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The external mechanisms responsible for morphological variability in Recent Ostracoda: seasonality and biotope situation: an example from Lake Titicaca

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ABSTRACT

The environmental mechanisms directly responsible for variations recorded in the ornamentation of ostracods are well known. They concern mainly the carbonate equilibrium at the water/sediment interface (reticulation phenomenon *sensu lato*) and the impact of the input of fine-grained and all allochthonous matter on biotopes (nodation and microconation phenomena).

Although these processes can be observed in all sorts of environments, whether continental shelf, coastal, lagoonal or estuarine, it is difficult to determine the factor(s) governing such equilibria.

Studies in Lake Titicaca revealed the existence of two major groups of factors responsible for the morphological variability of ostracods (mainly in the intertropical zone):

1) contrasting seasonality i.e. alternation between a dry and wet season with all the subsequent effects on the circulation, input from the flanks of the basin and chemical equilibria at the water-sediment interface.

2) biotope positioning. A maximum of species and morphs were observed at the borderline between the phytal and 'deep' zones.

With present-day conditions, where the seasonal contrast is relatively important, polymorphism is high. Conversely, when climatic conditions were different, polymorphism changed from being very intense under contrasting seasons (7500 BP), into monomorphism (towards 4500 BP) under almost uniform climatic conditions during all seasons. This is perhaps the first step towards speciation.

Ostracoda and Global Events

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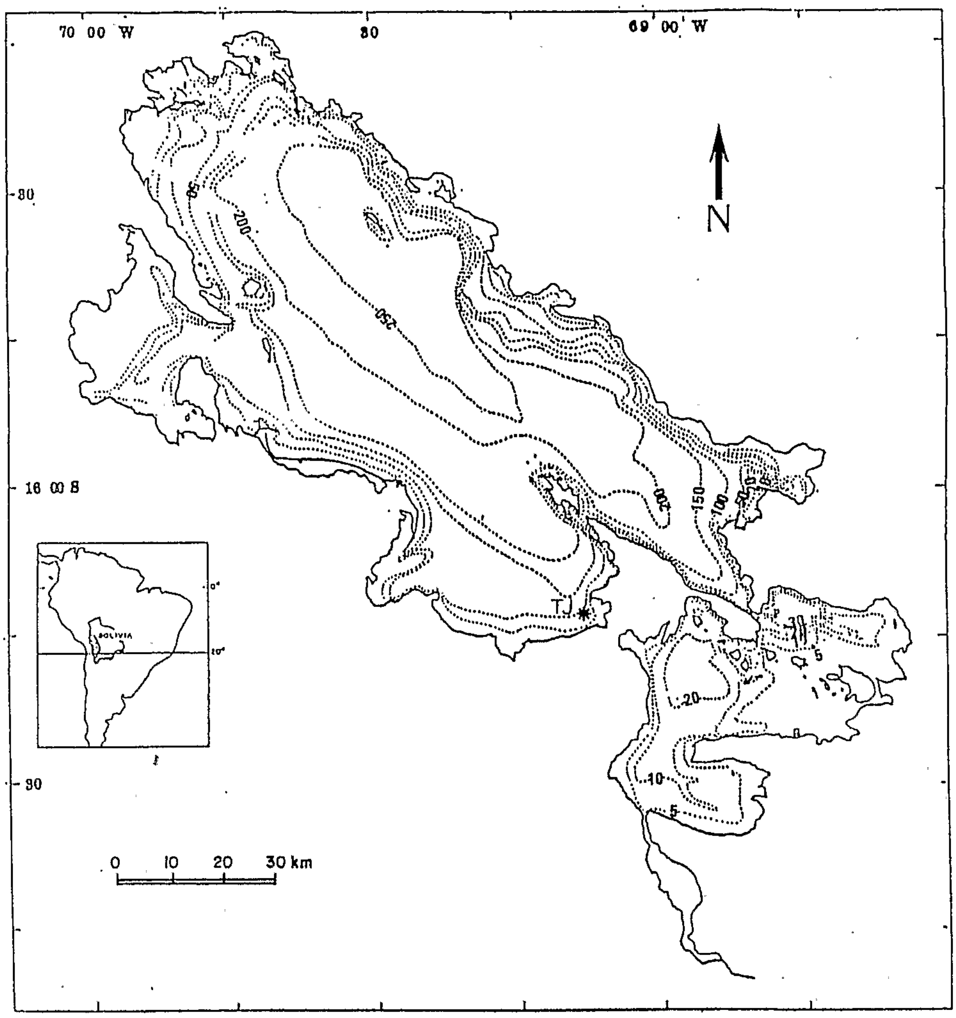

Fig. 1. Lake Titicaca, location map - site of core TJ.

When global climatic changes occurred, e.g., during the Pretiglian glacial and the Tiglian interglacial in North West Europe in inner shelf environments, very similar aspects as those described above must have existed.

INTRODUCTION

Some aspects of morphological variability in ostracods are more or less governed by variations in the chemical equilibria at the water-sediment interface. Ostracods take all the components of their shells from the water during each moulting stage without storing them in the soft parts (Turpen & Angell, 1971). This morphological variability is mainly expressed as 3 types of variation that can sometimes be observed together on the carapace:

1) reticulation, depending upon carbonate equilibria: this is the 'agradation-degradation' phenomenon defined by Peypouquet *et al.* (1987, 1988),

2) nodation, spinosity and microconation, connected with the supplies of fine-grained sediment and allochthonous organic matter,

3) size (not examined here).

These phenomena are observable in all environments; marine, lagoonal, lacustrine. Our aim is to show that ostracod variability is not haphazard but linked to the fluctuation of global parameters operating at the water-sediment interface where most ostracods live and moult.

First, we discuss the morphological variability which exists only in certain places and later the succession of valves with different morphologies on the bottom, representing each stage of the seasonal cycle. The example chosen is present day ostracod fauna living in Lake Titicaca, particularly two groups of *Limnocythere*.

VARIABILITY IN *LIMNOCYTHERE* FAUNA IN THE PRESENT DAY ENVIRONMENTS OF LAKE TITICACA

Lake Titicaca is located between the Andean Cordillera at 3800m above sea level (Fig. 1). It has an area of about 8000km^2 and its maximum depth is approximately 220m. It is subdivided into the Great Lake and Little Lake (or Lake Huynaymarca) connected by the Tiquina Strait. The Great Lake is considered to be a warm monomictic and eutrophic lake (Hutchinson & Löffler 1956) with a productivity of 500g cm^{-2} yr^{-1}. The Little Lake with a maximum depth of 40m (main part < 10m), is oligotrophic and has a productivity of 20g cm^{-2} yr^{-1}. Its ecology shows 2 phases (Fig. 2):

1) homothermy and homogenization during the austral winter,

2) stratification during summer and autumn.

Such a contrast entails, in the hypolimnion, an increase of CO_2 (caused by the consumption of organic matter by bacteria) and a decrease of pH during the stratification phase and later, saturation of O_2, with the recycling of chemical elements during the homogenization phase.

BATHYMETRIC ZONATION

The distribution of ostracods is the same in both parts of the lake. In the shallower parts, their distribution is controlled by that of phytal communities. Six successive zones are distinguished from the shallowest to the deepest parts of the lake (Fig. 3):

1) 0-2.5m, coastal zone. Low diversity of phytal fauna living on plants with *Elodaea* and *Myriophyllum*, generally less than 1m deep. This zone is physically very unstable and has a high energy level.

2) 2.5-4.5m, *Totora*. Ostracods are absent (oxygen depletion on the bottom): vegetative parts of *Totora* are developed on the water surface.

3) 4.5-7.0m, *Chara*. Weakly calcified ostracods living on *Chara*. No evidence of thanatocoenosis.

4) 7.5-12.5m, lower boundary of vegetation. Maximum number of species, individuals and morphs. This is particularly true for *Limnocythere*.

5) 12.5-20.0m, aphytal zone. Decrease in abundance and diversity of species.

6) more than 20m, deep zone. Ostracods rare.

In zones 5 and 6, which are deeper and less rich in nutrients than those above, ostracods become fewer and less diversified. The plants serve as regulators of food and energy levels and live under the direct influence of annual climatic variations.

This distribution is schematic, local characteristics exist, such as the density of *Totora* and the extension of zones 4, 5 and 6 depending on topography and water circulation. In the Great Lake, zones 4 and 5 are extended between 8-30m and 30-60m respectively, because of steeper slopes.

The abundance and morphological variability of *Limnocythere* are greatest in zone 4. This area is, therefore, the key sector where the impact of seasonal parameters is highest without any evidence of interference because of the filtering action of the water plants.

THE *LIMNOCYTHERE* FAUNA IN LAKE TITICACA

The *Limnocythere* fauna living in Lake Titicaca is abundant (often the main group) and diverse (Mourguiart, 1987). A taxonomic study of this group is in process and we will give only the principal elements necesssary to the understanding of the present paper. Seven species have been identified: *Limnocythere titicaca* Lerner-Segueev and the *Pampacythere* group Whatley & Cholich,

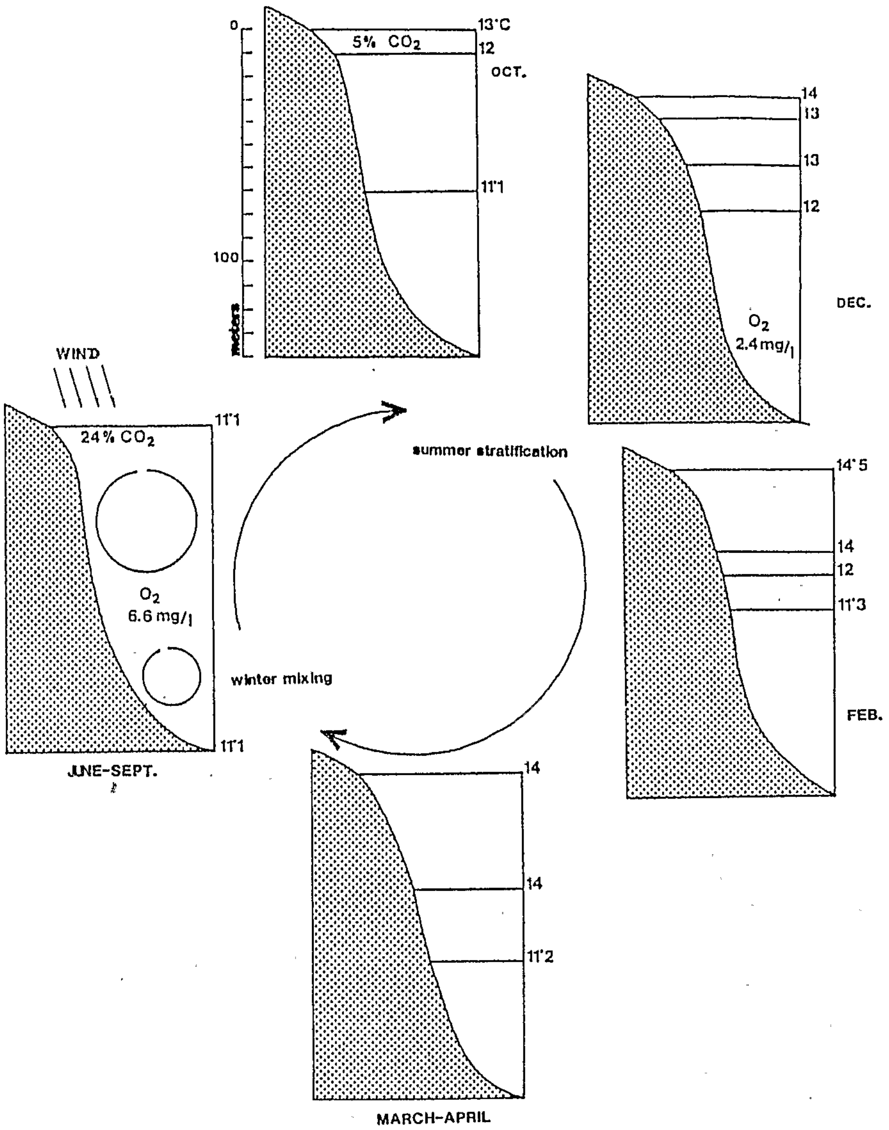

Fig. 2. Seasonal changes of water circulation in Lake Titicaca.

L. bradburyi Forester, *L.* sp. X Mourguiart, *L.* sp. Y Mourguiart, *L.* sp. Z Mourguiart, L. gr. 'A' Mourguiart and L. gr. 'B' Mourguiart. These species can be grouped together into 2 or 3 genera, but the confusion existing concerning their recognition (with the exception of *Pampacythere* and the type-genus) as well as the lack of interpretation of the soft parts, are the reasons why we have chosen to retain the denomination '*Limnocythere*' for the whole group. Two specific groups are particularly variable: *Limnocythere* gr. 'A' and 'B'. Their abundance and wide distribution account for their being chosen for this study. The main differences between the two groups are the following:

	Group 'A'	Group 'B'
Lateral view	subrectangular to slightly reniform	pseudorectangular
Dorsal view	oval	flat anteriorly
Calcification	variable, generally weak	variable, weak
Ant. margin	rounded, large with relief	rounded and flat
Dors. margin	straight	straight
Ventr. margin	ant. 1/3 slightly concave	ant. 1/3 slightly concave
Size	medium to large (L/H=0.53)	large (L/H=0.46)
Overlap	RV=LV	RV=LV

The morphological variability observed in both groups is similar (Fig. 6). In the group 'A', 4 'morphotypes' are recognized, A1 standard, A2 with one spine per valve, A3 with tubercle and microcones, A4 with some expansions similar to *Neolimnocythere haxaceros* Delachaux. In the group 'B', 8 'morphotypes' occur; these include B1 standard, B2 with one spine, B3 with microcones, B4 with expansions and B7 living on *Chara*. Members of group 'A' occur more frequently than those of group 'B', possibly due to ecological differences.

SEASONAL VARIATION OF *LIMNOCYTHERE* GROUP 'A' AND 'B'

Seven successive phases can be observed throughout the year with respect to the lake's ecology (Mourguiart, 1987).

1) During the austral winter (Fig. 4a) the water mass is homogeneous, the bottom is anoxic with no possibility for ostracods to live.

2) At the end of winter in September (Fig. 4b) maximum photosynthesis occurs and supersaturation of carbonates at the water-sediment interface gives rise to very large shells.

3) At the end of September (Fig. 4c), detritus from plants yields nutrients and elements of macrophytes are dissolved resulting in the occurrence of spines.

4) In the austral spring (October) (Fig. 4d), with increasing temperature, the water column begins to be stratified. The diatom bloom entails a strong depletion in silica and the death of these organisms (Carmouze *et al.*, 1984) gives rise to a rain of

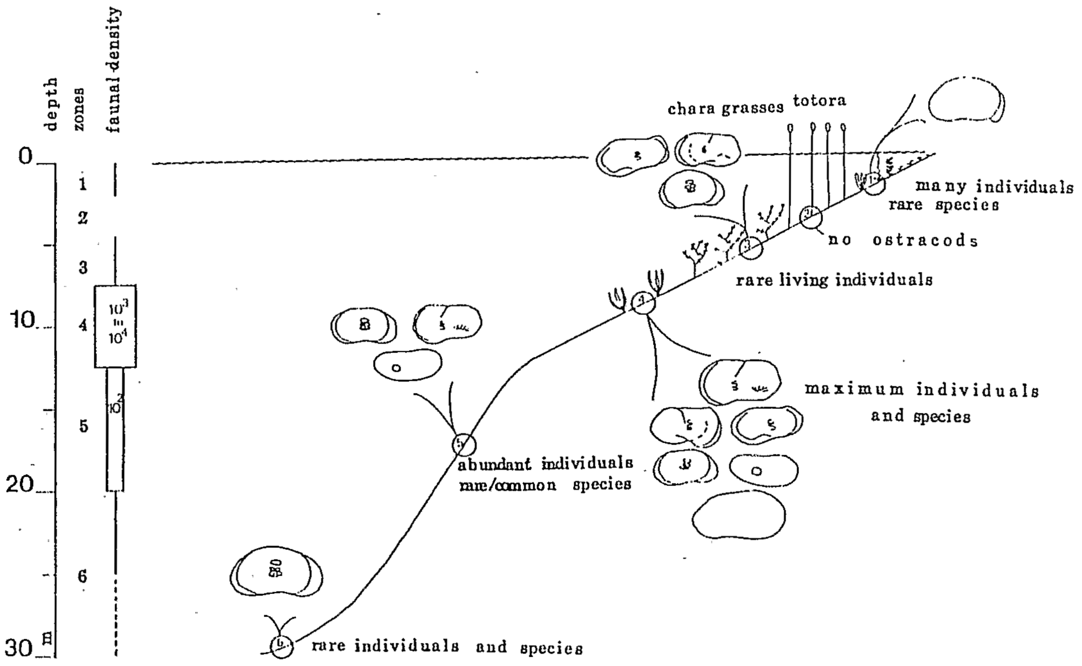

Fig. 3. Bathymetric zonation of the ostracod assemblages.

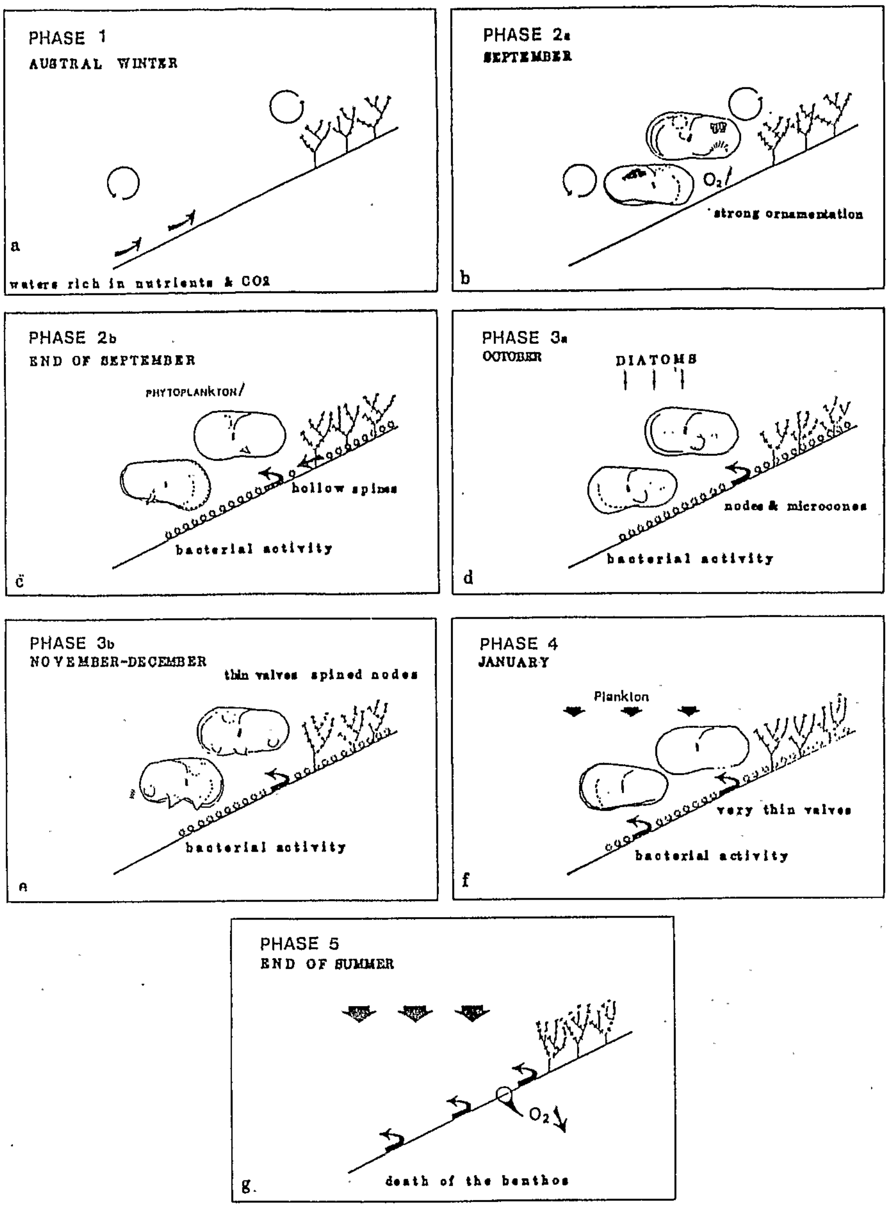

Fig. 4. Seasonal variability of *Limnocythere* gr. 'A' and 'B'.

frustules, comparable to the input of fine detritus (Kirk, 1985). This rain induces the development of microcones and nodes on the surface of the valves (Mourguiart, 1987). This mechanism is similar to that described by Abe & Choe (1988, 371) for the formation of microcones in *Pistocythereis bradyi* (morph D). 'Small sub-conical projections on the muri of *P. bradyi* are well developed around the pores of sensory hairs which are situated only at the junction of the muri and they are naturally assumed to affect the function of the sensory organ, perhaps by protecting the hair or preventing the

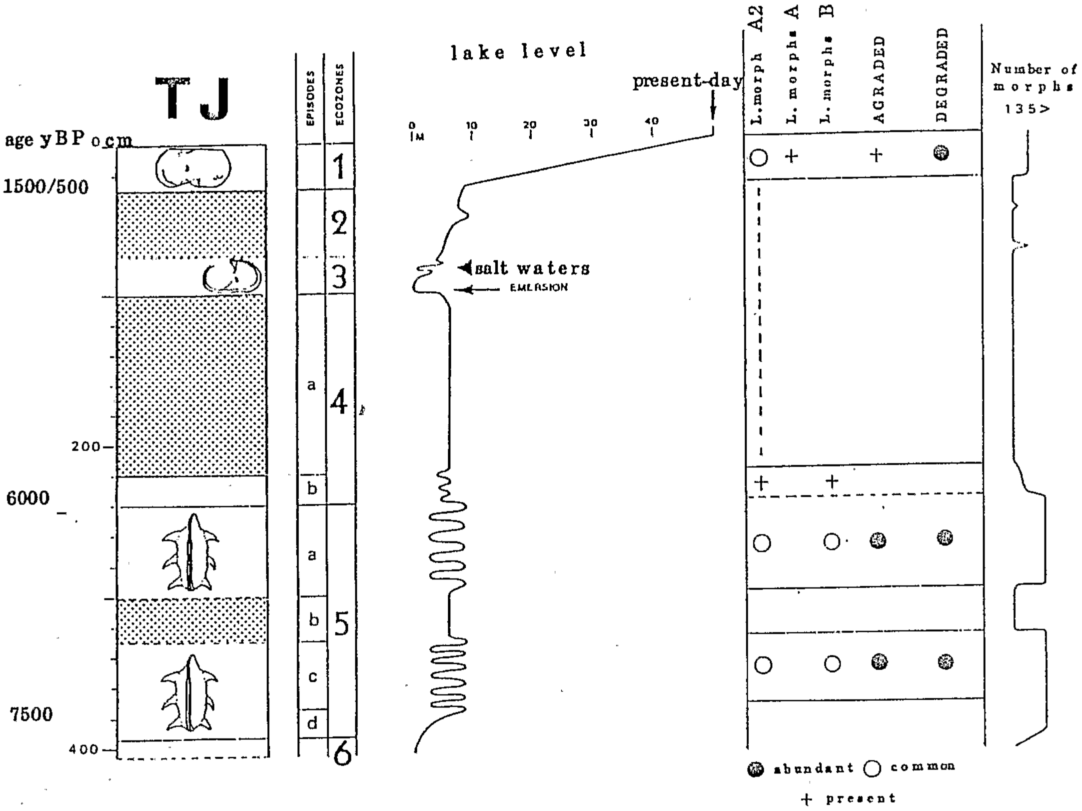

Fig. 5. Core TJ, zonation.

intrusion by foreign matter.'

5) In the austral spring (November-December) (Fig. 4e), the calcification of the shells decreases (with increase of CO_2 due to intense bacterial activity). Recycling of dissolved elements causes the development of spined nodes.

6) During the austral summer (Fig. 4f), primary productivity increases. Ostracod carapaces become very thin, as bioprecipitation of $CaCO_3$ is very difficult under these conditions.

7) At the end of summer (Fig. 4g) the water column is completely stratified; the bottom becomes almost depleted of oxygen. Calcite bioprecipitation becomes impossible (Kelts & Hsu, 1978). Most of the benthos dies.

Fig. 4 shows the successive seasonal stages in the morphological variability of *Limnocythere* groups 'A' and 'B' within an average climatic situation, i.e. a situation with a well-marked but not strong seasonal contrast. It is interesting to examine the response of *Limnocythere* to the environment under palaeoclimatic situations where seasonal contrasts were similar to those prevalent today.

THE PALAEOFAUNA OF LAKE TITICACA DURING THE HOLOCENE

We have selected a core from the Great Lake in Yunguyo Bay (Fig. 1) (50m deep), i.e. with a present day water depth that is sufficient for the recording of important variations of the lake level. This core is 4.06m long. An overall analysis of the fauna (Carbonel *et al.*, 1988) shows a zonation of 6 ecozones (Fig. 5). From bottom to top these are:

1) Ecozone 6, beach deposits with gypsum and without ostracods.

2) Ecozone 5, (394-240cm), zone with strong fluctuations. Maximum polymorphism occurring

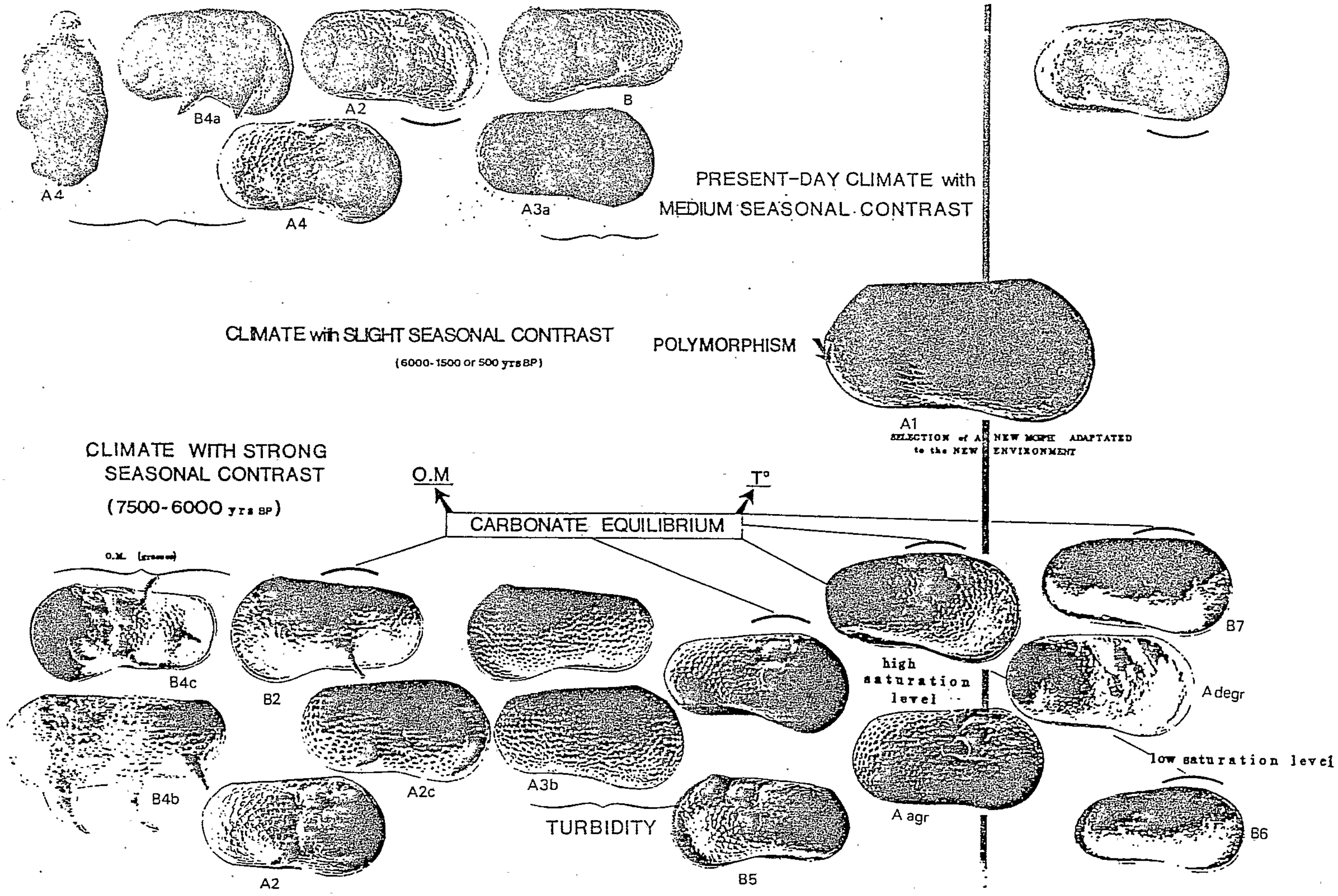

Fig. 6. Core TJ, polymorphism of *Limnocythere* gr. 'A' and 'B' during the last 7500 years.

at the same time as the maximum development of the ostracod fauna (Mourguiart, 1987).

3) Ecozone 4, (240-100cm), proximity of *Chara*. Very slight polymorphism changing into monomorphism.

4) Ecozone 3, (100-75cm), very low lake level with emergent phases giving rise to greater water concentration (occurrence of *Cyprideis*).

5) Ecozone 2, (75-30cm), similar to ecozone 4.

6) Ecozone 1, (30 cm-top), typical present-day fauna in this part of the lake. High polymorphism (less than in ecozone 5).

Three main phases can be observed in the morphological variability of *Limnocythere* (Fig. 6), maximum in ecozone 5 (7500-6000 BP), minimum in ecozones 2 and 4 (6000-4500 and 2000-500) and medium in ecozone 1 (500-present day).

Each type of variability can be related to a type of climate. Between 7500 and 6000 BP, the lake's level increases very slowly in association with a summer monsoon with intense stormy and rainy periods and very strong winter aridity. This phenomenon coincides with the sinking of the Inter Tropical Convergence Zone (ITCZ) towards the Bolivian Altiplano (Servant & Fontes, 1984).

Between 6000 and 4500 BP, and 2000 and 500 BP, the seasonal contrast decreases and the climate is characterized by rain showers, a stabilization of the lake's level and a large extension of the peat-bog in the high valleys. This change results probably from the rise of the ITCZ to the North, a rise that is stronger than that of today. This rise occurs together with a strong jet-stream on the top of the Andes and with an intensification of the El Niño phenomenon on the coasts (Martin *et al.*, 1987). In the final phase, the lake's level is comparable to the present day and the seasonal contrast recurs with the summer precipitations.

Variations in the seasonal contrast associated with the displacement of ITCZ seem to be indirectly related to the morphological variability of *Limnocythere*. This last point raises the following question. Is the selection of morphs by the environment (*sensu* Clark, 1976) the starting point for speciation? In the example given, it is impossible to know with certainty because the time factor is very short.

The same question can be asked for a longer period of time. Is it possible that a long term climatic situation can lead to speciation through geographical isolation and long term environmental stability? Several examples exist showing the same selection effects and stabilization and expansion of new morphs, and perhaps species, during longer time periods when intense climatic changes occur as, for example, during the Palaeocene (Peypouquet *et al.*, 1988) and during the initial glacial phases around the Plio-Quaternary boundary (Kasimi, 1966; Braccini, 1988).

CONCLUSIONS

The morphological variability of the *Limnocythere* groups appears in very specific areas of a limnic system (the same observation can be made in a marine coastal system) immediately beneath large phytal asemblages. This variability also depends on the seasonal evolution of the equilibria at the water-sediment interface, controlled by the seasonal contrast. During phases without seasonal contrast, there is only one morph present, while during phases with strong seasonal contrast, many morphs can be observed. The succession of such phases in the past may have probably resulted in the formation of new species. From a general point of view, can polymorphism be a necessary step towards speciation? The discussion is open.

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