Fossil rodent middens and wetland deposits from the central Atacama Desert (22° to 24°S) indicate increasing summer precipitation, grass cover, and groundwater levels from 16.2 to 10.5 calendar kiyoles before present (ky B.P.). Higher elevation shrubs and summer-flowering grasses expanded downslope across what is now the edge of Absolute Desert, a broad expanse now largely devoid of rainfall and vegetation. Paradoxically, this pluvial period coincided with the summer insolation minimum and reduced adiabatic heating over the central Andes. Summer precipitation over the central Andes and central Atacama may depend on remote teleconnections between seasonal insolation forcing in both hemispheres, the Asian monsoon, and Pacific sea surface temperature gradients. A less pronounced episode of higher groundwater levels in the central Atacama from 8 to 3 ky B.P. conflicts with an extreme lowstand of Lake Titicaca, indicating either different climatic forcing or different response times and sensitivities to climatic change.

The tropics are believed to be an important source of global climate variability at various time scales, yet their role is poorly understood. Ice age cooling (−5°C) of the tropics is now evident from many tropical ocean and land records (1), raising questions about climate forcing by high versus low latitudes. Precise chronologies of tropical climate change are becoming increasingly necessary to place empirical constraints on competing theories and models. Here, we focus on monsoonal circulation and tropical rainfall over the central Andes. One measure of monsoonal circulation over the central Andes is the variability of summer precipitation (December to March) that spills over from the Altiplano to the Atacama Desert, representing the abrupt, tail end of the tropical rainfall belt.

A history of vegetation change and ground-water fluctuations was reconstructed from 14C-dated fossil rodent middens (2) and wetland deposits (3) at sites straddling the Tropic of Capricorn (23.5°S) in the central Atacama Desert (Figs. 1 and 2). In the Atacama, several rodents (Lagidium, Phyllostis, Abrocoma, and Octodontomys) make urine-hardened cove deposits rich in plant remains akin to North American packrat middens (2). Rodent middens afford high taxonomic, spatial, and temporal resolution of past vegetation growing on dry hillslopes and in this study provide important evidence for seasonality of rainfall. Midden records, however, are stratigraphically discontinuous and represent only snapshots of flora through time. In contrast, paleosprings, fed by precipitation in the Andes (>3500 m), have left behind diatomaceous wetland deposits (3) that provide a more continuous record of sustained hydrologic changes in the Atacama Desert. The two data sets are strongly complementary and together provide a record of paleoclimatic change that is unprecedented for the region.

Most of the annual precipitation in the Ca-lama and Salar de Atacama basins (Fig. 2) falls in summer but shifts to winter (June to September) only 200 km to the south (Fig. 1). This summer-winter transition is reflected in southern limits of −22° to 24°S for most plants that flower in summer versus northern limits of −25° to 27°S for those that flower in winter (4).
Vegetation zonation in the study area parallels orographic effects. The 0°C mean annual isotherm marks the upper limit of vascular plants at ~4500 m. Between 3800 and 4500 m, mean annual precipitation of 150 to 230 mm supports Andean steppe grasses (*Festuca ortophylla*, *Jarava frigida*, *Stipa chrysophylla*, and *Deyeuxia* spp.) and cushion plants (*Azorella compacta*). Between 3200 and 3800 m, precipitation of 70 to 150 mm supports Tolar shrubs (*Parastrephia* spp., *Chuquiraga* spp., *Lampaya medicinalis*, *Junellia seriphoides*, and *Fabiana* spp.), columnar cacti (*Trichocereus atacamensis* and *Oreocereus leucotrichus*), and summer annuals (Poaceae and Asteraceae). Salt-tolerant shrubs (*Atriplex imbricata*), cushion cacti (*Opuntia camachoi*), and a few annuals (Boraginaceae, Malvaceae, Portulacaceae, and Solanaceae) characterize the Prepuna from 2600 to 3200 m, where mean annual temperature is ~10°C and annual precipitation ranges from 20 to 70 mm. The Prepuna gives way to the Absolute Desert, a vast, barren landscape that lacks vegetation because of years or decades without any rain.

Plant macrofossils were identified from 49 dated middens between 3200 and 2400 m. Most of the middens come from Lomas de Tilocalar and Lomas de Quilvar at the southeastern end of Salar de Atacama (Fig. 2). Modern plant cover within 100 m of the middens, roughly the foraging range of the rodents, is <1% and is produced by <five species. The total number of taxa identified across all middens was 41, and individual middens contained from 6 to 25 taxa. We focused on grass point occurrence in fossil middens because local grasses are excellent indicators of both the amount and seasonality of past rainfall (Fig. 3); more importantly, grasses do not presently grow near any of our sites.

The lack of middens from some intervals, such as 35 to 22 ky B.P., may reflect aridity and decreased midden production rather than simple decay of older middens. Four middens, dated >40 ky B.P., suggest that degradation of older middens is not a major issue. We cannot totally rule out preservation factors, however, so we limit our inferences to the past 22 ky B.P. The oldest midden with a finite date (22 ky B.P.) has low taxonomic richness and grass abundance (Fig. 3), compared with middens dated at 16.2, 13.2, and 12.5 ky B.P. Clustering of 15 middens between 11.8 and 10.5 ky B.P., with rich florlas dominated by grasses (average point occurrence of 58%) and higher elevation shrubs, indicates that this was the wettest period of the past 22 ky. Midden florlas between 16.2 and 10.5 ky B.P. contain perennial *C*3 steppe grasses (*Stipa chrysophylla*, *Nasella arcuata*, and *Anatherostipa venusta*), summer-flowering *C*4 perennial grasses (*Enneapogon desvauxii* and *Pappophorum* sp.), *C*4 annual grasses (*Munroa decumbens*, *Aristida adscensionis*, and *Chondrosarn simplex*), summer annual herbs (*Schkahiria multiflora* and *Tagetes multiflora*), and Tolar shrubs (*Junellia seriphoides*, *Adesmia* sp., and *Krameria lappaceae*) and cacti (*Trichocereus* sp.) that no longer occur at the midden sites. *Nasella arcuata* is now rare in the central Atacama but common above 3800 m on the Bolivian Altiplano and in the Andes near the Peru-Chile border.

Fig. 1. Digital Elevation Map (DEM) of the subtropical Andes showing precipitation seasonality in the Atacama Desert and key sites. Approximate elevations are >4000 m (blue), 4000 to 3500 m (pink), 3500 to 3000 m, 3500 to 2500 m (brown), 2500 to 1000 (yellow), and <1000 m (green). Broad areas of pink denote the Bolivian/Peruvian Altiplano. The steep north-south gradient in rainfall seasonality between 24° and 26°S is attributable to the extreme rain shadow imposed on the easterly trades by the Chilean Andes in summer and the equally abrupt blocking of the southern westerlies by the South Pacific Anticyclone in winter.
and the total number of Tolar taxa declines sharply after 10.5 ky B.P. This pattern persists until after 7.1 ky, when Tolar taxa (Trichocereus sp., Krameria lappacea, and Junellia seriphoides) reappear. Mid-Holocene middens resemble modern assemblages but are punctuated by more taxa, occasional appearances of Tolar taxa, and C4 grasses (most notably Aristida adscensionis and Pappophorum sp.), with noticeable increases in grass point occurrence at 6.2, 5.1, 4.8, and 3.9 ky B.P. Ten middens from 6.2 to 3.9 ky average ~7% grass, whereas the remaining eleven middens postdating 3.0 ky B.P. average <2%.

Paleowetland deposits at Tilomonte provide comparable evidence of hydrological changes. Tilomonte encompasses two adjacent spring complexes (Tarajne and Rio Tulán) at the base of the Andes between 2500 and 2700 m, <10 km from the Lomas de Tilocalar and Lomas de Quilvar midden sites. Spring-related sediments are composed of fluvial sands and gravels, interbedded with organic-rich diatomites, tufas, and silt deposited in wetlands. Radiocarbon dates on carbonized wood, organic matter encased within tufas, and residual and humate fractions of organic mats provide a chronology of water-level fluctuations free from hard-water effects (6). Paleowetland deposits at Tarajne are higher above the current water table than those at Rio Tulán. The Tarajne deposits date between 15.4 and 9.0 ky B.P. (Fig. 4), thus recording when groundwater levels were highest during the late glacial–early Holocene. After 9.0 ky B.P., the water table dropped to near modern levels. Between 8.2 and 3.0 ky B.P., paleowetland deposits within Rio Tulán record a less pronounced water table rise of ~11 m above the current levels (Fig. 4). Eleven meters of incision by Rio Tulán accompanied a second water table drop between 3.0 and 0.8 ky B.P.

Synchronicity between Tilomonte and three wetland records argues for shared paleohydrologic controls and rapid responses to climate changes in their collective recharge area, the Chilean Andes. Lake levels on the southern Altiplano just to the east of Salar de Atacama display changes (7, 8) synchronous with wetlands at El Tarajne. Lakes rose between 15.5 and 14.0 ky B.P., peaked between 12.8 and 10.3 ky B.P., and disappeared between 9.5 and 9.0 ky B.P. (8) (Fig. 5). Paleowetland deposits at Rio Loa, Rio Salado, and Quebrada Puripica, fed by strongly contrasting hydrologic systems, also record the mid-Holocene discharge increase seen at Tilomonte (9).

The combined data from middens and wetland deposits provide a detailed and replicated record of climatic change during the past 22 ky B.P. The paucity of both kinds of deposits for the period 35 to 16.2 ky B.P. suggests either selective preservation or greater aridity that decreased both local vegetation and rodent activity and regional snowpack and recharge in the Chilean Andes. Between 16.2 and 10.5 ky B.P., and particularly between 11.8 and 10.5 ky B.P., lowering of species ranges by up to 1000 m suggests that annual precipitation increased to ~70 to 100 mm at our driest site (2600 m), which today receives ~20 mm, and to 150 mm between 3000 and 3200 m, which now gets ~50 to 70 mm. Southward displacement of northern species and preponderance of summer-flowering herbs and C4 grasses show that the precipitation increase happened in summer. Wetland deposits at Tilomonte identify higher groundwater levels between 15.4 and 9.0 ky B.P., consistent with increased precipitation in the Chilean Andes, but are not specific about
the seasonality of precipitation or time of maximum recharge and discharge (Fig. 4). Greatly diminished grasses abundance and taxonomic richness suggest abrupt drying between 10.5 and 10.3 ky B.P. (Fig. 3), whereas Tilomonte stratigraphy indicates lowering of the water table to modern levels between 9 and 8 ky B.P. (Fig. 4). After 8.0 ky B.P., the water table gradually rose until 3.0 ky B.P. This is consistent with slightly more mesic midden florals between 7.0 and 3.0 ky. The periods 9 to 8 ky B.P. and after 3.0 ky B.P. mark times when vegetation and groundwater tables approached modern levels, perhaps the driest episodes in the past 22 ky B.P.

Our well-dated record for the central Atacama differs in several respects from paleoclimatic reconstructions elsewhere in the central Andes. Such discrepancies are common in paleoclimatic records throughout the region and may arise from poor dating, differences in regional climatologies across the broad (0° to 24°S) areas under discussion, or ambiguities between precipitation and temperature effects on glacial and lake budgets. For the past 22 ky B.P., the main disagreement is in the timing of maximum wetness and aridity since the Last Glacial Maximum. On the Bolivian Altiplano, maximum wetness is inferred from integration of the present Poopó, Coipasa, and Uyuní basins into the Taucá Phase highstand (3760 m), forming a ~50,000 km² paleolake (10, 11). The chronology for the Taucá Phase, based on 14C dates of lacustrine carbonates, shows that lake levels began rising at ~18.4 ky B.P., reaching the highest stand between 16.2 and 14.0 ky B.P. Lake levels dropped sometime after 13.9 ky B.P. (Ticaña Event), but a moderate-sized lake (Coipasa Event) appeared persistently until 9.5 ky B.P. (11/2) (Fig. 5). Problems with hard-water effects on 14C dates and detrital contamination on U-series dates make the lake desiccation chronology uncertain. The relation between lake desiccation and deglaciation in the central Andes is poorly known. In the tropical Andes (0° to 15°S), rapid ice recession is documented by 12.8 ky B.P. (12), well before the period (11.8 to 10.5 ky B.P.) of maximum summer precipitation in the central Atacama.

A clear discrepancy with other regional records is our inference for a wet phase between 8 and 3 ky B.P., with groundwater discharge peaking between 5 and 3 ky B.P (Fig. 4).

Although mid-Holocene middens contain mostly summer-flowering species, we acknowledge the possibility that greater winter snowpack in the High Andes could have raised regional groundwater levels without substantially increasing precipitation in the Prepuna–Absolute Desert transition. The mid-Holocene wet period in the central Atacama contrasts with the extreme lowstand of Lake Titicaca (15° to 17°S), 100 m below the present water level, between >6 and 3.8 ky B.P. (13), with high soluble and insoluble dust concentrations in the Sajama ice cores from 9000 to 3000 years ago (14), and with limnological evidence for drier conditions from Laguna Miscanti (15), just 30 km east of the Tilomonte spring complex (Fig. 2). Evidence for mid-Holocene aridity from Laguna Miscanti and other saline lakes on the Chilean Altiplano is uncertain because local 14C reservoir effects require age corrections of several thousand years (7, 8). The Lake Titicaca lowstand, however, is well dated and corroborated among multiple lines of evidence in the immediate vicinity of the lake (13). One exception is a wet episode between 4.5 and 3.9 ky B.P. recorded by fluvial terraces and shallow lakes along the Rio Desaguadero, the only outlet to Lake Titicaca (16). This wet episode was not registered in the Lake Titicaca cores but is evident in a pollen stratigraphy from Laguna Seca (~18°S, 200 km south of Lake Titicaca and only 30 km southwest of Sajama (17)). Resolution of these discrepancies may rest on better definition of response times and sensitivities to climatic events of varying duration and magnitude for vegetation, small and large lakes, and alluvial and groundwater systems.

Fig. 5. Estimates (solid lines) of lake-level and water-table fluctuations reconstructed from calibrated 14C ages or inferred ages (diamonds) from (A) Salares de Coipasa and Uyuní (11), (B) Laguna Lejía in the High Atacama (7, 8) and (C to E) wetland deposits from Quebrada Puripica (9) and our study sites.
5. Arged are reported as calendar kyiories B.P. All 14C dates in the text and figures were converted to calendar ages with the program CALIB v. 4.0 (Stuiver and Reimer, Radiocarbon 35, 215 (1993)). Grass abundance was measured as point occurrence on a 120-cell rectangular grid overlain on a sorting tray. A sediment matrix splitter was used to randomly segregate 100 ml of plant debris from each midden. Midden debris was spread uniformly across a 120-cell rectangular grid (each cell is 1 inch by 1 inch or 6.45 cm²); grass abundance was measured as point occurrence on the grid (the number of cells out of 120 where grass blades, florets, or seeds were identified). All plant remains were identified to the highest taxonomic level possible with a reference collection gleaned from herbarium specimens and our own field studies. In general, we met comparable success as with identifications of plant macrofossils in North American pacrat middens.

6. Vascular plant remains, including carbonized wood, twigs, and leaves, are abundant in the wetland deposits. Other organic-rich samples are too fine grained or decomposed to identify the source and could occur in hard-water effects on 14C dates if partly algal in origin. Groundwater from springs in the Atacama displays hard-water or reservoir effects, typically containing 25±6% 14C % modern carbon [R. Aravena and D. Suzuki, Water Resources Res. 35, 2887 (1999)]. Evidence against a hard-water effect includes excellent stratigraphic coherence between deposits of 4.9 and 3.5 ky B.P. Upper portions of the mid-Holocene wetland deposits are too fine-grained to be dated by 14C methods on humates from a modern black mat.


9. Extensive paleowetland deposits dating to the mid-Holocene are present on both the Río Salado and Río Loa, located 150 km north-northwest of Tilomonte. Mid-Holocene wetland deposits crop out 5 to 7 m above the modern wetlands. At the Río Loa, the base of these deposits is not exposed, whereas samples from the middle and top of the section yield ages of 4.9 and 3.5 ky B.P. Upper portions of the mid-Holocene wetland deposits at Río Salado yielded ages between 6.7 and 4.3 ky B.P. Wetland deposits at Quebrada Puripica, dating between 7.1 and 4.4 ky B.P., were initially interpreted as paleowetland deposits formed from side-canyon damming by debris flows (Grosjean et al., Paleobiology 26, 2887 (1999)). We found that the wetland deposits at Puripica were not debris-flow dammed but instead are similar to the deposits at Tilomonte and formed as a result of higher ground-water levels during the mid-Holocene.


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Structural Evidence for Evolution of the β/α BarreI Scaffold by Gene Duplication and Fusion

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Enzymes from metabolic pathways are among the best-studied examples of protein function and structure. There are catabolic pathways, like glycolysis, or anabolic pathways, like tryptophan biosynthesis, where an almost complete database of protein structures is available. It is evident that many enzymes in these pathways have evolved either by gene duplication and fusion or by the assembly into functional oligomers (1, 2). Molecular relations of proteins of the histidine and tryptophan biosynthesis pathways were postulated by structure prediction (3) and multisequence alignment methods (4). Many proteins in these pathways and other biological processes are folded as eightfold βα barrels (5, 6). Their evolution has been discussed (7, 8) and has recently been mimicked in a directed evolution experiment (9). Here, we compare atomic structures of two enzymes in the histidine biosynthesis pathway and provide evidence for the evolution of βα barrels from an ancestral half-barrel. The observation that ancestral folding units may comprise subdomain structural units has broad applications in searching genome sequences for related gene products and their functional interactions in biological processes (2, 10–12).

The crystal structures of the monomeric gene products HisA and HisF from the hyperthermophile Thermotoga maritima were deter-