Studies carried out on two cores from Lago Huiñaimarca, TD and TD1 (see Chapter III.1), have demonstrated great variations in the palynological content of sediments and reveal the presence in the lower layers of large quantities of Isoetes, an aquatic fern not recorded at present in Lake Titicaca, but abundant in the high Bolivian valleys at between 4250 and 4750 m altitude (Collot, 1980).

To interpret the fossil spectra in paleoclimatological terms, it is therefore necessary to know the present-day pollen sedimentation pattern in lakes whose environment would appear to correspond as closely as possible to that which Lake Titicaca experienced in the past. The lakes selected for this study were, firstly, those in the Hichu Kkota valley close to Lake Titicaca and situated in a botanically high altitude environment (Fig. 1 A and B) and secondly, Lake Poopo, characterised by a halophytic flora (Figs 1 A and C).

The paleobathymetric interpretations are derived from the comparison of present-day spectra obtained from analysing superficial samples taken along transects across these lakes as well as in Lake Titicaca with a Mondsee corer (Figs 1 and 2).

The fossil samples analysed were taken at 10 cm intervals on cores TD and TD1 and were then processed using the following steps:
- treatment with 10% HCl, with boiling 15% KOH, acetolysis, densimetric separation using bromoform with d = 2, mounting in glycerine/gelatine.

The palynomorphs identified in the analyses were lumped into 4 large groupings in terms of their dominant ecological origin: terrestrial habitats or wetland habitats (marshes, bogs, flood-plains bordering the lake) or their biological origin: aquatic macrophytes or planktonic organisms.

The taxa making up these groupings are given in the legends to the pollen diagrams.

Location of the sampling transects for the present-day samples and their corresponding environments

The Hichu Kkota valley, situated to the east of Lake Titicaca, belongs to the Puna region, a high Andean province also known as the “Puna Brava”
which is typified by its very sparse vegetation dominated by tussock-forming grasses. The mean annual temperature is 5.4°C at 4310 m altitude and the thermal gradient is of the order of 0.53°C per 100 metres (Ostria, 1987). Annual precipitation averages 834 mm, with a peak in January-February.

Ostria (1987) and Collot (1980) have studied the vegetation of this valley and have established the altitudinal distribution of the various plant species. Among the taxa recognised in the palynological preparations are: Nototriche violacea recorded above 4900 m; Valeriana, present between 4650 and 4750 m in dry areas; Caryophyllaceae and liguliflorous Compositae, which are especially abundant above 4500 m; Gentiana present between 4300 and 4800 m, but most abundant around 4500 m; Juncaceae which make up most of the vegetation of the bogs (known as “bofédales”) above 4550 m, where they are associated with numerous mosses and liverworts; Plantago, abundant below 4500 m in the bottom of damp valleys; Elodea, Myriophyllum, Lilaeopsis, Ruppia and Schoenoplectus tatora, whose upper limits of occurrence are respectively 4700, 4500, 4400 and 4300 m; Isoetes, present in all the lakes between 4250 and 4750 m.

The phytoplankton (Iltis, 1984) is represented by Botryococcus braunii, Spirogyra, Zygnema, Staurastrum, Mougeotia and Pediastrum, to mention only those taxa recognisable in our preparations. It should be noted, however, that Pediastrum is absent from Jankho Kkota, the highest lake.

One transect was studied for each of the main lakes in the valley (Fig. 1): Khara Kkota (4310 m), Khotia (4450 m) and Jankho Kkota (4690 m), lakes with mean water temperatures of 9.6°C, 8.8°C and 7°C respectively (Iltis, 1988).

Lake Titicaca is situated in the province of Puna sensu stricto, at a mean altitude of 3810 m; it is subject to a cold and semi-arid climate with a mean annual temperature of 8°C and rainfall of between 790 and 950 mm per year. The herbaceous vegetation is dominated by Gramineae, but Compositae and Chenopodiaceae are also well represented. Trees are infrequent, the main species being Polylepis tomentella, Buddleya incana, Cantua dependens and Eucalyptus sp. introduced in the last century.

The aquatic macrophytes recognised in our preparations were Lilaeopsis, Hydrocotyle, Myriophyllum, Elodea, Schoenoplectus tatora, Potamogeton and a small amount of Ruppia. It is noteworthy that Lilaeopsis, which flowers regularly in Lakes Khara Kkota and Khotia, has never been found flowering in Lake Titicaca.

The phytoplankton found in our preparations is composed mainly of Botryococcus braunii, Pediastrum, Ankistrodesmus, Spirogyra, Mougeotia, Zygnema and Staurastrum.

The mean surface water temperature is 12 to 14°C for Lago Grande and 10 to 16°C for Lago Huiñammarca (Iltis, 1987).

Three transects were studied (Fig. 2), the first in Lago Grande extending from Achacachi Bay in the direction of Sun Island, the two others in Lago Huiñammarca, from Suana Island in a southerly and south-westerly direction.
Figure 1. Map showing location of study lakes.
respectively. The deepest samples (D × 6 and D × 7) were taken with a Züllig type grab (Figs 2 and 3).

Lake Poopo, situated at 3690 m altitude, is also in the province of Puna sensu stricto, but is in an area with a colder and more arid climate than Lake Titicaca. The mean annual temperature is 6 to 8 °C and rainfall is between 300 and 400 mm per year.

The surrounding vegetation is a mountain steppe dominated by Gramineae and Compositae, with frequent cactuses in rocky areas. Because of the saline soils, the vegetation around the lake itself is composed mainly of Chenopodiaceae.

The water is generally saline (up to 50 g l⁻¹), so Myriophyllum and Schoenoplectus are rare. The most abundant aquatic plant is Ruppia which covers nearly 60% of the lake area. The phytoplankton is dominated by the genera
Figure 3. Composite palynological diagram of the Lake Titicaca transect.
Nodularia, Oscillatoria, Dictyosphaerium, Peridinium and Cyclotella (Iltis et al., 1990).

One transect was studied in the southern part of the lake, extending northwest from Quillacas (Fig. 1).

Present-day distribution of palynomorphs in relation to water depth and environmental factors

Analysis of superficial samples (Ybert, in prep.) has demonstrated a direct relationship between the distribution of the palynomorphs and the zonation of aquatic macrophytes, which itself is related to water depth (Collot, 1980).

The main features of this distribution, which is well marked on the transect in Lago Grande (Fig. 3), can be summarised as follows:

The taxa from terrestrial environments are on the whole abundant (12 to 35%) from the lake shore down to 1 m depth, with a maximum of 60 to 80% at about 40 cm. Their proportion then decreases rapidly to 5 to 15% between 1 and 2 m and then stays around 5% down to 8 to 10 m depth. After 10 m it increases again (10%) as a result of the input of allochthonous components and wind-dispersed taxa;

The taxa from wetland habitats are very abundant in the shoreline zone, where fungal spores dominate. They remain abundant (15 to 35%) from 40 cm to 2 m depth, where they are made up essentially of fungal spores and Cyperaceae pollen. They then decrease rapidly so as to represent only 2 to 5% of the palynological spectrum from 4 m onwards;

Aquatic macrophytes occur at less than 4% in the shoreline zone (between 0 and 40 cm depth), then increase to 15 to 40% in the *Myriophyllum* zone (between 40 cm and 2 m), then decrease rapidly so as to disappear almost completely from 4 m depth;

Algae are poorly represented (5%) down to 40 cm depth where they are made up essentially of *Spirogyra*. *Botryococcus* appears between 0 and 20 cm, increases slightly (3 to 10%) down to 2 m and then becomes dominant (80 to 90%) after 10 m. *Pediastrum* appears around 60 cm depth and remains at levels of between 2 and 10% until about 4 m, then becomes dominant between 4 and 10 m (50 to 70%) and then decreases (<5%). *Ankistrodesmus* (10 to 15%) is common in the *Myriophyllum* zone but not abundant elsewhere.

On the whole, this distribution was found to be almost identical in all the transects studied; however, the composition of the 4 main groupings of palynomorphs varies in relation to the ambient environment and characterises certain abiotic factors.

The altitudinal factor (Fig. 4) is characterised by:
- much higher percentages of *Valeriana* at Jankho Kkota (2%) than at Khotia (<0.2%);
- progressively higher percentages of Amaranthaceae-Caryophyllaceae (0.1
to 0.4%), liguliflorous Compositae (<0.1 to 1%) and Juncaceae going from Lake Titicaca to Lake Jankho Kkota;
- the absence of *Valeriana*, *Gentiana* and Juncaceae from the superficial sediments of Lake Titicaca;
- the proportion of *Gentiana* ranging 2 to 4% at Khotia and less than 1% at Jankho Kkota and Khara Kkota;
- high percentages of *Isoetes* at Khara Kkota (21% on average for all spectra, 80% between 0.1 and 3.5 m depth) but lower at Khotia and Jankho Kkota (2 and 10% respectively) and very low in Titicaca (<0.2%);
- high percentages of *Plantago* in the shallow water samples at Khara Kkota (33%) and Khotia (20%), but very low at Jankho Kkota (<1%) and Titicaca (<2%);
- high percentages (>25%) of Cyperaceae between 1.8 and 4 m depth in Titicaca, less than 5% in Khara Kkota and Khotia and less than 1% at Jankho Kkota;
- the absence of *Pediastrum* in Jankho Kkota, percentages of less than 3% in Khotia and Khara Kkota and greater than 20% in Titicaca;

![Composite palynological histograms of the lakes arranged according to altitude.](image)

*Figure 4.* Composite palynological histograms of the lakes arranged according to altitude.
The salinity factor is characterised by:

- high percentages (10 to 20%) of *Ruppia* in Lake Poopo, less than 0.2% in Titicaca and absence from the high altitude lakes;
- high percentages (up to 70%) of Chenopodiaceae in Lake Poopo, around 10% in Titicaca and less than 2% in the Hichâu Kkota valley;
Figure 6. Composite palynological diagram of core TD1.
- percentages of *Myriophyllum* exceeding 40% in Achacachi Bay (Titicaca) and less than 0.2% in Lake Poopo;
- percentages of *Pediastrum* of less than 0.6% in Lake Poopo, but at times exceeding 60% in Titicaca.

**Deductions concerning the Lake Titicaca environment over the last twenty thousand years**

Interpretation of the palynological diagrams for cores TD and TD1 (Figs 5 and 6), in comparison with the present-day data summarised above, leads us to propose the following succession of environmental conditions in the central-west basin of Lago Huyñamarka:

Palynological zone E, at the base of core TD1, before 21,000 BP.

The presence of *Valeriana, Gentiana, Isoetes* and Juncaceae is evidence of a ‘Puna Brava’ environment, with a temperature close to that currently occurring at about 4500 m altitude, or 3 to 5°C below present temperatures.
Ancient lake environments (deduced from pollen analysis) 59

The lake was shallow and the shorelines were occupied by “bofédales” identical to those occurring in the Hichu Kkota valley above 4500 m. The lake bottom was vegetated by Isoetes and not by totora as is the case now (Photos 1 and 2).

Palynological zone D, base of core TD, 400–200 cm on TD1, between about 21,000 and 17,500 BP.

In general terms the environment stays the same, but there is firstly a drop in lake level (sub-zone D3), then a progressive rise from 3 to 15 metres.

The presence of Valeriana and Juncaceae, and the total absence of Pediastrum in the sub-zone D2, indicates an environment comparable to that of Lake Jankho Kkota. The temperature was therefore 5 to 7°C lower than at present, and then 2 to 5°C lower in D1.

Palynological zone C, 425–320 cm on TD, 200–150 on TD1, between about 17,500 and 11,000 BP.

Isoetes is still numerous in sub-zone C2, Pediastrum and Plantago are present, but Valeriana and Juncaceae have disappeared. This association is equivalent to that of the superficial sediments in Lake Khara Kkota. The temperature has increased to reach values close to those at present and at the same time the lake level has risen significantly to 2 to 10 m below the present level. The “bofédales” with Juncaceae have disappeared from the margins to be replaced by meadows with Plantago.

During the period corresponding to sub-zone C1, Isoetes and the wetland palynomorphs disappear completely and Pediastrum increases. The lake environment becomes more or less the same as at present. Temperatures are the same as or slightly higher than at present and the lake level is about 5 m higher.

There is then the start of a drop in temperature and lake level from 12,000 or 11,500 BP (corresponding to the top of the C zone).

Palynological zone B, 320–110 cm on TD, 150–85 cm on TD1, between about 11,000 and 4100 BP.

The drop in level started in C1 is accentuated, and from about 10 500 BP the depth of the lake decreases rapidly so as to become of the order of 2 to 5 m only. The depth then decreases even more and varies between 0 and 1 m, the lowest levels being between about 7700 and 6500 BP and then about 4500 BP.

The temperature was lower than at present by 1 to 3°C during the period corresponding to sub-zone B5 (about 11,000–9500 BP), close to the present value between 9500 and 5500 BP, with slight cooling at about 8700 and 6500 BP, and then again 1 to 2°C cooler from about 5000 BP.

The predominance of fungal spores, Spirogyra and Chenopodiaceae pollen, the presence of Ruppia and the rarity of Myriophyllum and Pediastrum indicate a saline environment comparable to that of Lake Poopo.

Palynological zone A, top of TD and TD1, from about 4100 BP.
This zone is marked by a rapid increase in the percentage of algae and the almost complete disappearance of wetland palynomorphs, which indicates a major rise in lake level. The water level was 10 to 15 m below the present level between about 3000 and 2000 BP, then at the same level from 2000 to 1500 BP. A well-marked drop occurred about 2500 BP together with oscillations of an amplitude of about 5 m marked by sharp increases in the percentage of *Pediastrum*. Temperatures were close to those at present, but slight cooling could have taken place at about 3000, 1200 and 600 BP. The absence of *Pediastrum* during the first half of the period corresponding to the sub-zone A3 (before 3600 BP) indicate that the waters were still saline. The proportion of Cyperaceae then increased at the start of the sub-zone A2 and it is only from about this period (about 3000 years BP) that totorases must have developed, giving Lake Titicaca the appearance by which it is known today.
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