needs to be founded upon a sound taxonomy. This can only be achieved by considering characters of the soft-part anatomy.

Further studies are needed to elucidate the processes responsible for the geographical distribution of past and present ostracod diversity in the Andes. However, it is increasingly evident that rather than being species depauperate, the Andean plateau harbours surprisingly high levels of diversity for some aquatic taxa (e.g. ostracods). Unfortunately, many of the questions raised in this chapter can presently be addressed only on the basis of speculation and hypothesis, and there is a clear and urgent need for further studies of the remarkable morphological variation in certain Andean ostracod species. This must be done in tandem with taxonomic studies based on soft parts, especially the morphology of the copulatory processes of the hemipene, which represent more conservative characters to diagnose species accurately, and on genetic material. The application of molecular DNA techniques, as used so fruitfully on other ancient lake faunas by several contributors in this volume, seems certain to play an important role in Lake Titicaca. With a sound taxonomy in place, such studies of the limnocytherinid faunas of these Andean lacustrine environments should provide unique insights into allopatric and sympatric evolutionary processes.

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