Hyaenodontidae), others are more indicative of pre-Wasatchian age (Arctostylopidae, certain uintatheres and pantodonts). The Gashato fauna was long considered to be of late Paleocene age (21), but it is probably earliest Eocene and at least partly correlative with the Clarkforkian (8, 12, 22).

Our much-improved knowledge of the Clarkforkian Land-Mammal Age and its fauna allows better correlation with European and Asian faunas and demonstrates that the Paleocene-Eocene transition was a time of substantial faunal interchange between North America and both Europe and Asia.

## KENNETH D. ROSE

Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560

#### **References and Notes**

- D. E. Savage, Rev. Mus. Argen. Cienc. Nat. "Bernardino Rivadavia" Inst. Nac. Invest. Cienc. Nat. Cienc. Zool. 8, 53 (1962); R. H. Tedford, Proc. North Am. Paleontol. Conv. Part F (1970), p. 666; D. E. Savage, Contrib. Primatol. 5, 2 (1975). Land-Mammal ages are biochrons of about Age magnitude, but most are not hered on corresponding time stratigraphic not based on corresponding time-stratigraphic stages
- stages.
  M. O. Woodburne, J. Paleontol. 51, 220 (1977).
  H.E. Wood, 2nd, R. W. Chaney, J. Clark, E. H. Colbert, G. L. Jepsen, J. B. Reeside, Jr., C. Stock, Bull. Geol. Soc. Am. 52, 1 (1941).
  W. J. Sinclair and W. Granger, Bull. Am. Mus. Nat. Hist. 31, 57 (1912).
  W. D. Matthew and W. Granger, ibid. 34, 4, 311, 429 (1915); ibid. 38, 565 (1918).
  G. L. Jepsen, Proc. Am. Philos. Soc. 69, 463.
- 4.
- 6. G. L. Jepsen, Proc. Am. Philos. Soc. 69, 463
- (1930). G. G. Simpson, Am. Mus. Novit. No. 954 (1937).
- K. D. Rose, thesis, University of Michigan, Ann Arbor (1979); Univ. Mich. Mus. Paleontol.

Pap. Paleontol., in press (includes description of new species of Plesiadapis).
R. C. Wood, Breviora No. 257 (1967).
G. L. Jepsen, Proc. Am. Philos. Soc. 83, 217 (1967).

- 10. G
- (1940).P. D. Gingerich, Univ. Mich. Mus. Paleontol. Pap. Paleontol. 15, 1 (1976).
- 12.
- 12.  $\frac{1}{39}$  and K. D. Rose, Geobios Mem. Spec. 1,  $\frac{39}{1977}$ . 13. K. D. Rose, J. Paleontol. **51**, 536 (1977).
- 14.
- for reports of possible Clarkforkian specimens of Hyracotherium in southern North America, see W. J. Morris, Contrib. Sci. L.A. Cty. Mus. No. 151 (1968); J. A. Schiebout, Bull. Tex. Mem. Mus. 24, 1 (1974). University of Michigan project personnel have been unable to substan-tiate the late Tiffanian record of *Hyracotherium* reported by G. L. Jepsen and M. O. Woodburne [Science 164, 543 (1969)].
- 16. C. L. Gazin, Smithson. Misc. Collect. 131 (No. 7), 1 (1956).

- 7), 1 (1956).
   7). P. D. Gingerich, Contrib. Mus. Paleontol. Univ. Mich. 24, 237 (1977); ibid. 25, 1 (1978); T. M. Bown and K. D. Rose, ibid., 89 (1979); D. W. Krause, J. Paleontol., in press.
   18. P. D. Gingerich and G. F. Gunnell, Contrib. Mus. Paleontol. Univ. Mich. 25, 125 (1979).
   19. P. D. Gingerich, ibid. 24, 135 (1975).
   20. G. G. Simpson, Bull. Geol. Soc. Am. 58, 613 (1947); D. E. Russell, Mem. Mus. Nat. Hist. Nat. Paris Ser. C 13, 1 (1964); D. E. Savage, Abh. Hess. Landesamtes. Bodenforsch. 60, 154 (1971); M. C. McKenna, Ann. Mo. Bot. Gard. 62, 335 (1975). 62, 335 (1975).
- W. D. Matthew, W. Granger, G. G. Simpson,
   Am. Mus. Novit. No. 376 (1929); F. S. Szalay
   and M. C. McKenna, Bull. Am. Mus. Nat. Hist.
   144, 269 (1971). 21.
- D. Dashzeveg and M. C. McKenna, Acta Pa-laeontol. Pol. 22, 119 (1977). 22
- This report summarizes part of a dissertation submitted to the Rackham School of Graduate 23 Studies, University of Michael Science of Graduate Studies, University of Michael Andrews, Michael A. Dorr, Jr., M. C. McKenna, P. Myers, and G. R. Smith for guidance and ad-vice on aspects of the research presented here, and T. M. Bown, R. J. Emry, D. E. Savage, and an anonymous reviewer for their critical re-views of the meanscript Eveldwork and rewhich an anonymous reviewer for their critical re-views of the manuscript. Fieldwork and re-search were supported by grants from the NSF and the University of Michigan to P. D. Ginger-ich, and by grants from the Geological Society of America, American Society of Mammalogists, and University of Michigan to K.D.R.

26 November 1979: revised 29 February 1980

## Saturn's Luminosity and Magnetism

Abstract. The Pioneer 11 results for Saturn's large heat output, small magnetic field, and near-axisymmetry of the field may all be explained by an interior model in which the helium is undergoing phase separation and is nonuniformly distributed. Substantial depletion of helium from the atmosphere is predicted.

All published models for Saturn are essentially similar to those for Jupiter: they consist of a rock and ice core (or central concentration) of order ten Earth masses, surrounded by a shell of fluid, metallic, uniformly mixed hydrogen and helium, surrounded in turn by a fluid envelope of a molecular hydrogen-helium mixture (1). Three aspects of the Pioneer 11 results lead to doubts concerning this supposed similarity of Jupiter and Saturn. First, the conventional explanation of Jupiter's excess heat output (gradual homogeneous cooling) does not appear to explain Saturn's observed excess heat output (2). Second, the observed magnetic field at Saturn (3) is smaller than expected on the basis of scaling from Jupiter. Third, the magnetic dipole is aligned to within 1° of the rotation axis, unlike the substantial dipole tilt that characterizes other planets.

It is proposed to explain all these observations by an ongoing gravitational differentiation of helium from hydrogen within Saturn. The potential importance of differentiation as an additional energy source has long been known (4) and the essential features of the process have been described by Salpeter (5). Differentiation not only provides energy, but limits the convecting metallic region to deeper within the planet, thereby reducing the external field. Furthermore, an inhomogeneous, stably stratified metallic fluid layer above the dynamo region (see Fig. 1) is in differential rotation because of the equator-to-pole temperature difference. This flow tends to make the external field axisymmetric. These assertions are elaborated below.

The difficulty of reconciling Saturn's heat output with a homogeneous evolution (one in which the composition at each point within the planet does not change with time) is indicated by detailed evolutionary calculations (6) but can be readily understood in terms of quite simple considerations (7). To a good approximation, the "age" of a homogeneously evolving Jupiter or Saturn (defined as the time the planet takes to cool from an initially hot state to its present observed effective temperature) is proportional to the Kelvin time, defined as the ratio of present heat content to present excess heat output. (The constant of proportionality is about 0.25.) For Jupiter (8), the present excess heat output is  $(4 \pm 1) \times 10^{24}$  erg/sec and the present heat content can be calculated from interior models (9). The resulting age for Jupiter is  $(5 \pm 1.3) \times 10^9$  years, consistent with the age of the solar system. For Saturn, the excess heat output (2) is  $(1.1 \pm 0.3) \times 10^{24}$  erg/sec, and the heat content of Saturn can be evaluated from published models (1). The resulting homogeneous age of Saturn is (2.8  $\pm$  1.2)  $\times$  10<sup>9</sup> years, less than the solar system age. The error includes observational error, the assumption of an interior adiabat based on a temperature (T) of 140 K at a pressure (P) of 1 bar, the uncertainty in the specific heat of dense molecular hydrogen, and all the corrections and sources of error discussed by Hubbard (10). For the reasons discussed by Stevenson and Salpeter (7), an even larger uncertainty is possible, so the failure of a homogeneously cooling model is not certain. Nevertheless, these calculations suggest the need for an additional energy source.

The largest and most likely additional source is the gravitational energy release from a downward partitioning of the more dense helium. Theoretical calculations (11) show that insolubility of helium must eventually occur, beginning at the lowest pressure at which hydrogen is pressure-ionized [around 2 Mbar (12)] and for  $T \leq 10^4$  K. Helium raindrops form, grow to  $\sim 1$  cm in size, and fall under the influence of gravity, releasing energy by viscous dissipation on a small length scale. These raindrops dissolve deeper down where the temperature is higher. The molecular envelope (including the atmosphere) is in convective communication with the region of phase separation and is progressively de-

0036-8075/80/0516-0746\$00.50/0 Copyright © 1980 AAAS

pleted in helium. A three-zone structure evolves in the hydrogen-helium region (see Fig. 1) in which the intermediate zone is highly stable with respect to large-scale vertical motions because of a helium gradient (7).

The energy release from differentiation is around  $1.7 \times 10^{12}$  to  $2.5 \times 10^{12}$ ergs per gram of helium removed from the molecular envelope, the uncertainty being caused by current uncertainties in interior models (especially the rock-ice core). A depletion from an initial 25 percent helium by mass in the molecular envelope to a present value of 15 percent by mass would provide sufficient energy to sustain the present excess heat output for about  $2 \times 10^9$  years. A much smaller depletion (corresponding to the lowest value of excess heat output permitted by the observations) would be inconsistent with the proposed interpretation of the magnetic field. A much higher depletion does not increase the present-day heat output (because most of the depletion would have taken place long ago, when the heat output was much higher) and would be difficult to reconcile with current theoretical solubility models (11). Both theoretical and observational uncertainties prevent more precise predictions.

Attempts to understand the magnitudes of planetary magnetic fields are an endless source of amusement and frustration [for example, see (13)]. Assuming a dynamo mechanism and negligible precessional effect, the most general scaling law for the magnetic dipole moment Mcan be written (electromagnetic units) as

$$M = kR_c^3(\rho\lambda\Omega)^{1/2}R_0^a R_M^b P_e^c R_e^d \quad (1)$$

where k is a dimensionless constant of order unity;  $R_c$  is the core radius;  $\rho$  is the core density;  $\lambda$  is the magnetic diffusivity;  $\Omega$  is the rotation rate; and  $R_0$ ,  $R_{\rm M}$ ,  $P_{\rm e}$ ,  $R_{\rm e}$  are the Rossby, magnetic Reynolds, Péclet, and ordinary Reynolds numbers, respectively, all based on  $R_{\rm c}$  as a length scale and  $(F/\rho)^{1/3}$  as a velocity scale, where F is the heat or energy flux responsible for the dynamo (14). The exponents a, b, c, and d are not known but are expected to be small in magnitude. For the "magnetic Bode's law'' (14), b = -a = 1/2 and c = d = 0. Of all the relevant parameters, only Fand  $R_{\rm c}$  are substantially different between Jupiter and Saturn. The core heat flux is 50 percent larger in Jupiter, but M is only a weak function of F. The value of R<sub>c</sub> for conventional Jupiter and Saturn models should correspond to the  $P \simeq 2$ -Mbar level at which the hydrogen becomes metallic (12); this is  $R_c = 5.6 \times$ 16 MAY 1980



10<sup>9</sup> cm (Jupiter) and  $R_{\rm c} \simeq 3.0 \times 10^9$  cm (Saturn).

With these choices and with M = $1.4 \times 10^{30}$  G-cm<sup>3</sup> for Jupiter (15) and  $M = 4.8 \times 10^{28}$  G-cm<sup>3</sup> for Saturn (3), it is difficult to reconcile Eq. 1 with the expectations of small magnitudes for the exponents. For example, the magnetic Bode's law requires  $R_{\rm c} \simeq 2.3 \times 10^9 \, {\rm cm}$ for Saturn (13). This suggests that the region of dynamo generation is even deeper than conventional Saturn models would suggest. The differentiating model proposed here is consistent with this, since the inhomogeneous, stable metallic zone does not participate in the dynamo process. The thickness of this zone is difficult to estimate (7) but may be of order 5000 km.

Although the inhomogeneous layer has no large-scale vertical motions, horizontal flows are expected because of an equator-to-pole temperature difference arising from the atmospheric boundary condition and the rotational inhibition on convection in the molecular envelope (16). The resulting thermal wind takes the form of a differential rotation described by (17)

$$2\Omega\cos\theta\,\frac{\partial u}{\partial z} = -\alpha g\,\frac{\partial T}{\partial y} \tag{2}$$

where *u* is the azimuthal velocity,  $\theta$  is the colatitude, *z* is the vertical coordinate,  $\alpha$  is the coefficient of thermal expansion, *g* is the gravitational acceleration, and *y* is the local meridional coordinate. If  $\Delta T$  is the equator-to-pole temperature difference, then *u* has a characteristic magnitude ~  $10\Delta T$  cm/sec, the Richardson number for the inhomogeneous layer is ~  $10^{10}/(\Delta T)^2$ , ensuring high stability, and the magnetic Reynolds number  $R_{\rm M}$  is ~  $10^7\Delta T$ , ensuring hydromagnetic coupling for any reasonable  $\Delta T$ . A plausible choice is  $\Delta T \sim 10^{-3}$  K (16).

Neglecting ohmic dissipation (that is,

Fig. 1. Schematic representation of Saturn models (dimensions only approximate). Conventional models [all detailed models published; see (1)] do not explain Saturn's heat output or the magnitude and geometry of the magnetic field. The proposed differentiating model has an intermediate, inhomogeneous layer in which helium raindrops form. Energy is released, and the external field is reduced and tends to be axisymmetric.

assuming  $\Delta T >> 10^{-7}$  K), the effect of *u* on the magnetic field is given (in spherical coordinates) by

$$\frac{\partial H_r}{\partial t} = -\frac{u}{r \sin \theta} \frac{\partial H_r}{\partial \phi}$$
(3)

$$\frac{\partial H_{\phi}}{\partial t} = \frac{1}{r} \frac{\partial}{\partial r} (r u H_r) + \frac{1}{r} \frac{\partial}{\partial \theta} (u H_{\theta})$$
<sup>(4)</sup>

and the equation for  $H_{\theta}$  has the same form as Eq. 3. The axisymmetric components of  $H_r$  and  $H_{\theta}$  are unaltered, whereas the nonaxisymmetric components are progressively twisted and altered by the nonuniform differential rotation. Large, localized radial field gradients are produced, eventually to be balanced by small-scale ohmic dissipation. Meanwhile, the axisymmetric toroidal field is progressively amplified, presumably until it reaches magnetostrophic balance  $(H_{\phi} \sim 10^4 \Delta T^{1/2} \text{ G})$ , while nonaxisymmetric azimuthal components undergo no net amplification. The resulting steady state would be exceedingly difficult to evaluate and would ultimately require solution of the dynamo as well (since the large toroidal field modifies the boundary conditions for the dynamo) but an approximate analysis indicates that differential rotation causes rapid radial attentuation of the nonaxisymmetric parts of  $H_r$  and  $H_{\theta}$ , provided  $R_{\rm M} >> 1$ . This is consistent with the Pioneer 11 observations.

The harmonic spectrum and time variability of the magnetic field will play an important role in future attempts to interpret the internal structure and dynamics of Jupiter and Saturn (18). However, the most important prediction is a substantial (perhaps a factor of 2) depletion of helium from the atmosphere.

D. J. STEVENSON Department of Earth and Space Sciences, University of California, Los Angeles 90024

### **References and Notes**

- W. L. Slattery, *Icarus* 32, 58 (1977); V. N. Zhar-kov and V. P. Trubitsyn, *Physics of Planetary Interiors* (Pachart, Tucson, Ariz., 1978).
   A. P. Ingersoll, G. S. Orton, G. Münch, G. Neugebauer, S. C. Chase, *Science* 207, 439 (1979).
- (19/9).
  E. J. Smith, L. Davis, Jr., D. E. Jones, P. J. Coleman, Jr., D. S. Colburn, P. Dyal, C. P. Sonett, *ibid.*, p. 407.
  H. H. Kieffer, J. Geophys. Res. 72, 3179 (1967);
  R. Smoluchowski, Nature (London) 215, 691 (1967) 3.
- 4.
- (1967). E. E. Salpeter, Astrophys. J. Lett. 181, L83 5. È
- E. E. Saipeter, Astrophys. J. Lett. 104, 105 (1973).
   J. B. Pollack, A. S. Grossman, R. Moore, H. C. Graboske, Jr., Icarus 30, 111 (1977).
   D. J. Stevenson and E. E. Salpeter, Astrophys. 15, 220 (1977).
- J. Suppl. Ser. 35, 239 (1977). A. P. Ingersoll, G. Münch, G. Neugebauer, G.
- 8. S. Orton, in Jupiter, T. Gehrels, Ed. (Univ. of Arizona Press, Tucson, 1976), p. 197. D. J. Stevenson and E. E. Salpeter, in *ibid.*, p.
- 9.
- 10. W. B. Hubbard, Icarus 30, 305 (1977).

- 11. D. J. Stevenson, Phys. Rev. B 12, 3999 (1975); J.
- D. J. Stevenson, *Phys. Rev. B* 12, 3999 (1975); *J. Phys. F* 9, 791 (1979).
   P. S. Hawke, T. J. Burgess, D. E. Duerre, J. G. Huckel, R. N. Keeler, H. Klapper, W. C. Wallace, *Phys. Rev. Lett.* 41, 994 (1978).
   C. T. Russell, *Nature (London)* 281, 552 (1979).
   This is instance of an infection with the formation of the sector.
- 14. This is just one of an infinite number of ways of writing a generalized scaling law. It has the ad-vantage of arising naturally from hydromag-netic considerations [for example, D. J. Stevenson, Geophys. Astrophys. Fluid Dyn. 12, 139 (1979)]
- 15. E. J. Smith, L. Davis, Jr., D. E. Jones. in Juniter, T. Gehrels, Ed. (Univ. of Arizona Press,
- Tucson, 1976), p. 788. A. P. Ingersoll and C. C. Porco, *Icarus* 35, 27 (1978). 16.
- P. H. Stone, in *Jupiter*, T. Gehrels, Ed. (Univ. of Arizona Press, Tucson, 1976), p. 586.
   R. Hide and S. R. C. Malin, *Nature (London)*
- 280, 42 (1979) 19. I thank A. P. Ingersoll and E. J. Smith for com-
- municating their results before publication and F. H. Busse for useful discussions.

26 November 1979

# **Endothelial Cells of Bovine Pulmonary Artery Lack Receptors** for C3b and for the Fc Portion of Immunoglobulin G

Abstract. Bovine pulmonary endothelial cells do not possess receptors for the 3b component of complement (C3b) or for the Fc portion of immunoglobulin G. The lack of these receptors may help explain the nonthrombogenic function of endothelial cells. Our findings rule out the possibility that endothelial cells participate in pulmonary immune complex disease through the binding of C3b or Fc fragments.

It is generally agreed that the lungs are a major target organ in some forms of immune complex disease (1). The lungs appear to be a major site of deposition of immune complexes in which antigen is in slight excess over antibody (2, 3). Our study was begun to help clarify the role, if any, of pulmonary endothelial cells in binding of immune complexes as they may occur within the circulation. Specifically, we examined for the presence of receptors for the Fc portion (crystallizable fragment) of IgG (immunoglobulin G) and for C3b (3b component of complement). We were interested in C3b both because of its role in immune adherence and immune conglutination (4) and because bovine serum contains conglutinin, which appears to have specificity for bound C3b. We have found that bovine pulmonary endothelial cells in culture (initial isolates through the ninth passage) do not possess receptors for C3b or the Fc portion of IgG.

We obtained the endothelial cells by scraping bovine pulmonary artery with a scalpel. The cells were dissociated in 0.1 percent collagenase and cultured in Medium 199 containing 20 percent fetal calf serum. We used methods similar to those described previously (5). The cells were identified by structural and functional criteria: monolayer growth with cobblestone appearance; ultrastructural characteristics of endothelial cells including frequent caveolae and occasional Weibel-Palade bodies (5-7); presence of angiotensin-converting enzyme activity (6-10); and reactivity with antibodies to human factor VIII and  $\alpha_2$ -macroglobulin (5).

The rosette method (11) was used to assay for Fc receptors. Sheep erythrocytes (E), either alone or sensitized with IgG antibody (EA), were purchased from Cordis Laboratories. The sheep E and EA were washed three times and adjusted to a concentration of 0.5 percent in ice-cold Hanks buffered saline solution (HBSS) (12). To perform the assay, approximately  $2 \times 10^5$  endothelial cells in 0.1 ml of HBSS were incubated with 0.1



Fig. 1. (a) Cow pulmonary artery endothelial cells in the fifth passage were removed from their flasks with a rubber policeman. Approximately  $2 \times 10^5$  endothelial cells were incubated with 3 ml of 0.5 percent EAC at 37°C for 15 minutes, then at 4°C for 2 hours. Endothe lial cells did not bind EAC ( $\times$ 800). (b) Human buffy coat was incubated with 0.5 percent EAC as described for endothelial cells. Rosettes formed between B lymphocytes and EAC (×800).

action mixture was then centrifuged very gently, at approximately 25g for 5 minutes, and incubated for an additional 2 hours at 4°C. The cells were resuspended and examined in a Zeiss photomicroscope with phase optics. Endothelial cells did not bind EA (Fig. 1a). Prior treatment and length of time in culture did not appear to be important factors. Fresh isolates were unreactive as were cells in monolayer culture (passages 4 through 9; tested 24 hours after passage). Cells detached mechanically by scraping or enzymatically (0.5 percent trypsin with EDTA) did not bind EA. The quality of the EA was verified by reaction with B lymphocytes, cells known to possess Fc receptors (Fig. 1b).

ml of EA at 37°C for 15 minutes. The re-

The immune adherence assay (13)was used to test for C3b receptors. The cellular intermediate, EAC14b2a3b (EAC1423) was prepared as described (14). The cells were suspended in a dextrose-gelatin Veronal buffer containing 0.15 mM calcium and 0.5 mM magnesium, pH 7.3 (13), and adjusted to a concentration of  $8 \times 10^7$  cells per milliliter. To confirm that C3b was bound to the EA, monospecific goat antibody to human C3b was added to the coated red cells and clumping occurred. This indicated that the cellular intermediate was EAC1423, as expected. Three dilutions of complement-bearing red cells,  $4 \times 10^7$ ,  $4 \times 10^6$ , and  $4 \times 10^5$  per milliliter, were used. Endothelial cells were used at a concentration of  $5.5 \times 10^5$  per milliliter. For control tests we used human red cells (O positive) at 8  $\times$  10<sup>7</sup> per milliliter. Pulmonary endothelial cells showed no agglutination when incubated with EAC1423. When the test was carried out under identical conditions with normal human red cells, clumping did not occur.

Since a primary function of endothelial cells is to provide a smooth, gliding surface for the passage of blood, it is not surprising that these cells do not possess receptors for C3b and the Fc portion of IgG. In particular, the properties of C3b immune adherence could be extremely disadvantageous for the normal functioning of endothelial cells. Nonetheless, recent results (2, 3) indicate that the soluble immune complexes can gain access to the interstitial space of the lungs. The route taken by the immune complexes from blood to interstitium is not yet evident. What is evident is that endothelial cells do not participate by way of receptors for C3b, nor do they possess receptors for the Fc portion of IgG, unlike epithelial cells of the kidney which do possess receptors for C3b (15). Our results do not rule out the possibility that other