



## Nocturnality in Dinosaurs Inferred from Scleral Ring and Orbit

### Morphology

Lars Schmitz and Ryosuke Motani

*Science* **332**, 705 (2011);

DOI: 10.1126/science.1200043

*This copy is for your personal, non-commercial use only.*

If you wish to distribute this article to others, you can order high-quality copies for your colleagues, clients, or customers by [clicking here](#).

Permission to republish or repurpose articles or portions of articles can be obtained by following the guidelines [here](#).

**The following resources related to this article are available online at [www.sciencemag.org](http://www.sciencemag.org) (this information is current as of December 26, 2012 ):**

**Updated information and services**, including high-resolution figures, can be found in the online version of this article at:

<http://www.sciencemag.org/content/332/6030/705.full.html>

**Supporting Online Material** can be found at:

<http://www.sciencemag.org/content/suppl/2011/04/12/science.1200043.DC1.html>

A list of selected additional articles on the Science Web sites **related to this article** can be found at:

<http://www.sciencemag.org/content/332/6030/705.full.html#related>

This article **cites 22 articles**, 4 of which can be accessed free:

<http://www.sciencemag.org/content/332/6030/705.full.html#ref-list-1>

This article has been **cited by** 4 articles hosted by HighWire Press; see:

<http://www.sciencemag.org/content/332/6030/705.full.html#related-urls>

This article appears in the following **subject collections**:

Paleontology

<http://www.sciencemag.org/cgi/collection/paleo>

# Nocturnality in Dinosaurs Inferred from Scleral Ring and Orbit Morphology

Lars Schmitz<sup>1,2\*</sup> and Ryosuke Motani<sup>2</sup>

Variation in daily activity patterns facilitates temporal partitioning of habitat and resources among species. Knowledge of temporal niche partitioning in paleobiological systems has been limited by the difficulty of obtaining reliable information about activity patterns from fossils. On the basis of an analysis of scleral ring and orbit morphology in 33 archosaurs, including dinosaurs and pterosaurs, we show that the eyes of Mesozoic archosaurs were adapted to all major types of diel activity (that is, nocturnal, diurnal, and cathemeral) and provide concrete evidence of temporal niche partitioning in the Mesozoic. Similar to extant amniotes, flyers were predominantly diurnal; terrestrial predators, at least partially, nocturnal; and large herbivores, cathemeral. These similarities suggest that ecology drives the evolution of diel activity patterns.

In animals, bouts of activity are distributed throughout a 24-hour period (diel activity pattern), and the temporal patterns of such activity are classified into four types: diurnal (day-active), nocturnal (night-active), cathemeral (day-and night-active), and crepuscular (twilight-active) (1, 2). Conventional wisdom holds that temporal niche partitioning in the Mesozoic was dictated by phylogeny; that is, nocturnality in mammals evolved as consequence of the dominance of diurnal dinosaurs (3–5). It has been difficult to test this hypothesis because reliable information on diel activity pattern of fossil taxa was unavailable. However, it recently has been shown that optical information recorded in orbit and scleral ring morphology enables quantitative distinction of activity patterns. We used this approach (6) in conjunction with morphological data on extant species with known activity patterns and a time-calibrated phylogeny to make inferences about diel activity pattern in Mesozoic archosaurs.

Our approach is based on optical principles and the relation between form and function of the eye (7). Ocular image formation relates to retinal illumination, or the brightness of the projected image. Three groups of ocular image formation, which are correlated with diel activity pattern, exist: (i) photopic (diurnal), with no activity in dim light; (ii) scotopic (nocturnal), with activity in dim light only; and (iii) mesopic (cathemeral), with activity in all light levels. We included crepuscular species, or those that are active during twilight, in the mesopic group, and we classified species that are diurnal plus crepuscular, cathemeral plus crepuscular, or nocturnal plus crepuscular as phototics, mesotics, and scototics, respectively. Ocular image formation can be identified in fossils that preserve

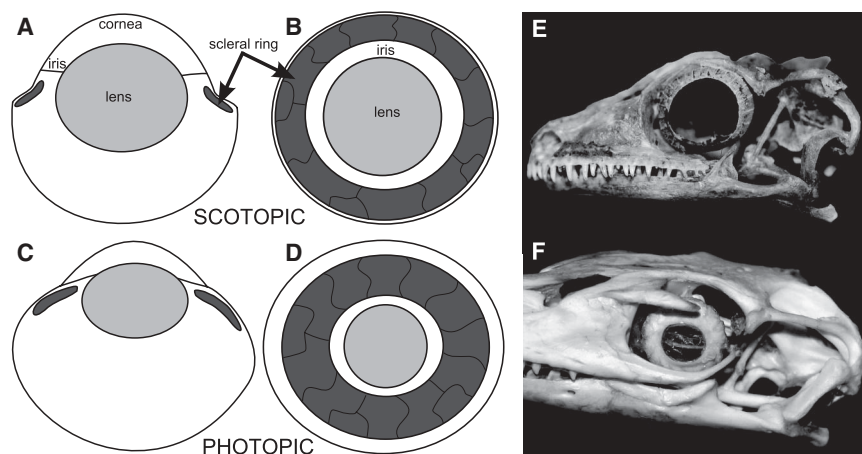
orbit length and diameter of the scleral ring (external and internal) because both are correlated with optical function (8, 9) and informative for classification (7).

Ocular image formation corresponds to eye shape (6, 7, 10). Scototics improve retinal illumination with a large aperture for given focal length and retinal area. The osteological equivalent is a large internal scleral-ring diameter relative to external diameter and orbit length (Fig. 1). Photopic species have a relatively small aperture and a small internal scleral-ring diameter for a given eye size, emphasizing acuity. Small maximum aperture probably minimizes the energy required to contract the iris for better depth of focus and prevention of retina overstimulation. A large eye facilitates both high acuity and sensitivity, a characteristic important for mesotics. Scleral ring and orbit dimensions in 33 Mesozoic archosaurs (10) (Fig. 2, Table 1, and tables S1 and S2) varied, with external diameters of scleral rings ranging from 9.56 mm (*Pterodactylus*

*antiquus*) to 92.6 mm (*Saurolophus osborni*). The latter is more than twice as large as that of the emu (*Dromaius novaehollandiae*, 34.9 mm) (9) but is still less than half the size of scleral rings found in ichthyosaurs, marine reptiles of the Mesozoic (11). The shape and size diversity of scleral rings and orbits in our sample of fossil archosaurs indicates variety in ocular image formation, which we can confirm quantitatively.

The quantitative discrimination of ocular image formation with osteological features has its foundation in comparative data on extant avians and squamates (6). This taxonomic bracket enables analyses of fossil archosaurs that fall between avians and squamates in a phylogenetic tree (12). However, there is phylogenetic signal in the correlation between form and ecology of amniote eyes (6). This phylogenetic signal can potentially lead to false inferences of activity pattern, and we therefore analyzed the data set with a discriminant analysis accounting for the phylogenetic signal (10) (figs. S1 and S2).

To determine the activity pattern of fossil archosaurs, we performed phylogenetic discriminant analysis at Pagel's lambda, a measure of the strength of phylogenetic signal, of 0.08, the optimal value for correlation between ocular image formation and hard-tissue traits (6). For classification purposes, we allowed an error of 0.01 around the optimum because the vertex of the likelihood distribution is wide. To make inferences about the activity pattern in fossil archosaurs, we modified a published script to allow inclusion of data with unknown activity pattern (10). Prior probabilities are based on proportions of phototics, scototics, and mesotics among extant amniotes (squamates, avians, and mammals) (10) (Fig. 2 and tables S3 and S4). Although archosaurs are nested within the saurian lineage (12), the amniote prior is reasonable. A prior based on extant saurians alone would misrepresent the ecological diversity recognized in



**Fig. 1.** Scotopic (nocturnal) species [(A) cross section, (B) lateral view along the optical axis] have a much larger lens and aperture for given eye size compared with phototics [diurnals (C and D)]. Scototics and phototics can also be distinguished with skeletal structures alone [(E) the scotopic *Rhachodactylus* and (F) the photopic *Varanus*]. Not to scale.

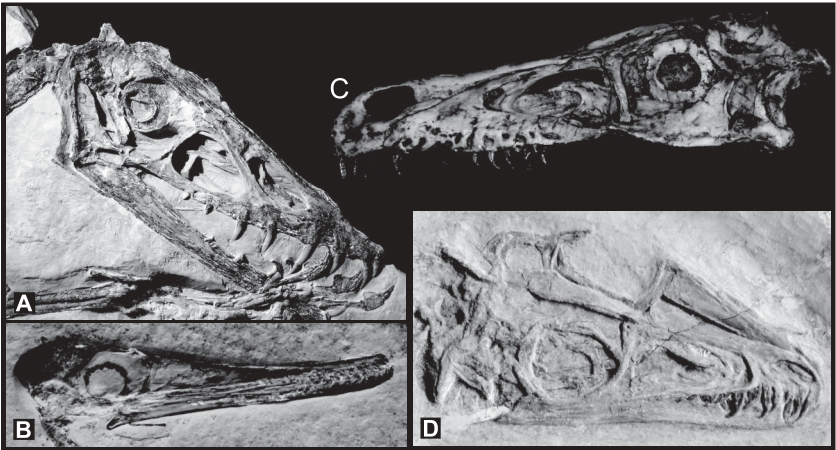
<sup>1</sup>Department of Evolution and Ecology, University of California, Davis, CA 95616, USA. <sup>2</sup>Department of Geology, University of California, Davis, CA 95616, USA.

\*To whom correspondence should be addressed. E-mail: lschmitz@ucdavis.edu

Mesozoic archosaurs. Ecological niches previously occupied by nonavian dinosaurs are now filled by mammals, and thus the inclusion of mammals is integral for accurate prior probabilities. We estimate that the majority of extant amniotes are photopic (58.5%), followed by scotopics (27.1%) and mesopics (14.4%). Photopics are dominant among active flyers (77.5%), whereas scotopics and photopics form the largest proportions among the terrestrials, or nonflyers (41.6% and 41.0%, respectively) (Fig. 3).

Our results (Table 1) suggest that a variety of ocular image formations existed in the Mesozoic. Fourteen species were identified as mesopics, 9 as scotopics, and 8 as photopics, whereas 2 were ambiguously classified as mesopic/scotopic. There is no clear phylogenetic clustering of ocular image formation. *Euparkeria capensis* and *Proterosuchus vanhoepeni*, both found near the base of the archosaur tree (13), were scotopic and mesopic, respectively. This finding is congruent with the hypothesis that archosaur ancestors had visual pigments adapted to dim light (14). Given the plasticity of ocular image formation across clades in extant amniotes and fossil archosaurs, however, estimates of ancestral states should be postponed until we have sampled more species. Moreover, *E. capensis* and *P. vanhoepeni* may require further investigation because they occurred near a polar circle (table S5). Polar species experience periods of continuous sunlight or darkness depending on season. However, the majority of the examined archosaurs inhabited low and temperate latitudes (table S5).

Comparisons with extant amniotes suggest that proportions of activity patterns are ecology-specific and largely independent from phylogeny. Similar to extant amniotes, the majority of flyers in our sample, including three pterosaurs and all four avians, were photopic. Four pterosaurs were scotopic; another one, mesopic. *Ctenochasma elegans*, *C. taqueti*, and *Rhamphorhynchus muensteri* were likely piscivorous and possibly had diel activity patterns comparable to those of nocturnal procellariiform birds (15). The filter-feeder *Pterodaustro guinazui* may have had diel activity similar to nocturnal filter-feeders among anseriform birds (16). Nocturnality in an extinct flyer has been suggested for an omithurine bird, on the basis of the relative size of brain region impressions (17). Anurognath pterosaurs may have been nocturnal as well (18), yet we could not test this because a specimen with preserved scleral ring is currently unavailable. Five of the analyzed pterosaurs are part of the Late Jurassic Solnhofen fauna (early Tithonian; Hybonotum Zone, Solnhofen Limestone), which allows for examination of temporal niche partitioning (19). Our results suggest that the Solnhofen pterosaur fauna is characterized by a photopic (*Archaeopteryx lithographica*, *Pterodactylus antiquus*, and *Scaphognathus crassirostris*) and a scotopic (*Ctenochasma elegans* and *Rhamphorhynchus muensteri*) group.



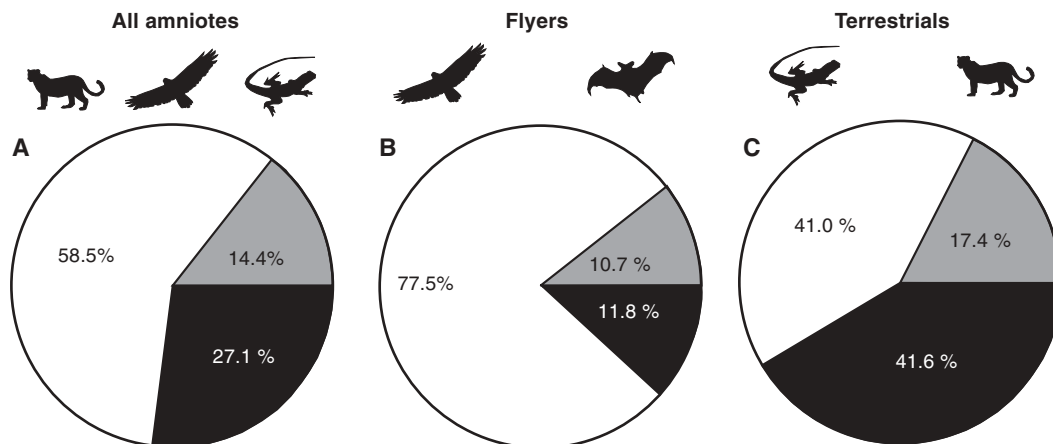
**Fig. 2.** Scleral rings used to infer diel activity pattern in fossil archosaurs. (A) The pterosaur *Scaphognathus crassirostris* was photopic (diurnal), whereas the pterosaur (B) *Ctenochasma elegans* and the theropod dinosaurs (C) *Velociraptor mongoliensis* and (D) *Juravenator starki* were scotopic (nocturnal). Not to scale.

**Table 1.** Inferred ocular image formation in fossil archosaurs.

	Ocular image formation	Ecology
<i>Basal archosaurs</i>		
<i>Euparkeria capensis</i>	Scotopic	Predator
<i>Proterosuchus vanhoepeni</i>	Mesopic	Predator
<i>Pterosaurs</i>		
<i>Ctenochasma elegans</i>	Scotopic	Flyer
<i>Ctenochasma taqueti</i>	Scotopic	Flyer
<i>Pterodactylus antiquus</i>	Photopic	Flyer
<i>Pterodaustro guinazui</i>	Scotopic	Flyer
<i>Rhamphorhynchus muensteri</i>	Scotopic	Flyer
<i>Scaphognathus crassirostris</i>	Photopic	Flyer
<i>Tapejara wellnhoferi</i>	Mesopic	Flyer
<i>Tupuxuara</i> sp.	Photopic	Flyer
<i>Ornithischian dinosaurs</i>		
<i>Agilisaurus louderbacki</i>	Photopic	Herbivore
<i>Corythosaurus casuarius</i>	Mesopic	Herbivore
<i>Prosaurolophus maximus</i>	Mesopic	Herbivore
<i>Protoceratops andrewsi</i>	Mesopic	Herbivore
<i>Psittacosaurus mongoliensis</i>	Mesopic	Herbivore
<i>Saurolophus osborni</i>	Mesopic	Herbivore
<i>Basal saurischian dinosaur</i>		
<i>Herrerasaurus ischigualestensis</i>	Mesopic	Predator
<i>Sauropodomorph dinosaurs</i>		
<i>Diplodocus longus</i>	Mesopic	Herbivore
<i>Lufengosaurus huenei</i>	Mesopic/scotopic	Herbivore
<i>Nemegtosaurus mongoliensis</i>	Mesopic	Herbivore
<i>Plateosaurus longiceps</i>	Mesopic	Herbivore
<i>Riojasaurus incertus</i>	Mesopic	Herbivore
<i>Nonavian theropods</i>		
<i>Garudimimus brevipes</i>	Mesopic	Herbivore
<i>Juravenator starki</i>	Scotopic	Predator
<i>Megapnosaurus kayentakatae</i>	Scotopic	Predator
<i>Microraptor gui</i>	Scotopic	Predator
<i>Ornithomimus edmontonicus</i>	Mesopic/scotopic	Herbivore
<i>Sinornithosaurus</i> sp.	Mesopic	Predator
<i>Velociraptor mongoliensis</i>	Scotopic	Predator
<i>Avians</i>		
<i>Archaeopteryx lithographica</i>	Photopic	Flyer
<i>Confuciusornis sanctus</i>	Photopic	Flyer
<i>Sapeornis chaoyangensis</i>	Photopic	Flyer
<i>Yixianornis grabaui</i>	Photopic	Flyer



**Fig. 3.** Estimated proportions of photopic (diurnal, white), scotopic (nocturnal, black), and mesopic (catheymal, gray) extant mammals, squamates, and avians. Photopics are common when all species are considered (A). The dominance of photopics is pronounced among flapping flyers [(B) avians and chiropterans combined], whereas photopics and scotopics are equally common among other terrestrial species (C). We used proportions in (A) as prior probability for phylogenetic discriminant analysis.



We also recognized similarities between extant and fossil amniote activity patterns for herbivores. All herbivores in our analysis were found to be mesopic, except for the photopic ornithischian *Agilisaurus louderbacki*, the smallest analyzed herbivore, and two, *Lufengosaurus huenei* and *Ornithomimus edmontonicus*, ambiguously classified as mesopic/scotopic. These results confirm previous hypotheses, based on thermoregulatory considerations (20), of partially nocturnal behavior in large dinosaurs. Recently, the relatively large orbit size of the ceratopsian dinosaur *Protoceratops andrewsi* was interpreted as a nocturnal adaptation (21); however, our results suggest that *P. andrewsi* was adapted to mesopic light levels. Constraints for foraging time and thermoregulation likely influenced diel activity pattern of herbivorous dinosaurs, as is the case for extant herbivores (22). The daily foraging budgets of herbivores increase with body mass, and a study (22) suggests that herbivorous mammals exceeding a body mass of 423 kg are expected to forage more than 12 hours a day. Constraints on foraging time in herbivorous dinosaurs, often exceeding extant terrestrial vertebrates in size, are reasonable from anatomical and energetic perspectives. Lower metabolic rate (23) could decrease food requirement and daily foraging time. Furthermore, sauropodomorphs may have had higher food intake rates and shorter daily foraging time budgets because they did not masticate (24). However, thermoregulatory constraints as consequence of size dictate a shift to catheymality, in particular in the light of high mean annual temperatures in the Mesozoic (25). Many terrestrial vertebrates avoid high mid-day temperatures and show bimodal diel activity to minimize overheating (22, 26, 27), a substantial problem for large animals. The change in diel activity pattern as response to high mid-day temperatures, in combination with the necessity to meet food requirements, can lead to partially nocturnal behavior.

Nocturnal or catheymal activity was also common among predators, as our results suggest. All terrestrial predators in our sample were either scotopic or mesopic, which matches the pattern seen in extant mammalian carnivores (28). Our

results are consistent with the interpretation that sensory areas in the brain of the small theropod *Conchoraptor gracilis* were adapted to a crepuscular or nocturnal lifestyle (29). Differences in relative orbit size have led to suggestions of niche separation in this group, with small theropods being nocturnal and large theropods being diurnal (30). Although we confirm that some small theropods were at least partially scotopic, data on ocular image formation of large theropods are not available yet. However, we can make an inference of predator-prey interaction. *Velociraptor mongoliensis* from the Campanian Djadokhta Formation (Upper Cretaceous) in Mongolia was scotopic, whereas an herbivore of this fauna (*P. andrewsi*) was mesopic. It is plausible that the *Velociraptor* attack on *Protoceratops*, one of the few examples of predatory behavior directly documented in the vertebrate fossil record (31), occurred in twilight or low-light conditions.

Our results suggest that the previous assumption of a dichotomous split in temporal habitat and resource use among terrestrial amniotes in the Mesozoic, with archosaurs being diurnal and mammals being nocturnal (3–5), is inaccurate. Although quantitative inferences of Mesozoic mammals are not available yet, our results show that many Mesozoic archosaurs were active day and night. We reject the hypothesis of a phylogenetic split between nocturnal and diurnal activity patterns. Instead, we argue that partition of diel activity pattern depends on body size, diet, and habitat in both extant amniotes and Mesozoic archosaurs. In conclusion, ecology emerges as major evolutionary driver of diel activity patterns.

#### References and Notes

- I. Tattersall, *Folia Primatol.* **77**, 7 (2006).
- D. J. Curtis, M. A. Rasmussen, *Folia Primatol.* **77**, 178 (2006).
- A. W. Crompton, C. R. Taylor, J. A. Jagger, *Nature* **272**, 333 (1978).
- H. J. Jerison, *Evolution of the Brain and Intelligence* (Academic Press, New York, 1973).
- J. A. Wiens *et al.*, in *Community Ecology*, J. Diamond, J. Case, Eds. (Harper & Row, New York, 1986), pp. 145–153.

- R. Motani, L. Schmitz, *Evolution*, published online 7 April 2011 (10.1111/j.1558-5646.2011.01271).
- L. Schmitz, R. Motani, *Vision Res.* **50**, 936 (2010).
- M. I. Hall, *Anat. Rec.* **292**, 798 (2009).
- L. Schmitz, J. Morphol. **270**, 759 (2009).
- Materials and methods are available as supporting material on Science Online.
- R. Motani, B. M. Rothschild, W. Wahl, *Nature* **402**, 747 (1999).
- M. S. Y. Lee *et al.*, in *Assembling the Tree of Life*, J. Cracraft, M. J. Donoghue, Eds. (Oxford Univ. Press, Oxford, 2004), pp. 451–467.
- D. B. Weishampel *et al.*, Eds., *The Dinosauria* (Univ. of California Press, Berkeley, 2004).
- B. S. Chang, K. Jönsson, M. A. Kazmi, M. J. Donoghue, T. P. Sakmar, *Mol. Biol. Evol.* **19**, 1483 (2002).
- F. Mougeot, V. Bretagnolle, *J. Avian Biol.* **31**, 376 (2000).
- R. McNeil, P. Drapeau, J. D. Goss-Custard, *Biol. Rev. Camb. Philos. Soc.* **67**, 381 (1992).
- E. N. Kurochkin, G. J. Dyke, S. V. Saveliev, E. M. Pervushov, E. V. Popov, *Biol. Lett.* **3**, 309 (2007).
- S. C. Bennett, *Paläont. Z.* **81**, 376 (2007).
- N. Kronfeld-Schor, T. Dayan, *Annu. Rev. Ecol. Syst.* **34**, 153 (2003).
- F. Seebacher, G. C. Grigg, L. A. Beard, *J. Exp. Biol.* **202**, 77 (1999).
- N. R. Longrich, in *New Perspectives on Horned Dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium*, M. J. Ryan, B. J. Chinnery-Allgeier, D. A. Eberth, P. Dodson, Eds. (Indiana Univ. Press, Bloomington, 2010), pp. 308–327.
- R. N. Owen-Smith, *Megaherbivores: The Influence of Very Large Body Size on Ecology* (Cambridge Univ. Press, Cambridge, 1988).
- B. K. McNab, *Proc. Natl. Acad. Sci. U.S.A.* **106**, 12184 (2009).
- P. M. Sander *et al.*, *Biol. Rev. Camb. Philos. Soc.* **86**, 117 (2011).
- B. W. Sellwood, P. J. Valdes, *Sediment. Geol.* **190**, 269 (2006).
- S. K. Maloney, G. Moss, T. Cartmell, D. Mitchell, *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **191**, 1055 (2005).
- I. R. Swingland, J. G. Frazier, in *A Handbook on Biotelemetry and Radio Tracking*, C. J. Amlaner, D. W. Macdonald, Eds. (Pergamon, London, 1979), pp. 611–615.
- J. L. Gittleman, *J. Mammal.* **67**, 23 (1986).
- M. Kundrát, J. Janáček, *Naturwissenschaften* **94**, 769 (2007).
- D. J. Chure, *Gaia* **15**, 233 (1998).
- K. Carpenter, *Gaia* **15**, 135 (1998).

**Acknowledgments:** We thank D. Brinkmann, S. Carlson, I. Schwab, G. Vermeij, and P. Wainwright for comments. C. Cicero, A. Engilis, I. Engilis, D. Evans, M. Flannery, P. Holroyd, M. Koelbl-Ebert, J. McGuire, C. Mehling,

M. Norell, R. Papendieck, O. Rauhut, M. Sander, K. Seymour, B. Shaffer, D. Unwin, X. Xu, and Z. Zhou granted specimen access. The project was supported by NSF grant EAR 0551024 to R.M. and Durrell Funds of the Department of Geology, University of California Davis, an M. A. Fritz Award of Royal Ontario Museum, a doctoral stipend of German Academic Exchange Service,

and a postdoctoral fellowship of German Research Foundation to L.S.

### Supporting Online Material

www.sciencemag.org/cgi/content/full/science.1200043/DC1  
Materials and Methods  
SOM Text

Figs. S1 and S2  
Tables S1 to S5  
References

5 November 2010; accepted 16 February 2011  
Published online 14 April 2011;  
10.1126/science.1200043

# Saturn's Curiously Corrugated C Ring

M. M. Hedman,<sup>1\*</sup> J. A. Burns,<sup>1,2</sup> M. W. Evans,<sup>1</sup> M. S. Tiscareno,<sup>1</sup> C. C. Porco<sup>3</sup>

In August 2009 the Sun illuminated Saturn's rings from almost exactly edge-on, revealing a subtle corrugation that extends across the entire C ring. This corrugation's amplitude is 2 to 20 meters and its wavelength is 30 to 80 kilometers. Radial trends in the corrugation's wavelength indicate that this structure—like a similar corrugation previously identified in the D ring—results from differential nodal regression within a ring that became tilted relative to Saturn's equator plane in 1983. We suggest that this initial tilt arose because interplanetary debris struck the rings. The corrugation's radial extent implies that the impacting material was a dispersed cloud of debris instead of a single object, and the corrugation's amplitude indicates that the debris' total mass was  $\sim 10^{11}$  to  $10^{13}$  kilograms.

The Cassini spacecraft obtained numerous images of Saturn's rings within a few months of Saturn's equinox in August 2009, when the Sun illuminated the rings from almost exactly edge-on. Many of these observations were designed to investigate ring features that would be highlighted by this unusual lighting geometry, such as shadows cast by embedded moonlets or inclined ringlets. Among

the most surprising structures revealed by these images was a series of regularly spaced bright and dark bands extending throughout the entire C ring (Fig. 1). Because this periodic banding was not seen in earlier Cassini images, it cannot be ascribed to simple variations in the ring's density or optical depth. Instead, these bands appear to be caused by a vertical corrugation extending across the entire C ring. Broad-scale corrugations have previously been identified in Saturn's D ring (1) and Jupiter's main ring (2); both these structures appear to have formed within the last few decades when the relevant ring suddenly became tilted relative to its planet's equatorial plane (1, 3). The C-ring corrugation seems to have been similarly generated, and

indeed it was probably created by the same ring-tilting event that produced the D-ring's corrugation.

The amplitudes and wavelengths of the C-ring's periodic brightness variations have been measured using Fourier analyses of selected images (SOM text 1). The amplitudes of the observed brightness variations change with viewing and illumination geometries as expected for a vertically corrugated ring (SOM text 2). The corrugation amplitudes derived with a simple photometric model range between 2 and 20 m throughout the C ring (Fig. 2A; SOM text 2 describes systematic uncertainties associated with these estimates), and are thus well below the few-hundred-meter amplitudes of the previously identified D-ring corrugations (1). Meanwhile, the corrugation wavenumber systematically decreases with increasing distance from Saturn throughout the entire C ring (Fig. 2B), suggesting that the observed corrugations are part of a single coherent structure. Extrapolating the observed trends interior to the C ring shows that the predicted wavenumber is close to the expected wavenumber of the previously observed, larger-amplitude D-ring corrugation. The latter has been interpreted as the result of differential nodal regression of an initially inclined ring (1), which suggests that the C-ring corrugations could have been produced by the same process (Fig. 3). Indeed, the radial trends seen in Fig. 2B are consistent with such a model.

<sup>1</sup>Department of Astronomy, Cornell University, Ithaca, NY 14853, USA. <sup>2</sup>Department of Mechanical Engineering, Cornell University, Ithaca, NY 14853, USA. <sup>3</sup>CICLOPS—Space Science Institute, Boulder, CO 80301, USA.

\*To whom correspondence should be addressed. E-mail: mmhedman@astro.cornell.edu

**Fig. 1.** Mosaic of images of Saturn's C ring obtained during Cassini's orbit 117, along with close-ups of selected radial regions showing the periodic bright and dark bands that extend across the entire C ring. The contrast has been adjusted in each close-up image to better show the periodic structure. Horizontal bands within these close-ups are camera artifacts (22).

