speculate that the 30-ky cycle is restricted to the tropical Indo-Pacific Ocean (*14*), because the ENSO is characteristic of that area. However, the CO_2 record from the Vostok ice core also reveals a 30-ky cycle (*30*). Cross-spectral analyses indicate that the productivity series are highly coherent with the CO_2 record at the 30- and 23-ky periods, and that low CO_2 values are associated with high productivity (Fig. 3) (*6*). It is therefore possible that, with primary production acting as a significant sink in the carbon cycle, the 30-ky record in global CO_2 is the signature of ENSO-like control of biological production in the equatorial Indo-Pacific. This is consistent with a significant role of the low-latitude biological pump in controlling atmospheric CO_2 concentrations (*31*).

We have identified two independent forcings responsible for 60% of the long-term equatorial Indo-Pacific productivity dynamics. The first forcing concerns the response of the depth of the equatorial thermocline to global climatic variations. The second forcing is related to changes in the equatorial east-west thermocline tilt and is linked to the 23-ky period of Earth's precession. This precession-related variability could reflect the influence of low-latitude insolation on ENSO, as a predictive ENSO model stipulates (*16*). A similar dual "precession-glacial" forcing has been described recently on New Guinea corals (*32*). The 23-ky signal precedes ice volume variations by about 2 ky. Thus, long-term ENSO dynamics provide a possible causality for the growing body of evidence that low-latitude climates are early responders to orbital forcing (*9, 10, 22, 33–35*). Although minor, a 30-ky period is also evidenced. It is characteristic of the equatorial Indo-Pacific coherent with a similar period found in Vostok CO_2 record. That coherency attests to the importance of biological carbon fixation in the equatorial Indo-Pacific in controlling variations of atmospheric CO_2. Therefore, because of its early response and its possible effect on the carbon cycle, the 23-ky ENSO-like cycle is likely to have played a significant role in global climate dynamics.

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39. We thank IFRTP for financial and technical support for the Marion-Dufresne coring during IMAGES III cruise, Lamont-Doherty laboratory core repository for the samples from Core RC13-110, G. Ganssen for providing samples and stratigraphy from Core TY93-929, and M.-P. Aubry, L. Lourens, and two anonymous reviewers for reviewing an earlier version of the manuscript. Supported by NATO (L.B.) and by INSU ad'hoc ocean and CNRS ECLIPSE grant (L.B.).

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Embryonic Skulls of Titanosaur Sauropod Dinosaurs

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Little is known about the cranial anatomy of the taxonomically diverse and geographically widespread titanosaurs, a paucity that has hindered inferences about the genealogical history and evolutionary development of the latest sauropod dinosaurs. Newly discovered fossil eggs containing embryonic remains from the Late Cretaceous of Argentina provide the first articulated skulls of titanosaur dinosaurs. The nearly complete fetal skulls shed light on the evolution of some of the most notable cranial features of sauropod dinosaurs, including the retraction of the external nares, the forward rotation of the braincase, and the abbreviation of the infraorbital region.

Chiappe *et al.* (*1*) reported embryonic remains of sauropod dinosaurs from incomplete skull remains from the Late Cretaceous nesting site of Auca Mahuevo (Patagonia, Argentina) (*2*). Six newly discovered eggs from this site containing exquisitely preserved skulls provide nearly complete and articulated cranial material of sauropod embryos (*3, 4*). The subtriangular skulls (Fig. 1) have large, circular orbits exceeding one-third of the cranial length. A large, triangular antorbital fenestra perforates the short snout, whose dorsal margin is slightly stepped. A tall premaxilla broadly sutures to a robust maxilla bearing slender and cylindrical teeth. The enamel of the tooth crowns is smooth and devoid of serrations. The dentigerous portion of the maxilla occupies the rostral half of the element. The maxilla defines the rostral margin of a large ventral notch (Fig. 1A), which is caudally bound by the jugal and the quadratojugal. A similar large, ventral notch was reported for the Malagasy titano-

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saur *Rapetosaurus krausei* (*5*). The lacrimal is rostrodorsally inclined at a 45° angle, differing from the subvertically to caudodorsally oriented lacrimal of adult sauropods (*6*). The jugal is rostrocaudally long and, in contrast to adult sauropods, takes part in the ventral margin of the skull (Fig. 1). The inverted L-shaped postorbital bears a long and slender, rostrally slanting jugal process. Scleral plates are preserved inside the orbit of some specimens (e.g., MCF-PVPH-147, MCF-PVPH-272). The long, distally expanded rostral process of the quadratojugal extends to the middle of the orbit. Its dorsal process is short, without contacting the squamosal. The elongate and rostroventrally inclined infratemporal fenestra has a central constriction. Its ventral end barely underlies the caudoventral corner of the orbit. The quadrate is rostroventrally inclined at an angle of about 130° from the horizontal. This and the equivalent inclination of the squamosal (Fig. 1) suggest some degree of braincase rostral rotation. The width of the frontal and parietal (*4*) indicates that the embryos had a broad skull, with a width greater than half of its length. The lower jaw is low, especially in its rostral portion. Its caudal half is excavated by a large fenestra, unusual among sauropods (*7*).

Previously reported embryos from Auca Mahuevo (*8*) revealed characters supporting their identification as neosauropods within eusauropod dinosaurs (*9*). This phylogenetic hypothesis is corroborated by the newly discovered specimens. Anatomical information added by the new embryonic skulls includes several eusauropod synapomorphies (e.g., a snout with stepped rostral margin, a rostrally extended quadratojugal, the lack of quadratojugal-squamosal contact, and absence of an antorbital fossa) (*10*), as well as other derived characters diagnostic of neosauropods (e.g., postorbital bar broader transversely than rostrocaudally) (*10*). In addition, this new anatomical information clarifies the embryonic identification beyond Neosauropoda. The low rostral portion of the mandible is a derived feature known for the titanosaurs *R. krausei* (*5*), *Antarctosaurus wichmannianus* (*11*, *12*), and an undescribed, nearly complete skeleton from the Río Colorado Formation of Patagonia (*13*)—the same formation containing the embryos reported here. Furthermore, the extreme width of the skull and the presence of a large mandibular fenestra are derived characters also reported for the latter titanosaur (*13*), and a distinct ventral notch similar to that found caudal to the maxillary dentigerous margin of the embryos is present in *R. krausei* (*5*). These apomorphic similarities suggest that the Auca Mahuevo embryos are titanosaur sauropods (*14*).

Titanosaur skulls are very incompletely known (*15*–*17*). The specimens reported here are the first articulated skulls of this widespread sauropod clade. Notwithstanding their young ontogenetic age, anatomical information available in these embryos illuminates aspects paramount to sauropod skull evolution such as the retraction of the external nares, the forward rotation of the braincase, and the shortening of the infraorbital region.

The external nares are partially (e.g., *Camarasaurus lentus*, *Brachiosaurus brancai*) to completely (e.g., diplodocids, titanosaurs) retracted in all eusauropods (*5*, *10*), and the lacrimal—which roughly marks the narial caudal end—is oriented vertically or slightly caudally. It has been suggested (*17*) that the retraction of the nares could have been coupled to the braincase rostral rotation typical of diplodocids (*7*) and some titanosaurs (*5*, *13*), a modification that orients ventrally the occipital condyle. In the Auca Mahuevo embryos, the presence of dorsorostrally oriented lacrimals (Fig. 1, A and B) and frontals that nearly reach the rostral margin of the orbit (Fig. 1B) indicates that the caudal margin of the external nares laid in front of the orbit, with the narial opening dorsorostral to the antorbital fossa. Yet, the orientation of the quadrate and squamosal suggests some degree of braincase rotation. As with other

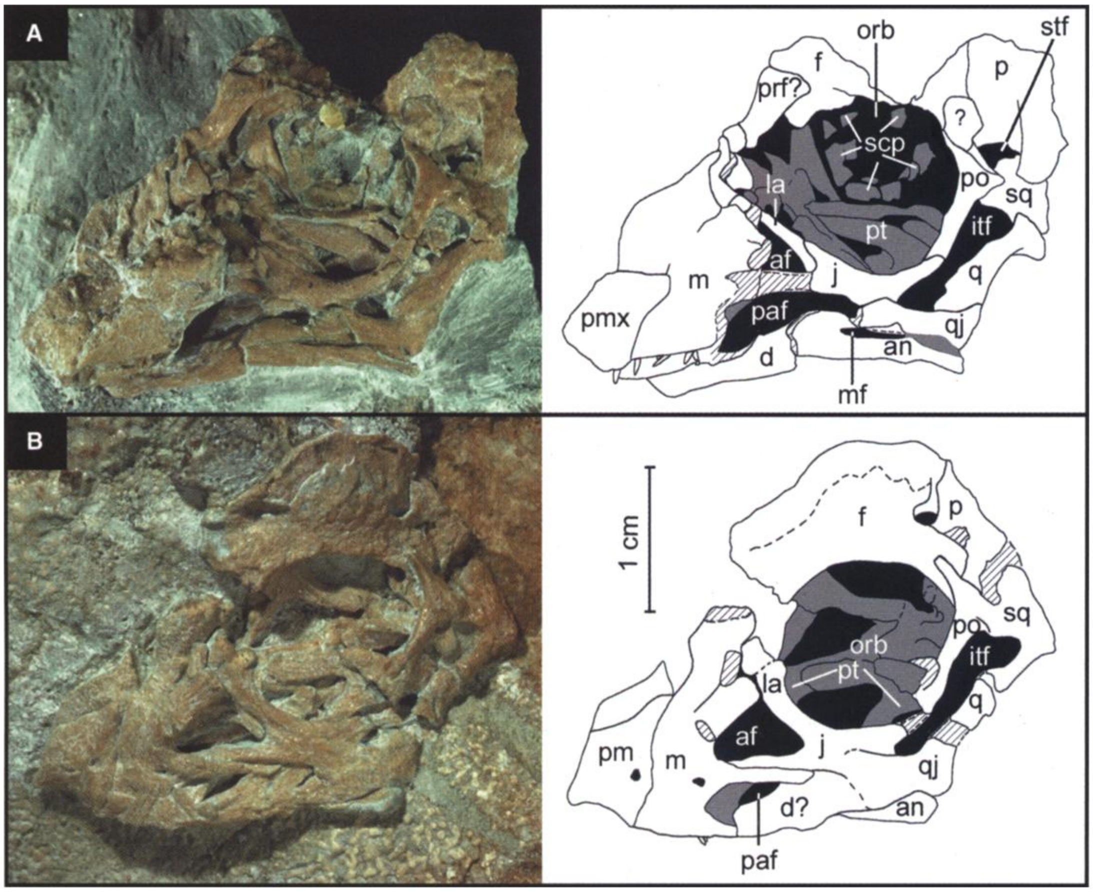

Fig. 1. Embryonic titanosaur skulls from Auca Mahuevo in left lateral view (photograph and interpretive drawing). (**A**) MCF-PVPH-272. (**B**) MCF-PVPH-263. Abbreviations: af: antorbital fenestra; an: angular; d: dentary; f: frontal; itf: infratemporal fenestra; j: jugal; la: lacrimal; m: maxilla; mf: mandibular fenestra; orb: orbit; p: parietal; pmx: premaxilla; po: postorbital; prf: prefrontal; pt: pterygoid; q: quadrate; qj: quadratojugal; scp: scleral plates; sq: squamosal; stf: supratemporal fenestra.

primitive features of the embryos (e.g., short snout, circular orbit, and elongated jugal), it is possible that the position of their nares migrated backwards during ontogeny. The extent to which ontogenetic development could have affected the partially to minimally retracted nares of the embryos is uncertain because their position (either partially or fully retracted) remains unclear for most adult titanosaurs (*15*, *16*), but in the newly described *R. krausei*, the external nares are placed on the top of the skull (*5*). The new embryonic evidence contradicts previous ideas coupling narial retraction to quadrate and braincase rostral rotation, which need not have evolved in concert (*16*).

Another notable transformation of the cranial architecture of sauropod dinosaurs is the abbreviation of the infraorbital region characteristic of neosauropods (*6*). In these dinosaurs, the jugal is short and does not contribute to the ventral margin of the skull. It has been suggested (*10*) that the evolution of this apomorphic position of the jugal could have been correlated to the infraorbital shortening experienced by these sauropods. The participation of the jugal in the ventral margin of the new embryonic skulls, whose orbital region is unabbreviated (Fig. 1), is congruent with this suggestion.

The discovery of the new embryonic sauropod skulls provides another example of how developmental data inform our understanding of evolutionary events (*18*). The new ontogenetic evidence suggests that whereas the narial retraction and braincase rotation of the sauropod skull likely evolved independently from each other, the infraorbital abbreviation and the exclusion of the jugal from the ventral margin of the skull could have evolved in concert.

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3. All embryonic remains from Auca Mahuevo belong to the vertebrate paleontology collection (MCF-PVPH) of the Museo Municipal "Carmen Funes" in Plaza Huincul (Province of Neuquén, Argentina).
4. The skull length of the best-preserved specimen (MCF-PVPH-272) is ~35.0 mm from the proximocaudal end of the quadrate to the tip of the rostrum; the horizontal length of its orbit is 13.5 mm. The parietal width, measured from its contribution to the supratemporal fenestra to the interparietal suture, is about 7.6 mm and 8.3 mm in MCF-PVPH-272 and MCF-PVPH-250, respectively. The teeth of the new and previously reported embryos are ~2.0 mm in length (*1*). Estimates based on limb measurements suggest that the total length of the most advanced embryos was ~300 mm (*20*).
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9. Wilson and Sereno (*10*) phylogenetically defined the clade Neosauropoda as the common ancestor of the Late Jurassic diplodocid *Diplodocus longus* and the latest Cretaceous titanosaur *Saltasaurus loricatus* plus all its descendants. These authors also defined the more inclusive clade Eusauropoda as sauropods more closely related to *S. loricatus* than to the Early Jurassic *Vulcanodon karibaensis*.
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Effects of Helpers on Juvenile Development and Survival in Meerkats

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Although breeding success is known to increase with group size in several cooperative mammals, the mechanisms underlying these relationships are uncertain. We show that in wild groups of cooperative meerkats, *Suricata suricatta*, reductions in the ratio of helpers to pups depress the daily weight gain and growth of pups and the daily weight gain of helpers. Increases in the daily weight gain of pups are associated with heavier weights at independence and at 1 year of age, as well as with improved foraging success as juveniles and higher survival rates through the first year of life. These results suggest that the effects of helpers on the fitness of pups extend beyond weaning and that helpers may gain direct as well as indirect benefits by feeding pups.

In social mammals whose young are reared principally by their parents and are rarely (or never) fed directly by other group members, competition for resources commonly increases in large groups, and breeding success either declines with increasing group size or shows no consistent relation to it (*1*, *2*). In contrast, positive relations between breeding success and group size are common in social mammals whose young are reared by helpers (*3*–*8*). Although these correlations suggest that the presence of helpers benefits juveniles in cooperative species, the ecological and behavioral mechanisms underlying them are poorly understood, and group size could affect several different processes that influence juvenile survival, including predation, infanticide, and starvation (*3*).

Like other social mammals whose young receive much of their food from helpers, juvenile survival increases in larger groups of Kalahari meerkats, *Suricata suricatta* (*9*). This cooperative mongoose lives in groups of 2 to 30, consisting of a dominant male and

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