

Evidence of colonial nesting and 'site fidelity' among ornithischian dinosaurs

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Recent discoveries in the late Cretaceous (Campanian) Two Medicine Formation of western Montana indicate that some dinosaur species, like some modern species of birds and crocodiles, nested in colonies. I report here evidence that members of one species returned to the same nesting area for many years. There are also indications that, after hatching, some species remained in their respective nests whereas others left the nest but remained in, or at least returned occasionally to, the nesting site. The area in which these discoveries were made is the Willow Creek Anticline of Teton County, where in 1978 a nest of fifteen, 1-m long hadrosaurs provided the first evidence of extended parental care among dinosaurs¹.

I have found in the same sediment horizon that produced the '1978 nest', a second nest of younger juvenile hadrosaurs (0.5 m long) and the weathered remnants of six unoccupied nests containing abundant eggshell remains (Fig. 1). All of the eight nests seem to have hosted conspecific hadrosaurs, of an as yet undetermined species, as the eggshell fragments from each site are structurally identical. Each nest appears to have been constructed as a circular or oval pit within a preconstructed mud mound (see ref. 1; Fig. 1). They were each found at an equal depth beneath a palaeosol, incorporated in a grey-brown mudstone interpreted as a floodplain deposit². Where erosion or cover has not destroyed or obscured parts of the nesting horizon, the nests are at least 7 m apart or approximately a distance equivalent to the length of an average adult hadrosaur from this area. There may, therefore, have been as many as 40 nests in the 10,000 m² area. The occurrence of eight nests along what appears to have been a single time horizon, within a relatively small area, suggests that these hadrosaurs were nesting in a colony.

With the exception of a single isolated juvenile in the nesting area, the remains of the young hadrosaurs were found in nests associated with eggshell. Although the skeletal elements of the young are relatively well ossified, even on the youngest individuals, there is no indication that they were precocial self-feeding individuals that would have ventured out of their respective nests without parental supervision, as suggested for

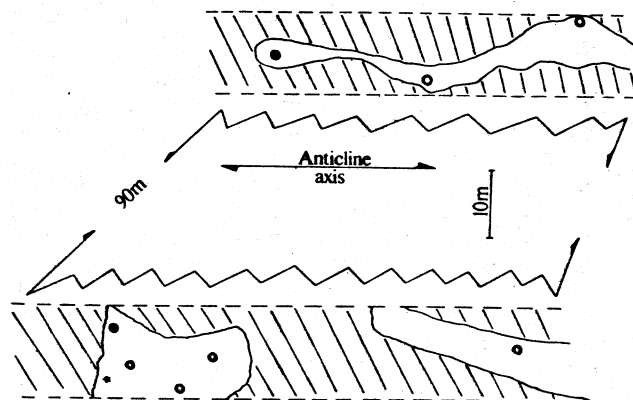


Fig. 1 Relationship of hadrosaur nests straddling Willow Creek Anticline. ●, Nests containing juveniles; ○, nests with eggshell concentrations and the asterisk indicates the location of the isolated juvenile. Broken lines represent the limit of the nest-bearing horizon. Cross-hatched areas are covered or missing.

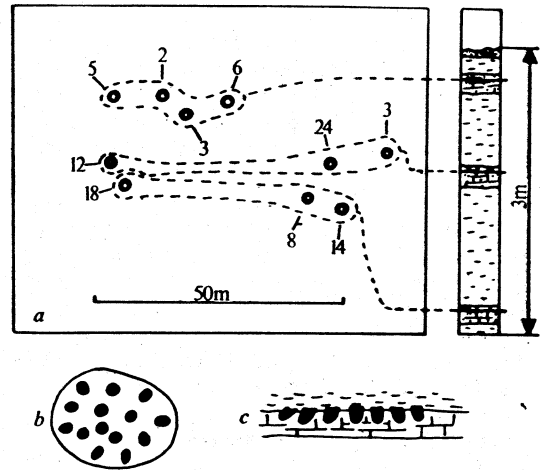


Fig. 2 a, Map and vertical section of the anticline showing the relationship of the egg clutches attributed to the hypsilophodont-like ornithopod. Values represent the number of eggs per nest, broken lines enclose clutches found on single horizons. b, Typical clutch arrangement viewed from above. c, Egg clutch viewed from the side showing how the lower portions of the eggs are located in siliceous carbonate sediment.

*Psittacosaurus*³. Early ossification may instead simply reflect rapid growth. As for the juveniles being too small for effective feeding by the adults, or possibly being crushed by an adult 'mis-step' (ref. 3), the fact that the crocodylians manage to overcome these difficulties⁴⁻⁶ implies that other archosaurs could also manage to do so. If by instinct or parental assistance, the young remained in their respective nests and the parent fed them from the nest perimeter, the young may have grown more rapidly, and there would have been less risk of infant mortality. Protection against predators would have been afforded by both nest confinement of the young and the closely-packed nests of the colony with the continued presence of many adults. As some adults foraged and gathered food for their young, the presence of other adults remaining in the nesting area may have thwarted potential predators, as is thought to be the case for many colonizing birds⁷. The presence of the two nests containing the remains of juveniles probably reflects this security in that they were not obviously preyed upon. Their deaths may have been due to starvation after the death of their parents.

A second nesting site (Fig. 2) on Willow Creek Anticline which has yielded several juvenile ornithopods, closely allied to the Hypsilophodontidae, offers evidence not only of colonial nesting but also of 'site fidelity' (multi-year use of nesting site) and the possibility of bird-like crèches. The 10 nests attributed to these ornithopods contain the hatched remains of up to 24 eggs per clutch. Clutches that do not appear to have suffered erosional damage are ~1 m in diameter, and were found along at least three different horizons, incorporated in brown, organic-rich, siliceous carbonates with mudstone inclusions². These are interpreted as products of soil formation where partially dried sediments were repeatedly disrupted and mixed in the process of nest construction and daily traffic². Although the exposed site of these nests is being excavated, the number of clutches so far found along these three horizons suggests colonial nesting for this species. The fact that they occur at different levels indicates that the members of the species returned to the site for many years. The elongate, ellipsoid eggs attributed to these ornithopods were meticulously laid with their smaller ends 'planted' upright to oblique, partially into the siliceous carbonate sediments (Fig. 2). On hatching, the young left through the top portion of the eggs, leaving the lower portions intact within the sediment. The fact that the lower portions were preserved rather than crushed and broken by trampling of the young, together with the fact that juvenile remains were not found in the nests, suggests that the young of this species did not remain in the nests long after hatching. It is possible, however, that

the juveniles from different nests assembled into bird-like crèches, as the remains of at least 12 small skeletons of varying sizes, have been found on the nesting horizons. Adults of this species appear to have been ~2.5–3 m long. The juvenile remains represent individuals ~0.5–1.5 m long, indicating that the young of this species either remained in the colony or returned to the site frequently, either of which may have been a result of parental care.

Considering the variety of nesting habits and social behaviours exhibited by the different crocodylian species or particularly by Recent birds, it is expected that the morphologically and ecologically diverse dinosaurs would also have exhibited a variety of behaviours.

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Lucy's limbs: skeletal allometry and locomotion in *Australopithecus afarensis*

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Precise information about the bodily proportions of early hominids is crucial for accurate functional and phylogenetic interpretations of early human evolution^{1–6}. The partial skeleton of *Australopithecus afarensis* (AL 288-1; 'Lucy'^{7,8}) recovered in 1974 from the Hadar area of Ethiopia⁹ permits the first direct assessment of body size, limb proportions and skeletal allometry in ancestral hominids that pre-date 3 Myr. Using allometric relationships for limb lengths in non-human catarrhine primates (as a whole and for African apes alone) as empirical base lines for comparison, I show here that the limb proportions of *A. afarensis* are clearly unique among hominoids. The data indicate that *A. afarensis* had already attained forelimb proportions similar to those of modern humans but possessed hindlimbs that were relatively much shorter; hence the 'intermediate' humerofemoral index of AL 288-1 (85.1) compared with *Homo sapiens* and great apes^{9,10}. It follows that relative and absolute elongation of the hindlimbs represents one of the major evolutionary changes in later human evolution. The bodily proportions of Lucy are not incompatible with some form of bipedal locomotion, but kinematic identity and functional equivalence with the bipedal gait of modern humans seem highly improbable. Reduced relative stride length in AL 288-1 probably implies both greater relative energy cost and relatively lower peak velocities of bipedal locomotion in *A. afarensis*.

Speculation about the limb proportions of the earliest hominids has long preoccupied palaeoanthropologists and functional anatomists^{1–6,11–15}, largely due to the obvious importance of such information for realistic reconstructions of locomotor behaviour and probable phylogenetic pathways. Due to the lack of associated, complete limb bones from both fore- and hindlimbs of *Australopithecus*, the earliest unequivocal hominid, comparisons of bodily proportions with modern *H. sapiens* have been necessarily tentative and inconclusive. Some

authors suspect that australopithecines possessed proportions virtually identical to those of modern humans, perhaps for the entire postcranial skeleton^{16,17} or just for the hindlimb^{2,18}. Others have proposed that the forelimbs were relatively long^{7,12,15} and/or the hindlimbs relatively short^{4,6,12,14}. The recently prepared, partial skeleton of *A. afarensis* (AL 288-1; 'Lucy') includes complete elements of forelimb (humerus) and hindlimb (femur), and therefore provides the first opportunity to test previous inferences about limb proportions and skeletal allometry in ancient hominids. As Walker³ notes, it is only when such data are available that "biomechanical analyses of the postcranial parts of *Australopithecus* will become more convincing than they are at present".

Based on a skeletal sample of 454 adult, non-human catarrhine primates (Old World monkeys, lesser apes and great apes) and wildshot body weights, I have established allometric relationships for humerus length and femur length in catarrhines as a whole (a size spread from *Miopithecus talapoin* to *Gorilla gorilla*) and in African apes alone (from female *Pan paniscus* to male *G. gorilla*)¹⁹. The sample includes 164 cercopithecines, 77 colobines, 116 hylobatid apes and 97 pongids. Body weights are taken from museum records and the literature. These scale relationships serve in this analysis as comparative, empirical baselines from which vertical deviations (d_{yx}) can be identified in AL 288-1, a sample of modern *H. sapiens* and a small female bonobo chimpanzee. For prediction and d_{yx} calculation, model I regression of \log_{10} -transformed data is regarded as more appropriate^{19–21} than model II methods (although principal axis solutions yield identical conclusions). Least-squares regression of \log_{10} (humerus length) and \log (femur length) on \log_{10} (body weight)^{1/3} yields the following predictions for catarrhines as a whole:

$$\begin{aligned} \text{Humerus: } \log_{10} Y &= 1.048 \log_{10} X + 0.862 \quad (r = 0.88) \\ \text{Femur: } \log_{10} Y &= 0.828 \log_{10} X + 1.192 \quad (r = 0.94) \end{aligned}$$

For African apes only, the predictive equations are:

$$\begin{aligned} \text{Humerus: } \log_{10} Y &= 0.815 \log_{10} X + 1.229 \quad (r = 0.99) \\ \text{Femur: } \log_{10} Y &= 0.437 \log_{10} X + 1.806 \quad (r = 0.94) \end{aligned}$$

Following Smith^{17,21}, percentage deviations ('prediction errors') for humerus length and femur length were computed from each equation as

$$\frac{\text{Observed value} - \text{predicted value}}{\text{Predicted value}} \times 100$$

for AL 288-1, a female Mbuti pygmy *H. sapiens* (MMC-18)²², male and female samples of caucasian *H. sapiens* and a female bonobo *P. paniscus* (T-29060). Body weight of Lucy has been estimated by her discoverers at 60 lb (27.3 kgf)⁷. A conservative 25.0–30.0 kgf range has been used in this analysis, consistent with independent estimates derived from both linear²³ and multiple (C. O. Lovejoy, personal communication) regression. Body weight of the Mbuti pygmy was calculated elsewhere²⁴, and the caucasian male and female values represent actual weights at death (Table 1). At 27 kgf the wildshot female bonobo falls at the lower limit of adult body size in *P. paniscus*. It is included in this analysis specifically because it is a pongid skeleton that is similar in size to both AL 288-1 and MMC-18.

Percentage deviations (Table 1) disclose a close similarity between AL 288-1 and both *H. sapiens* groups in relative humerus length. The humerus is slightly shorter than predicted in all the hominids, whereas that of the female bonobo is longer than expected. In contrast, prediction errors for femur length indicate a great disparity between modern humans on the one hand and Lucy and T-29060 on the other. With the exception of AL 288-1 relative to African apes, femoral deviations are positive in all cases, but those of the modern human groups are much greater than Lucy's. The same results obtain even if an estimate of 50 lb (22.7 kgf) is used for Lucy's weight. Inter-group allometric projections (Table 2) reinforce these observations. An AL 288-1 to caucasian projection results in near isometry ($k = 1.10$) for humerus length but extreme positive