Even though the water molecules are rotationally cold after the supersonic expansion, the ground state of ortho-water is \( J = 1 \). Hence, we expect a further splitting of the trajectories, corresponding to the different possible projections of the rotational axis with respect to the magnetic field direction (9). Figure 2, B and C, demonstrate the substantial effect that the velocity spread and the finite size of the source have on the width of the focused beam in our setup; in contrast, the rotational splitting for water molecules in the \( J = 1 \) rotational state is small and has only a minor effect (<5%) on the final width of the water beam.

Figure 3 shows the experimental profile we measured when scanning the perpendicular position of the aperture. The aperture was located 1.6 m from the source. The profile of the water partial pressure (blue circles) shows that our setup successfully produces a focused beam of ortho-water, with a narrow (1.5-mm FWHM) profile. The spatial focusing of ortho-water, as opposed to the diverging trajectories of para-water, necessarily leads to a very low content of para-water in the vicinity of the signal peak intensity: For example, a region 1.5 mm in diameter centered around the signal peak contains only 3% of para-water molecules (10). In contrast, sampling the water off the main peak (moving the aperture from the center) allows progressive enrichment of the para-water content of the beam up to a maximal content of 50% para-water; however, the intensity is generally weaker for the unfocused para-water beam.

The dashed line in Fig. 3 is the calculated profile of the beam, at a distance of 1.6 m from the source, taking into account the diameter of the scanning aperture (0.5 mm) and the three mechanisms mentioned above: a 10% velocity spread; a 0.5 mm diameter, given by the skimmer diameter; and a rotational magnetic moment value of 0.66 nuclear magneton. (19). The calculated peak width is in good agreement with the experiment, supporting our estimation of the velocity distribution width (20). To confirm that the focusing effect is due to the proton nuclear magnetic moment, we replaced the \( {\text{H}}_2^{19}\text{O} \) water with deuterium oxide (\( {\text{D}}_2\text{O} \), using the same mixing ratio with krypton. This control experiment was practically identical in terms of the beam expansion parameters, but \( {\text{D}}_2\text{O} \) has a substantially smaller nuclear magnetic moment and was essentially unfocused by our setup, leading to the broad and low-intensity profile at the detector (Fig. 3, black diamonds). Finally, we also performed an aperture scan, using a beam of pure water vapor (without krypton; Fig. 3, red squares). The lack of a heavy monatomic carrier gas in the expansion results in molecular velocities of approximately 1000 m/s; as expected, we did not see any substantial magnetic focusing in this case.

The feasibility of producing a focused ortho-water molecular beam, which can be directed at the surface of a sample held under UHV conditions, enables a wide range of experiments. In particular, the focused molecular beam can be integrated with conventional surface-sciences phenomena. A review of the differential ad- sorption characteristics of the spin isomers and empirically address this controversial topic. Other promising approaches for spin isomer separation have been reported based on rotational state selection (21–23). However, a fundamental dif- ference between rotational state selection and the magnetic focusing we used is our ability to select a particular spin projection, a promising feature for future nuclear magnetic resonance (NMR) experiments.

Because our apparatus includes an adiabatic transition element from a hexapole field to a dipole field (24), followed by dipolar holding fields, the water molecules reach the end of the beam line with a well-defined spin projection. Thus, adsorbing these molecules onto a surface located in a magnetic field will lead to the formation of hyperpolarized water surface layers. The lifetime of the spin polarization on the surface is currently unknown; however, if it is sufficiently long to allow NMR measurements, a dramatic increase in NMR signal could be obtained in future experiments (for example, five orders of magnitude relative to a room-temperature-1-T NMR experiment).

Finally, we emphasize that the experimental setup we present can be extended to focus a variety of other relatively light molecules in a spin-selective fashion. The mass of the carrier gas and the nozzle temperature need only be tuned in accord ance with the magnetic moment of the molecule, thus obtaining the desired focal length. A demonstration of such an experiment with methane is shown in fig. S1.

References and Notes
patchy fossil record (3) that, until recently, seemingly lacked evidence of the earliest growth stages: embryos and neonates. Consequently, ideas concerning the reproductive biology of these animals have been largely inferred via comparisons with birds, from which it was assumed that pterosaurs were oviparous, undertook contact incubation (implying rigid-shelled eggs), and hatched altricial young that were cared for by their parents until they could fly (1, 4–6).

The recent discovery of eggs with embryos from the Lower Cretaceous of China (7,8) and Argentina (9) and the recognition of hatching and/or early juvenile growth stages in several species of pterosaurs (2, 4, 10–15) have provided direct insights into pterosaur reproduction (Fig. 1). These finds have confirmed that pterosaurs were oviparous but, rather surprisingly, hint at a reptilian mode of reproduction involving highly precocial hatchlings that required little or no parental care (2) and a parchment-like eggshell, from which it has been inferred that the eggs were buried (8, 16, 17). These conclusions are at odds with the general assumption that pterosaur locomotory ability, physiology, respiration, and ecology were more like those of birds and bats than those of reptiles (1, 2, 5, 6, 18). Here we describe a pterosaur preserved in association with an egg (Fig. 2 and fig. S1). This fossil provides direct evidence for the gender of pterosaurs and implies that their reproduction was essentially reptilian in nature.

The fossil, ZMNH (Zhejiang Museum of Natural History, Hangzhou, Zhejiang Province, China) M8802, was purchased by the Zhejiang Museum of Natural History from a local farmer. It was recovered from upper Middle to lower Upper Jurassic sedimentary rocks of the Tiaojishan Formation (160 Ma) at Linglongta in Liaoning Province, China (19–22). The adult individual, seen in ventral aspect (Fig. 2A and fig. S1), is represented by a nearly complete skeleton, the missing parts of which are probably preserved on the counterslab (now apparently lost). The skeleton is naturally articulated, except for the left forearm, which is broken at its midpoint, and represents a medium-sized pterosaur with a skull length of 150 mm and an estimated wingspan of about 0.78 m (table S1). A combination of characters, including a relatively large skull with a highly elongate confluent nasoantorbital opening; slender, well-spaced teeth; a relatively long neck; a long tail; a short metacarpus; and a long fifth toe with a distinctly curved second phalanx permit assignment of this pterosaur to the basal monofenestratan *Darwinopterus* (20), already known from more than 10 individuals from the Tiaojishan Formation.

![Fig. 1. The fossil record of growth stages in *Darwinopterus* and other pterosaurs. Phylogeny is based on (20). Open circle, fossil found or identified during the past decade; solid circle, older record. Abbreviations are as follows: adult, A; egg and/or embryo, E; hatching, H; juvenile, J; subadult, S.](image)

![Fig. 2. A female individual of *Darwinopterus* associated with an egg from the Tiaojishan Formation of Liaoning Province, China (ZMNH M8802). (A) Skeleton with fractured forearm (arrow) and associated egg (double-headed arrow). Scale bar, 5 cm. (B) Sacrum, pelvis, and the associated egg. Scale bar, 2 cm. Abbreviations are as follows: articular end of sacral rib, as; caudal vertebrae, ca; cervical vertebrae, cv; dorsal vertebrae, dv; femur, f; humerus, h; ilium, il; ischiopubic, ip; impression of egg, ie; mandible, md; pes, ps; prepubis, pp; radius, ra; rib, ri; scapulocoracoid, sc; skull, sk; sacral vertebrae, sv; ulna, u; tail, ta; tibia, t; wing-phalanx 2, wph2.](image)
An egg, preserved immediately posterior to the pelvis (Figs. 2B and 3), indicates that this individual was female. Such associations, which permit unequivocal assignment of gender, are rare in the vertebrate fossil record. We suppose that this individual experienced a violent accident that fractured the forearm, rendering the pterosaur incapable of flight and precipitating her into a water body. After this, she drowned, her carcass became waterlogged, sank to the bottom, and, as decay processes began, the egg was expelled from her body.

Individual bony elements are well ossified, the skull bones are co-ossified, and composite structures including the scapulocoracoid, synarcapsals, synsacrum (fused sacral vertebrae and sacral ribs), pelvis, tibia and fibula, and tibia and proximal tarsals are fully fused, the one exception being the contact between the synsacrum and the pelvic girdles, which appears to have remained unfused. This general pattern of co-ossification and fusion indicates that ZMNH M8802 had reached the end of the main growth phase (4, 10, 13, 14) and, as the presence of the egg implies, had already shifted resource utilization from growth to reproduction.

The pelves of ZMNH M8802, certainly a female, and YH-2000 (Yizhou Museum, Yixian, Liaoning Province, China), a putative female, are relatively large. That of the former is almost the same size as the pelvis of ZMNH M8782, a putative male that in other respects is 113 to 126% larger than ZMNH M8802 (20) table S2). In addition, the pelvic girdles of ZMNH M8802 and YH-2000 splayed outward, did not meet along the ventral midline, and were not fused to the synsacrum (Fig. 2B), presumably allowing for some flexure during egg laying and forming a relatively wide pelvic canal. In contrast, the pelves of ZMNH M8782 and HGM 41HIII-0309A (Henan Geological Museum, Zhengzhou, Henan Province, China), another putative male, were relatively small (table S2), with pelvic girdles that appear to have been fused to the sacrum and to each other along the ventral midline (20, 21), resulting in a relatively narrow pelvic canal.

Sexual dimorphism in the pelvis of *Darwinopterus* is correlated with bimodal variation in the development of the cranial crests of this pterosaur: Females (ZMNH M8802 and YH-2000) lack a crest (Fig. 2A) (20), whereas males (ZMNH M8782 and HGM 41HIII-0309A) have a well-developed sagittal bony crest extending from the caudal end of the rostrum anterior to the nasoantorbital opening to the apex of the cranium (20, 21). Similar bimodal variation in pelvic morphology, observed in *Pteranodon* (23) and ornithocheirids, and cranial crests, present in approximately 40% of the 133 species of pterosaur described to date (1, 2), has often been interpreted as sexual dimorphism (1, 2, 23–26). The evidence from *Darwinopterus* supports this hypothesis.

The single egg is preserved as a continuous positive impression, immediately posterior to the pelvis (Figs. 2B and 3). A small portion of the impression that overlays the tail and thus was at a slightly higher level appears to have pulled away with the counterslab. The impression is distinguished by its yellowish-brown color and the presence of several surface features superimposed on a smooth background. The outer region bears multiple, subparallel, narrow concentric folds that pinch out laterally. Their peripheral location and greater frequency toward the poles are consistent with compression of the egg during early stages of burial. The inner region of the impression has an uneven, crumpled appearance and, at low magnifications, a fine pitting, possibly representing pore-like holes in the surface ornament of the egg. There is no trace of mineralized shell, cracking, or crazing, although bivalves and conchostracans from the Tiaojishan Formation have intact shells (19, 27), and the external features indicate that the egg had a relatively soft, parchment-like shell as reported for other pterosaurs (7, 8, 16, 17) and, for example, extinct squamates (17).

The presence of shell membranes that were sufficiently well developed to leave an impression suggests that the egg had reached a late stage of development and was probably close to oviposition. The impression has a prolate spheroid shape, is symmetrical about its major and minor axes, and measures 28 mm in length by 20 mm in breadth. The original egg may have been somewhat smaller, but in any case its maximum possible breadth, 20 mm, is consistent with our estimate of 20 mm for the width of the pelvic canal (22). Moreover, passage of the soft-shelled egg was probably assisted by its compliance and by flexure of the pelvic girdles.

The absence of evidence for taphonomic distortion of the fossil and the likelihood that the egg was close to its size at oviposition allows its mass at oviposition to be estimated [see (22)]. This initial egg mass (IEM), estimated to be 6.1 g, is relatively small compared to estimates of adult female mass (FM) and is similar to IEM/FM ratios for extant reptiles such as squamates (Fig. 4). The one other pterosaur for which this value can be estimated, *Pterodaustro* (9, 14), shows the same relationship. Extant birds of similar mass to that of ZMNH M8802, estimated to lie between 110 and 220 g (22), typically produce eggs that are nearly twice, and possibly up to almost three times, as large as the estimated mass of the fossil egg (10.3 to 17.8 g as compared to 6.1 g). This is most likely because these rigid-shelled eggs must contain all the resources needed for the development of the embryo to hatching stage. In contrast, evidence for a parchment-like shell points to the burial of pterosaur eggs in a nest (2, 16, 17), which would have permitted a substantial increase in mass after oviposition via water uptake during incubation. Assuming that the rate of water uptake was comparable to that seen in eggs of extant squamates, we estimate that the final egg mass for ZMNH...
Changes in Climatic Water Balance Drive Downhill Shifts in Plant Species’ Optimum Elevations

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Uphill shifts of species’ distributions in response to historical warming are well documented, which leads to widespread expectations of continued uphill shifts under future warming. Conversely, downhill shifts are often considered anomalous and unrelated to climate change. By comparing the altitudinal distributions of 64 plant species between the 1930s and the present day within California, we show that climate changes have resulted in a significant downward shift in species’ optimum elevations. This downhill shift is counter to what would be expected given 20th-century warming but is readily explained by species’ niche tracking of regional changes in climatic water balance rather than temperature. Similar downhill shifts can be expected to occur where future climate change scenarios project increases in water availability that outpace evaporative demand.

Climatic warming during the 20th century has led to a variety of responses from biota (7), including changes in phenology for plants (2, 3) and animals (4, 5), and shifts in the geographic distributions of species poleward in latitude (6, 7) or uphill in elevation (8, 9). Because climate-change scenarios project warming during the 21st century (10), changes in the distributions of species are predicted to continue, with shifts toward higher elevations and latitudes projected for species that are able to track changes in temperature (11). The assumption that temperature is the principal factor defining species’ distributions ignores the fact that many species, including plants, are constrained by energy and water availability (12, 13). Consequently, considering changes in temperature alone may be inadequate for understanding distributional shifts of plant species. Consistent with this, there is ample evidence of stasis and even downhill shifts in species’ distributions despite climatic warming (14–16). These seemingly inconsistent responses are attributed to changes in competitive interactions at range margins (17), human-induced landscape modification (14), legs in the effect of climatic warming (15), or idiosyncratic responses of individual species (18). As such, there has been limited progress in understanding the drivers of shifts in species’ distributions and their associated mechanisms.

We sought to determine how the altitudinal distributions of vascular plant species in California, USA, have changed during the 20th century and whether changes, if any, could be attributed to changing climatic parameters. We defined our study area based on the availability of long-term climate station data and spatial coverage of vegetation survey data in both historical (1930–1935) and modern (2000–2005) time periods (19). This region includes approximately one-half of the state (177,000 km²) and encompasses most of the major mountain ranges north of 35° latitude (Fig. 1). Mean annual temperatures in California increased by ~0.6°C during this time period, with warming occurring across the entire state (19). Changes in precipitation exhibited regional-