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8. A celestial mechanics experiment, similar to the Galileo experiment discussed here, was included on Pioneer 10 and 11 but not on Voyager. Previous results on the gravitational field of the Jupiter system can be found in G. W. Null, J. D. Anderson, S. K. Wong, *Science* **188**, 476 (1975); J. D. Anderson, in *Jupiter*, T. Gehrels, Ed. (Univ. of Arizona Press, Tucson, 1976), pp. 113–121; G. W. Null, *Astron. J.* **81**, 1153 (1976); J. K. Campbell and S. P. Synnott, *ibid.* **90**, 364 (1985). Because of the close Galileo flybys of Io and Europa, our recommended standard errors are considerably smaller than earlier realistic errors.
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Juvenile Skeletal Structure and the Reproductive Habits of Dinosaurs

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Skeletal ontogeny in extant archosaurians (crocodilians and birds) indicates that the morphology of the perinatal pelvic girdle is an indicator of overall developmental maturity [that is, altriciality (nestbound) versus precociality (mobile and relatively independent)]. Comparison of the skeletal anatomy of perinatal extant archosaurians and perinatal dinosaurs suggests that known dinosaur hatchlings were precocial. These data are consistent with the overall similarity in nesting behavior of dinosaurs and modern crocodilians.

Fossils of juvenile dinosaurs can provide key information regarding dinosaur life history and physiology. To evaluate whether hatchling dinosaurs were altricial or precocial, we examined the skeletal structure in a variety of extant, perinatal precocial birds [emu (*Dromaius*), Mallee-Fowl (*Leipoa*), ostrich (*Struthio*), brush turkey (*Talegalla*)], perinatal altricial birds [macaw (*Ara*), cockatoo (*Cacatua*), eagle (*Haliaeetus*), starling (*Sturnus*)], and perinatal crocodilians (*Alligator*, *Caiman*) (all crocodilians are precocial at birth) and compared their characteristics with the skeletal features of perinatal dinosaurs (*1*).

This comparison reveals that the extent of ossification of the pelves at hatching may be a reliable indicator of the altricial or precocial nature of archosaurian neonates. Specifically, the pelves of late-fetal crocodilians and precocial birds are more ossified than those of altricial birds (Fig. 1 and Table 1) (*2*). This observation is consistent with the structure of the major locomotor muscles of the hindlimb, many of which originate from the pelvic girdle in both crocodilians and birds. Juveniles that are active cursors immediately upon hatching require a rigid, stable site of origin for limb musculature. In contrast, pelves of perinatal altricial birds are poorly ossified. However, even altricial juveniles become active within the nest in a matter of days after hatching, and postnatal ossification of the pelvic girdle is relatively rapid. Nearly complete ossification may take place within the first week. Consequently, if a fossilized embryo with well-ossified pelvic elements can be reliably identified, this criterion for distinguishing altricial from precocial neonates may be applied with some assurance. Significantly, the pelvic girdles of embryonic *Maiasaura* and *Orodromeus* (*1*), as well as all other known dinosaur embryos, including *Hypacrosaurus* (Ornithischia) (*3*), *Oviraptor* (Theropoda) (*4*), and *Therizinosaurus* (Segnosauria) (*5*), were apparently well ossified. These observations indicate that precociality was possibly widespread in dinosaurs.

Earlier hypotheses regarding altriciality in certain ornithischian dinosaurs were based on long bone epiphyseal ossification (*1*, *6*). Long bone elongation in all extant fetal archosaurians (birds and crocodilians) is centered in a massive cartilaginous cone at each end of the shaft. The cartilaginous cone consists of a cap of articular cartilage that overlies a distinct growth zone of proliferating chondrocytes (cartilage-producing cells). These chondrocytes, in turn, rest above a large, temporary mass of hyaline cartilage.

At the perinatal stage in all extant archosaurians, whether altricial or precocial, the growth zone differentiates into distinct regions of proliferating and hypertrophying chondrocytes. The chondrocytes themselves are superficial to a region of calcified cartilage that is interspersed with spongy

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endochondral ossification (Fig. 2). Long bone elongation proceeds as chondrocytes continuously produce new cartilage that becomes calcified and is subsequently replaced by spongy endochondral bone. At this developmental stage and thereafter, the growth zone follows a curve roughly parallel to the articular surface, which consists of a superficial cap of undifferentiated cartilage and fibrocartilage. Identical patterns of long bone development in other altricial and precocial birds [for example, Muscovy duck (*Cairina*), rock dove (*Columba*), Japanese quail (*Coturnix*), finch (*Lonchura*), budgerigar (*Melopsittacus*), and barred buttonquail (*Turnix*)] have also been described elsewhere (*2*).

A series of skeletons from embryonic and hatchling ornithopod dinosaurs have recently been discovered. It has been suggested that apparently incompletely ossified femoral epiphyses in neonates of the hadrosaur *Maiasaura* (Archosauria: Ornithischia) indicates altriciality. The femoral epiphyses are composed of spongy endochondral bone overlain by a thin layer of calcified cartilage (*1*). There is no obvious indication of the articular fibrocartilaginous cap that is present on the long bones of all extant archosaurians. Consequently, the knee joint in nestling *Maiasaura* was assumed to have been functionally immature (*6*). However, the articular fibrocartilage cap is unlikely to fossilize (*7*). Moreover, the apparently incomplete epiphysis of *Maiasaura* does not

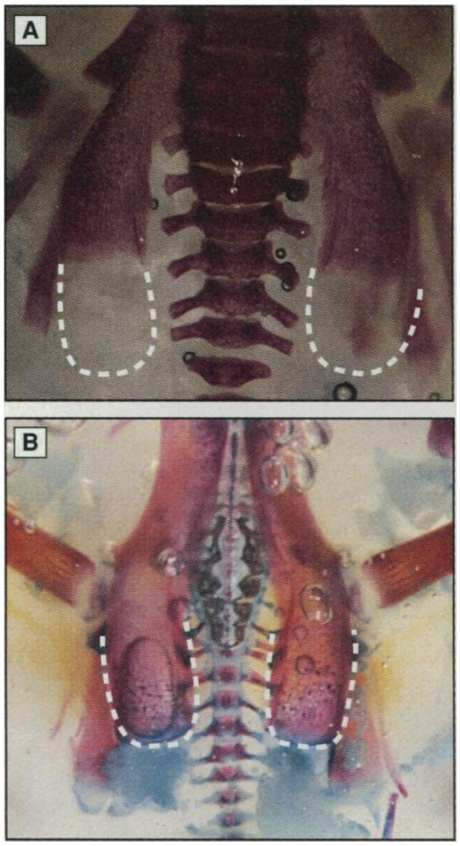

Fig. 1. Ossification of the pelves in representative hatchling birds: (**A**) altricial or nestbound [starling (*Sturnus*)] and (**B**) precocial or mobile [Mallee-Fowl (*Leipoa*) (Yale Peabody Museum, specimen 1171)]. The pelvis of *Leipoa* is completely ossified (the dashed line outlines the ossified posterior region of the ilium); the corresponding region of the ilium of *Sturnus* is cartilaginous. Pelves of perinatal altricial birds are significantly less ossified than those of perinatal crocodilians and precocial birds at equivalent stages of development (preparations are from cleared and stained specimens).

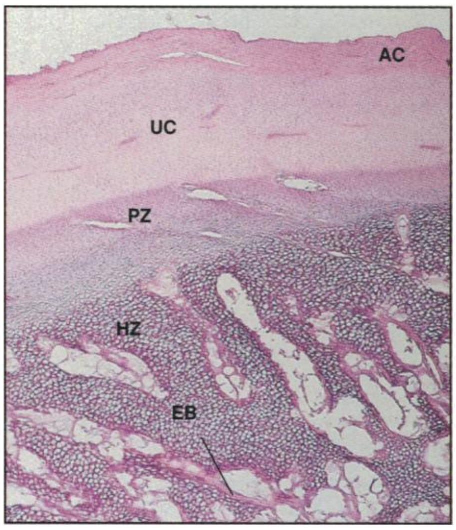

Fig. 2. Light micrograph of a longitudinal (sagittal) section of the distal femoral epiphysis in a 2-week-old emu (*Dromaius*). The pattern of long bone development illustrated here is typical of crocodilians as well as both precocial and altricial birds at equivalent stages of development. AC, articular fibrocartilage; EB, endochondral bone; HZ, zone of hypertrophication and calcification; PZ, zone of proliferation; UC, undifferentiated cartilage. Magnification: ×30.

Table 1. Hatchling condition (altricial or precocial) and pelvic development in a variety of birds and crocodilians. All known dinosaur perinates had well-ossified pelves.

Species	Hatchling condition (*11*)
Poorly ossified pelvis	
Budgerigar (*Melopsittacus*)*	Atricial
Cockatoo (*Cacatua*)	Altricial
Dove (*Columba*)*	Altricial
Finch (*Lonchura*)*	Altricial
Macaw (*Ara*)	Altricial
Starling (*Sturnus*)	Altricial
Eagle (*Haliaeetus*)	Semi-altricial
Well-ossified pelvis	
Brush turkey (*Talegalla*)	Precocial
Buttonquail (*Turnix*)*	Precocial
Duck (*Cairina*)*	Precocial
Emu (*Dromaius*)	Precocial
Mallee-Fowl (*Leipoa*)	Precocial
Ostrich (*Struthio*)	Precocial
Quail (*Coturnix*)*	Precocial
Alligator	Precocial
Caiman	Precocial

*Data from Starck (*2*).

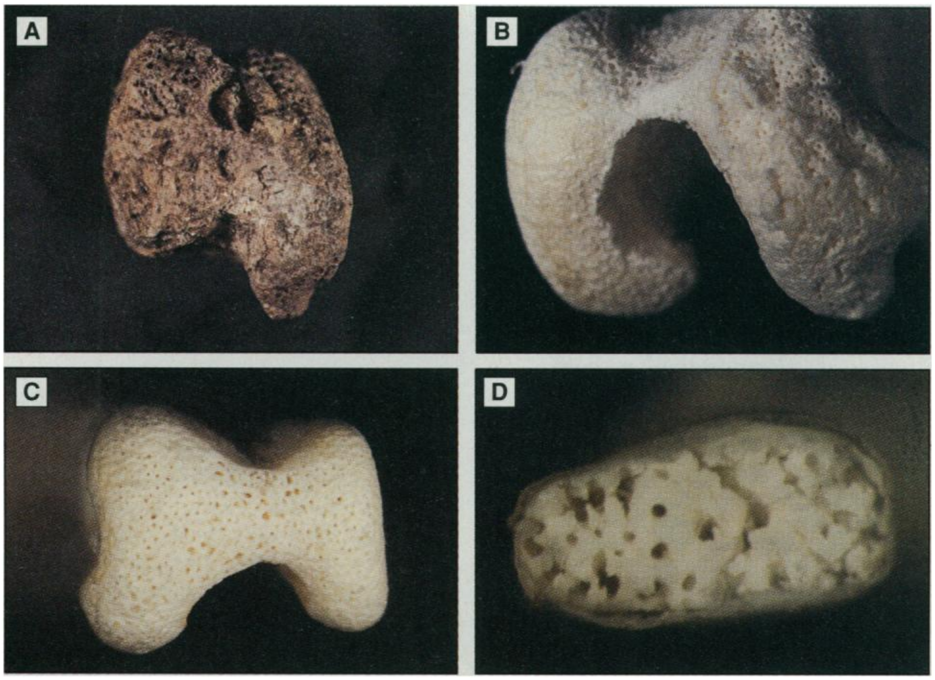

Fig. 3. Neonatal distal femoral epiphysis (frontal view) from (**A**) the ornithischian dinosaur *Maiasaura* (Princeton University Museum, specimen 23438) and from three precocial, extant archosaurians including (**B**) emu (*Dromaius*), (**C**) Mallee-Fowl (*Leipoa*) (Yale Peabody Museum, specimen 1195), and (**D**) alligator (*Alligator*). The distal femoral epiphysis of *Maiasaura* closely resembles those of extant archosaurians insofar as all are composed (in part) of endochondral bone overlain by a thin layer of calcified cartilage. The femora of the extant specimens were prepared by bacterial maceration to remove the articular cartilaginous caps.

differ significantly from the femoral epiphyses of extant juvenile crocodilians and precocial birds when the latter are prepared by bacterial maceration to remove the articular cartilage cap (Fig. 3). Thus, long bones of *Maiasaura* probably originally had a typical archosaurian articular fibrocartilaginous cap. In life, this dinosaur's long bones were probably similar to those of all extant archosaurians, whether altricial or precocial. Moreover, the femoral growth plate of perinatal *Maiasaura* is similar to that of a 2-week-old chicken (*Gallus*), a thoroughly precocial taxon (*8*).

Embryonic femora of the hypsilophodont ornithopod *Orodromeus* (Archosauria: Ornithischia) were described as having "well formed, smooth condyles which, although fully ossified in appearance, are formed entirely of calcified cartilage. Endochondral bone is not observed in the epiphyseal or metaphyseal regions" (*1*, p. 256). This description is problematic insofar as in extant, perinatal archosaurians, whether altricial or precocial, articular condyles of the long bones are not composed of calcified cartilage. Calcified cartilage forms in the deepest layer of the growth zone, where it is a scaffold for the deposition of new endochondral bone. Without the association between calcified cartilage and endochondral bone, there is no capacity for long bone elongation. Consequently, we suggest that interpretation of perinatal long bone structure in *Orodromeus* deserves reexamination.

Data from extant specimens indicate that there are no qualitative differences in the development of long bone epiphyseal structure in archosaurians, whether altricial or precocial. It has also been suggested that the lack of well-formed processes for muscle attachment (for example, trochanteric processes) in neonatal *Maiasaura* may be indicative of its altricial nature (*1*). However, well-formed processes did not exist in any of our precocial or altricial neonatal specimens. These processes apparently form much later in response to muscle-induced mechanical stresses on the long bones.

It has also been hypothesized that contemporaneous preservation of juvenile and adult *Maiasaura* in or near presumed colonial nesting sites somehow indicates that neonates were altricial and that the young were completely dependent on adult care. However, this evidence is equivocal: parents and juvenile crocodilians, as well as some precocial birds [for example, many shorebirds (Charadriiformes)], often remain in or near colonial nesting sites for some time after hatching (*9, 10*).

Similarly, the discovery of eggs in close association with an adult *Oviraptor* has been interpreted as evidence of birdlike parental behavior, including perhaps endothermy and incubation of eggs by adults (*11*). However, nest-attending and brooding behavior is widely distributed among extant crocodilians, lizards, snakes, and amphibians (*12–15*). For example, female crocodiles (*Crocodilus niloticus*) often rest their lower throat or thorax directly on the nest for the duration of the 90-day incubation period (*16*). Speculation regarding parental incubation of eggs and endothermy based on the apparent brooding behavior of *Oviraptor* are, at best, tenuous. Current evidence suggests that the nesting behavior of dinosaurs was likely similar to that of modern crocodilians.

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Concentrations of Tropospheric Ozone from 1979 to 1992 over Tropical Pacific South America from TOMS Data

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An estimate of tropospheric ozone concentrations was obtained from the difference in the Total Ozone Mapping Spectrometer (TOMS) data between the high Andes and the Pacific Ocean. From 1979 to 1992 the tropospheric ozone concentration apparently increased by 1.48 ± 0.40 percent per year or 0.21 ± 0.06 Dobson unit per year over South America and the surrounding oceans. An increase in biomass burning in the Southern Hemisphere can account for this trend in tropospheric ozone concentrations.

Tropospheric O_3 plays a key role in regulating the chemical composition and climate of the troposphere (*1*). The photolysis of O_3 forms $O(^1D)$, which reacts with H_2O to form reactive HO_x radicals in the troposphere. These radicals in turn undergo a series of chemical reactions that are important for the lifetimes of a large number of gases (for example, CH_4, CO, and CH_3X, where X is a halogen or nitrile). Moreover, O_3 is associated with air pollution. Its increase in the atmosphere is of concern because of its deleterious effects on vegetation and human health.

There is general agreement that tropospheric O_3 concentrations have increased in recent decades in the temperate zones in the Northern Hemisphere, but trends seem to vary geographically and temporally. A regional increase in tropospheric O_3 concentrations was first documented by Warmbt (*2*), who analyzed a 20-year record of surface O_3 measurements at stations in Germany between the mid-1950s and 1970s. Analyses of the vertical dependence of the O_3 concentrations were then attempted, based on the record of ozonesonde readings (*3–6*). These studies typically showed an increase in O_3 concentrations of about 1% per year in the lower troposphere.

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