

Although losers on the supply side may forgo opportunities in scientific advancement and economic benefits associated with earth resources sensing, the developing countries may gain, as the competition may lower the prices of satellite products and ease the terms for obtaining technical assistance in remote sensing.

References and Notes

1. C. K. Paul, *Technol. Rev.* **82**, 23 (October 1979).
2. T. W. Wagner and D. S. Lowe, *A.I.D.'s Remote Sensing Grant Program* (Report 111800-1-F, U.S. Agency for International Development, Washington, D.C., August 1978), p. 13.
3. M. T. Halbouty, *Am. Assoc. Pet. Geol. Bull.* **64**, 8 (January 1980).
4. A. O. Beall and C. H. Squyres, *Oil Gas J.* **78**, 107 (7 April 1980).
5. J. Fussell, *Geotimes* **25**, 19 (May 1980).
6. "Oil geologist picks Kiryat Gat sites," *The*

- Jewish Week*, 8 to 14 January 1981, p. 6.
7. J. B. Miller and J. V. Danakker, paper presented at the William Pecora Symposium, Sioux Falls, S.D., November 1977. Articles on the Sudan survey and oil exploration have appeared in *Oil Gas J.* **75**, 190 (25 July 1977); *ibid.* **77**, 42 (23 July 1979); *ibid.* **78**, 8 (25 February 1980).
8. I. S. Kikula, thesis, University of Dar es Salaam, Dar es Salaam (1980).
9. *Planning for a Civil Operational Land Remote Sensing Satellite System: A Discussion of Issues and Options* (National Oceanic and Atmospheric Administration, Rockville, Md., 1980), p. 9.

Interiors of the Giant Planets

W. B. Hubbard

Consider a sample of material from the sun or, almost equivalently, from the primordial material out of which the solar system formed. Cooled to planetary temperatures (about 100 K), the sample has the distribution of principal chemical

planets, but in amounts that vary from planet to planet. Such inferences are model-dependent, since we have no direct techniques for sampling the bulk composition of planets. Figure 2, a mass-radius diagram for the giant planets, il-

Summary. Unlike the terrestrial planets, the giant planets—Jupiter, Saturn, Uranus, and Neptune—have retained large amounts of the carbon, nitrogen, and oxygen compounds that were present in their zone of formation. A smaller fraction of the available hydrogen and helium was retained. The distribution and relative amounts of these components in the interiors of the Jovian planets can be inferred from theoretical and experimental data on equations of state and from the planets' hydrostatic equilibrium response to rotation.

constituents shown in Fig. 1. The various mineral species such as magnesium silicates ("rock") and iron that form the terrestrial planets are an extremely minor component of this distribution. The predominant component consists of gases that would not condense under any plausible primordial conditions, such as hydrogen and helium, as well as gases that could condense in bulk only at rather low nebular temperatures, such as water, methane, and ammonia (1). The fact that these gases are largely missing from the terrestrial planets suggests that they were somehow removed from the coexisting solid phase at around the time these planets were formed.

In the outer solar system, evidence indicates that large amounts of the gas-phase component were incorporated in

illustrates some of the general conclusions that can be drawn from a consideration of these two basic parameters. Shown are some approximate curves for spherical objects of various compositions at 0 K. As has long been known, hydrogen is a dominant constituent of Jupiter and Saturn but not of Uranus and Neptune (2). Therefore Uranus and Neptune represent compositions that have been altered from the original nebular material. From Fig. 2 we might conclude that Jupiter and Saturn are of primordial composition, but more detailed studies, outlined below, prove that they, too, have been somewhat depleted in gaseous constituents.

Current investigations of the interior structure of the Jovian planets are attempting to make the general conclusions above more quantitative and more detailed by means of modeling that takes into account the interaction of the atmo-

sphere and interior, heat flow measurements, and gravitational field parameters. Experimental and theoretical determination of the high-pressure behavior of important likely constituents plays a major role in this work.

In this article I present an assessment of our current understanding of the distribution of density and chemical composition in the Jovian planets. Heat flow measurements and their implications for the structure and evolution of the Jovian planets have been reviewed recently (3).

Geophysics of Giant Planets

Detailed knowledge of the earth's interior is provided primarily by seismology, which yields seismic wave velocities as a function of depth by inverting seismic travel times as a function of angular separation on the earth's surface. Such detailed information is unavailable for any other planet so far. For Jovian planets, another geophysical approach comes into play. In this technique, we use the response of the planet to rotation to provide a series of integral constraints on the interior equation of state.

Consider a rotating, liquid planet that is in hydrostatic equilibrium with its own gravitational field and rotational field. For solid-body rotation, we may write

$$Q = \frac{1}{2} \omega^2 r^2 \sin^2 \theta = \frac{1}{3} \omega^2 r^2 [1 - P_2(\cos \theta)] \quad (1)$$

where Q is the rotational potential in the fluid's comoving frame, ω is the angular rotation rate, r is the distance from the center of mass, θ is the colatitude, and P_2 is a Legendre polynomial. We can regard Q as a perturbation to the spherically symmetric gravitational potential that would prevail in the absence of rotation.

As a result of rotation, the planet's external gravitational potential is expressed as

$$V = \frac{GM}{r} \left[1 - \sum_{l=1}^{\infty} J_{2l} \left(\frac{a}{r} \right)^{2l} P_{2l}(\cos \theta) \right] \quad (2)$$

The author is a professor of planetary sciences at the University of Arizona, Tucson 85721.

where G is the gravitational constant, M is the mass, J_{2l} are dimensionless zonal harmonics, and a is a normalizing radius, usually taken to be the equatorial radius at a pressure of 1 bar for Jovian planets.

Examining Eq. 1, we see that Q consists of a purely spherical part and a purely quadrupole part. Therefore we might expect the response of the planet, V , to likewise terminate with the P_2 term. However, it turns out that an equilibrium body cannot respond in an exactly quadrupolar manner to a purely quadrupole perturbation. The initial quadrupole response at surfaces of discontinuity—the outer layer of the planet, a core-mantle interface, and so on—gives rise to a perturbation of order Q^2 , which then generates a response proportional to P_4 . Thus the coefficient J_2 represents the basic linear response of the planet to Q , while J_4 is the linear response to that part of the perturbation which has been transformed to Q^2 . Similarly, J_6 is the linear response to Q^3 , and so on (4). In general, one can write

$$J_{2n} = \sum_{l=n}^{\infty} \Lambda_{2l,l-n} q^l \quad (3)$$

where Λ_{2l} are dimensionless response coefficients and q is the dimensionless measure of the amplitude of Q

$$q = \omega^2 a^3 / GM \quad (4)$$

In general, we are unable to observe this hierarchy of perturbations in terrestrial planets. The process of successive accommodations to hydrostatic equilibrium must terminate when we reach scales over which the planet does not attain hydrostatic equilibrium. For the earth this occurs at a level of perturbation of about 10^{-6} , and since $q \sim 10^{-3}$ for the earth only the linear response term J_2 is observed, and even J_2 contains a measurable nonhydrostatic component. A similar situation obtains for Mars, while for Mercury, Venus, and the moon, q is too small for even the hydrostatic portion of J_2 to be measurable.

In the Jovian planets, q values range from 10^{-1} to 10^{-2} and the degree of adaptation to hydrostatic equilibrium is believed to be greater than for the solid terrestrial bodies. Therefore it seems possible to apply Eq. 3 to rather high order to obtain a series of integral constraints on interior structure. Attempts have been made to proceed further and develop formal inversion theories to yield interior models that satisfy the available integral constraints. Such theories are generally based on finding coefficients in a series expansion for the interior density distribution, but considerable

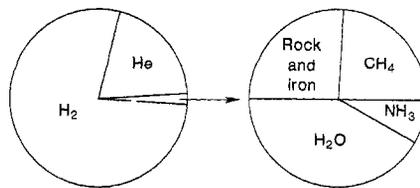


Fig. 1. Distribution by mass of compounds in primordial solar composition.

caution is needed in such an approach, since it is limited to a particular class of planetary models and therefore cannot guarantee a unique solution.

Jupiter and Saturn Models

As a first approximation one might try models with unmodified solar composition, assuming that accumulation processes for proto-Jupiter and proto-Saturn involved no fractionation of chemical species. Such a model does not work for either planet, and although the numerical demonstration of this fact requires lengthy calculations, it is also possible to understand it by means of a simplified model.

To a fairly good approximation, one may represent the pressure-density relation for solar composition material undergoing a reversible adiabatic charge by

$$P = K\rho^2 \quad (5)$$

where P is the pressure, ρ is the mass density, and K is a constant equal to about $2 \text{ Mbar cm}^6/\text{g}^2$. Equation 5 is valid for adiabatic paths with a starting temperature of about 150 K at $P = 1$ bar. It smooths over the assumed phase transition of hydrogen from the molecular to the pressure-ionized form at $P \sim 3$ Mbar; the corresponding temperature at this point is $\sim 10^4$ K. Different starting temperatures can be incorporated by changing the value of K slightly.

The lowest-order response coefficient, $\Lambda_{2,0}$, can be calculated exactly for Eq. 5, and we find (5)

$$\Lambda_{2,0} = 0.173 \quad (6)$$

while

$$J_2/q = 0.166 \pm 0.00005 \quad (7)$$

for Jupiter and

$$J_2/q = 0.12 \pm 0.0001 \quad (8)$$

for Saturn. Since the $\Lambda_{2l,0}$ are decreasing functions of degree of central condensation, we conclude that (i) Jupiter and Saturn are not homologous to each other and (ii) both are relatively more centrally condensed than would be expected for uniform solar composition. The latter result is particularly true for Saturn.

A further confirmation of quantitative differences in interior structure between Jupiter and Saturn follows from the fact that for Eq. 5 the radius is independent of mass, while Saturn's radius is actually about 85 percent of Jupiter's radius.

In retrospect, we do not find these results altogether surprising. According to one recent model for the formation of the Jovian planets, accumulation of planetesimals in the outer solar system is the initial step in the process (6). Because of the low temperature in the primordial solar nebula at heliocentric distances of about 5 astronomical units and beyond, one may well expect such planetesimals to contain substantial amounts of condensed H_2O in addition to chondritic abundances of rock and iron. At the orbits of Uranus and Neptune, and possibly Saturn, ammonia may also have condensed. Finally, at even lower temperature (Uranus, Neptune?), methane would also condense (2). Some investigators consider it possible that such primordial outer solar system planetesimals were virtually identical to the nuclei of comets. Assuming complete equilibrium condensation, the ratio of ice (H_2O , NH_3 , and CH_4) to rock and iron in such planetesimals would be about 2/1 to 3/1 by mass (1).

Accumulation of the noncondensable component, principally hydrogen and helium, requires some sort of gravitational collapse mechanism whereby aggregation of the planetesimals into a core triggers an instability in the surrounding nebula, causing hydrogen and helium to become bound to the core. The first quantitative investigation of such a collapse was made by Perri and Cameron (7). More recent work by Mizuno (6) has shown that collapse occurs when the planetesimals have aggregated into a protoplanetary core with a mass of about $10 M_E$ ($M_E = \text{earth mass}$). This appears to be a universal result, which is insensitive to the conditions of the primordial nebula, and thus would be consistent with the observation that all of the Jovian planets have similar-sized cores. Mizuno's calculations show that at the point of collapse an amount of hydrogen and helium approximately equal to the core mass is gravitationally bound to the planet. Thus his mechanism works well for Uranus and Neptune ($14.6 M_E$ and $17.3 M_E$, respectively), but would require further infall of matter in order to add more hydrogen to Jupiter and Saturn ($317 M_E$ and $95 M_E$, respectively).

Our picture of a Jovian planet then has a central core composed of the initial planetesimals (largely ice and rock) and an outer hydrogen-helium envelope

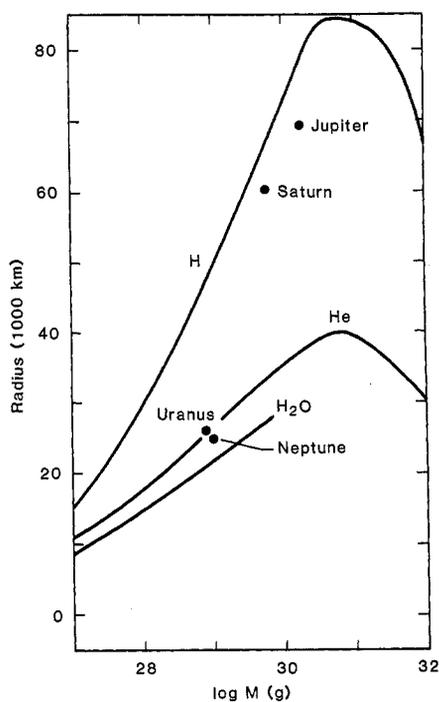


Fig. 2. Theoretical curves of radius versus mass (M) for zero-temperature spherical bodies composed of hydrogen, helium, and water. Observed values for the Jovian planets are also shown.

formed by gravitational collapse. In the limit of precise solar composition—that is, in the limit where the central core is accompanied by the full solar complement of hydrogen and helium—one expects the core mass to be approximately 1.8 percent of the total mass of the planet, and an even smaller percentage if portions of the core are redissolved into the envelope.

Detailed model calculations (2) indicate that the actual Jovian core mass is about 9 percent of the total planetary mass. For Saturn, the corresponding value is about 20 percent of the total mass. Such large values of the core mass are reflected in the values of J_2/q given in Eqs. 7 and 8; these numbers are lower than the value for a homogeneous planet, Eq. 6. It is also instructive to express core masses in absolute terms: $28 M_E$ for Jupiter and $19 M_E$ for Saturn. These results suggest that the cores of Jupiter and Saturn are similar in size to Uranus and Neptune as a whole.

All of these results on core masses depend heavily on the assumed pressure-density relation for the hydrogen-rich envelope. Thus it is necessary to check the adequacy of the physics in this region of the planet.

As molecular hydrogen is compressed, important changes take place in its structure. According to static compression experiments, the vibrational frequency of the molecule first increases with pres-

sure, and at still higher pressures it begins to decrease (8). The latter effect is presumably caused by other molecules, and at sufficiently high pressures the molecules will disintegrate. The latter transition has not been reliably observed, but according to calculations it occurs at $P \sim 3$ Mbar (9). Calculations also indicate that the hydrogen atoms simultaneously ionize at this point. At higher pressures, hydrogen is in the so-called metallic or pressure-ionized phase. It then resembles a simple alkali metal with proton cores and mobile electrons.

Figure 3, which schematically shows a cross section of a Jovian planet, illustrates how the observed composition of the planet's atmosphere may be affected by various interior interfaces. Following collapse of the hydrogen-helium envelope onto the protoplanetary core, portions of the core may, in principle, redissolve into the envelope. In the limit of complete redissolution of H_2O into the envelope, for example, we would expect a resulting enhancement of the H_2O/H_2 ratio, depending on the ratio of protoplanetary core mass to envelope mass. Although attempts have been made to theoretically calculate the degree of solubility of various chemical constituents in the hydrogen-helium envelope, the process depends sensitively on many poorly known parameters involving interspecies interaction energies at high pressure. Stevenson (10) has shown, for example, that helium has limited solubility in metallic hydrogen and that substantial amounts of gravitational energy can be released if helium comes out of solution and settles toward the center of the planet.

If the transition from molecular to metallic hydrogen represents a first-order phase transition, in equilibrium the abundances of various dissolved species must change across the interface. Therefore, even if there were unlimited solubility of all species in hydrogen, there would be a significant difference between the atmospheric abundances and the interior abundances. Moreover, according to Stevenson and Salpeter (9), the interface between metallic and molecular hydrogen may act as a barrier to convection and produce a specific entropy discontinuity.

If such effects are important, significant differences in the mass fraction of atmospheric helium might be expected between Jupiter and Saturn. Results from recent spacecraft investigations are not totally consistent. Orton and Ingersoll (11) found a helium mass fraction $Y = 0.18 \pm 0.05$ in Saturn's atmosphere

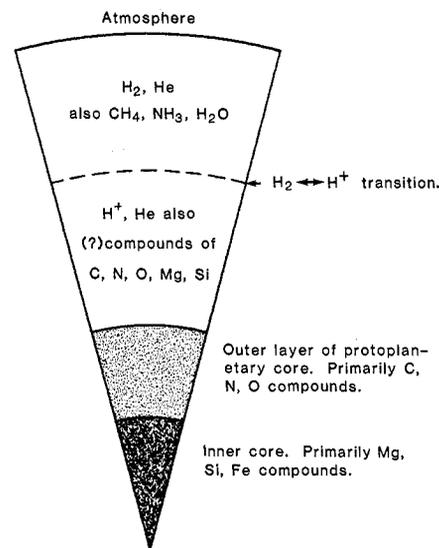


Fig. 3. A generic model for a Jovian planet. The transition from molecular hydrogen (H_2) to metallic hydrogen (H^+) occurs at a pressure of about 3 Mbar. This transition does not occur in Uranus and Neptune.

from an analysis of Pioneer 11 infrared data. On the other hand, Voyager data give $Y = 0.19 \pm 0.04$ for Jupiter's atmosphere and $Y = 0.11$ with an error of "a few percent" for Saturn's atmosphere (12).

In the absence of detailed experimental data on the high-pressure hydrogen phase transition, our best clue to processes in the envelopes of Jupiter and Saturn comes from examination of the higher-order gravity coefficient J_4 or, equivalently, the response coefficients $\Lambda_{4,0}, \Lambda_{4,1}, \dots$. The effect of different hydrogen equations of state can be studied as follows. For a given mass, equation of state, starting adiabatic temperature, core parameters, and abundance distribution, we can calculate a radius and response coefficients $\Lambda_{2l,i-n}$. Various parameters (typically the core mass and helium mass fraction) are adjusted to bring the radius and J_2 into agreement with observation. The resulting value of J_4 can then be compared with observation to determine whether the model is an acceptable one. We know J_2 to ± 0.03 percent for Jupiter and ± 0.11 percent for Saturn and J_4 to ± 1.2 percent for Jupiter and ± 4.1 percent for Saturn (2, 13). According to the theory, J_4 is grossly correlated with J_2 , so that a true test of equations of state is possible only when J_4 is known within a minimum uncertainty that turns out to be about ± 5 percent for Jupiter and Saturn.

Because of the need for detailed modeling of the equilibrium distribution of minor constituents between molecular and metallic hydrogen parts of the plan-

et, the phase transition has not been treated in detail in any current model of Jupiter and Saturn. Instead, other approaches have been taken. One approach is to assume that a continuous transformation takes place at the elevated temperatures that occur in Jupiter and Saturn ($\sim 10^4$ K). The form of the pressure-density relation in the vicinity of the transformation at $P \sim 3$ Mbar can then be treated as an unknown parameter, leaving the pressure-density relation fixed in other regions of the planet where the theory is more accurate. Figure 4 shows three alternative ways in which adiabats in a solar mixture of hydrogen and helium can be smoothly interpolated between the low-pressure molecular hydrogen region and the high-pressure metallic hydrogen region. Curve A approaches the exact high-pressure limit most rapidly, while curve C is closest to the equation of state of (metastable) metallic hydrogen and helium in the range of pressures less than 1 Mbar (2). Changes in the helium abundance and initial conditions of the adiabats shift all three curves but preserve their relative positions and differences in curvature. Adiabats of families A and C are not compatible with Jupiter's J_4 , while family B provide a satisfactory fit for both Jupiter and Saturn, although the helium abundance which is thereby derived is still very model-dependent. I emphasize that equation of state B is not a unique solution, and pressure-density relations with a density discontinuity remain to be investigated in detail. Clearly, accurate experimental measurements of the hydrogen equation of state in the vicinity of $P = 1$ Mbar will play an important role in constraining models.

Uranus and Neptune Models

Current models of Uranus and Neptune have a generic similarity to models of Jupiter and Saturn (Fig. 3). The principal difference is that hydrogen cannot be a major constituent according to the observed values for mass and radius. On the other hand, hydrogen is observed to be the major constituent in the atmospheres of both planets, and so we conclude that the outermost layer of both planets is mostly hydrogen, but that this layer contributes only a small fraction of the total mass. Therefore, the structure of the core is more gravitationally "exposed," and the calculated gravity field is much more sensitive to the relative layering of the ice and rock components than is the case for Jupiter and Saturn.

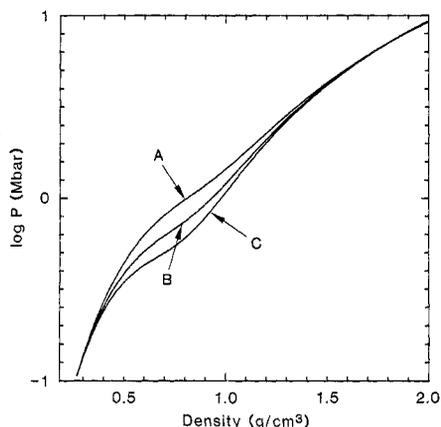


Fig. 4. Interpolated adiabatic pressure-density relations in molecular hydrogen and helium (lower left) and metallic hydrogen and helium (upper right).

Because of the shallow depth of the hydrogen layer, pressures remain well below 1 Mbar and so no metallic hydrogen is formed. Typical models of Uranus and Neptune have rock-iron cores of about $3 M_E$, $\text{CH}_4\text{-NH}_3\text{-H}_2\text{O}$ mantles of about $10 M_E$, and 1 to $2 M_E$ of hydrogen-rich atmosphere (2). In fact, they resemble Jupiter or Saturn with nearly all of the hydrogen envelope removed.

Accurate values for Λ_2 and approximate values for Λ_4 for Uranus are now available (14). These results indicate that the three-layer model mentioned above is not correct in unmodified form. An important component of this deduction is an improved laboratory measurement of the pressure-density relation for H_2O up to pressures of ~ 2 Mbar (Uranus and Neptune are probably about 50 percent water by mass) (15). The newer equation of state indicates that water is more compressible than was previously thought, so that the three-layer model has a smaller value of Λ_2 , significantly smaller than the observed value. In order to increase Λ_2 to the observed value, it is necessary to partially homogenize the planet, for example, by mixing the rock core with the ice mantle. This seems very unlikely because the ice component is surely molten. A more plausible alternative is to mix a gravitationally significant amount of $\text{CH}_4\text{-NH}_3\text{-H}_2\text{O}$ into the hydrogen-rich outer envelope. In fact, there is good observational evidence that CH_4 may be present in amounts as large as 40 percent of the mass in Uranus's atmosphere (16); this is about equal to the enrichment required to bring Λ_2 into agreement with the observed value. Such a model can be tested by comparing the value of Λ_4 with observation when the error bars become somewhat smaller.

There is a major qualitative difference between Jupiter-Saturn models and Uranus-Neptune models. There is no evidence from gravity data of any significant enhancement of $\text{CH}_4\text{-NH}_3\text{-H}_2\text{O}$ in the outer envelope of Jupiter or Saturn. Why is methane so enriched in Uranus's (and presumably Neptune's) atmosphere? Two possibilities need to be considered: (i) methane is strongly soluble in hydrogen at pressure of a few hundred kilobars, and there is enough convection in Uranus to cause mixing between the atmosphere and interior; and (ii) the hydrogen in Uranus's atmosphere is not primordial, but is produced by decomposition of methane at pressures greater than ~ 200 kbar (17). Either of these possibilities needs to be reconciled with the observation that the deuterium/hydrogen ratio in the atmospheres of Jupiter, Saturn, and Uranus is about the same and about equal to the primordial value (this ratio has not yet been obtained for Neptune). Since deuterium tends to concentrate in CH_4 , and also H_2O and NH_3 at temperatures low enough to condense these species, one expects that the planetary average value of the deuterium/hydrogen ratio in Uranus and Neptune should be at least four to five times the primordial value (18). The primordial value would be preserved in the hydrogen-rich atmosphere only if the atmosphere does not communicate in any way with the deeper interior of the planet.

Conclusions

The geophysical and geochemical study of the Jovian planets has many parallels to study of the earth and other terrestrial planets. In the Jovian planets the ices— CH_4 , NH_3 , and H_2O —and gaseous species such as H_2 and He play the role of minerals. The "surface" abundances that we observe in atmospheres may reflect complex processes of planetary accumulation, differentiation, and evolution. Thus, for example, the CH_4/H_2 ratio in the atmosphere may be diagnostic of whether methane condensed during formation of the protoplanetary core, or remained in the gas phase and was subsequently captured along with the H_2 and He. Future measurements in situ by means of atmospheric entry probes may give high-precision values for the abundances of many atmospheric constituents. Interpretation of these results will require continued work on interior modeling and on high-pressure geochemical studies.

References and Notes

1. V. N. Zharkov and V. P. Trubitsyn, *Physics of Planetary Interiors* (Pachart, Tucson, Ariz., 1978), p. 308.
2. W. B. Hubbard, J. J. MacFarlane, J. D. Anderson, G. W. Null, E. D. Biller, *J. Geophys. Res.* **85**, 5909 (1980); W. B. Hubbard and J. J. MacFarlane, *ibid.*, p. 225.
3. W. B. Hubbard, *Rev. Geophys. Space Phys.* **18**, 1 (1980).
4. ———, W. L. Slattery, C. L. DeVito, *Astrophys. J.* **199**, 504 (1975).
5. W. B. Hubbard, *Astron. Zh.* **51**, 1052 (1974).
6. H. Mizuno, *Prog. Theor. Phys.* **64**, 544 (1980).
7. F. Perri and A. G. W. Cameron, *Icarus* **22**, 416 (1974).
8. S. K. Sharma, H. K. Mao, P. M. Bell, *Phys. Rev. Lett.* **44**, 886 (1980); *Carnegie Inst. Washington Yearb.* **79**, 358 (1980).
9. D. J. Stevenson and E. E. Salpeter, in *Jupiter*, T. Gehrels, Ed. (Univ. of Arizona Press, Tucson, 1976), pp. 85–112.
10. D. J. Stevenson, *Phys. Rev. B* **12**, 3999 (1975).
11. G. S. Orton and A. P. Ingersoll, *J. Geophys. Res.* **85**, 5871 (1980).
12. R. Hanel *et al.*, *Science* **212**, 192 (1981).
13. G. W. Null, E. L. Lau, E. D. Biller, J. D. Anderson, *Astron. J.* **86**, 456 (1981).
14. J. L. Elliot, R. G. French, J. A. Frogel, J. H. Elias, D. J. Mink, W. Liller, *ibid.*, p. 444.
15. A. C. Mitchell and W. J. Nellis, *High Pressure Sci. Technol.* **1**, 428 (1979).
16. L. Wallace, *Icarus* **43**, 231 (1980).
17. M. Ross and F. Ree, *J. Chem. Phys.* **73**, 6146 (1980).
18. W. B. Hubbard and J. J. MacFarlane, *Icarus* **44**, 676 (1980).
19. Supported by NASA grant NSG-7045.

Similar Amino Acid Sequences: Chance or Common Ancestry?

Russell F. Doolittle

The ultimate goal in the study of protein evolution is the reconstruction of past events that have given rise to the vast inventory of proteins in existence today. It is altogether likely that the overwhelming majority of extant proteins—and certainly most enzymes—

of nucleic acid may be short, corresponding to a few amino acids, or extensive enough that microscopically visible pieces of chromosome are involved. Depending on whether or not the duplicated portions of the base sequence coexist within the boundaries set by the start and

Summary. The systematic comparison of every newly determined amino acid sequence with all other known sequences may allow a complete reconstruction of the evolutionary events leading to contemporary proteins. But sometimes the surviving similarities are so vague that even computer-based sequence comparison procedures are unable to validate relationships. In other cases similar sequences may appear in totally alien proteins as a result of mere chance or, occasionally, by the convergent evolution of sequences with special properties.

have evolved from a very small number of archetypal proteins. The premise is based on the notion that it is simpler to duplicate and modify proteins genetically than it is to assemble appropriate amino acid combinations de novo from random beginnings. In present-day living systems the invention of new proteins depends on gene duplications that lead to specific amino acid sequences being coded for by more than one segment of DNA (or RNA) in a given genome. The duplications are the results of various breakage and reunion events that occur more or less randomly in the genetic material (1).

Amino acid sequence studies have revealed that gene duplications occur in all kinds of organisms, prokaryotic and eukaryotic alike. The duplicated segment

stop signals for protein synthesis, the duplication may lead either to (i) an elongated polypeptide chain or (ii) two separate copies of the protein. The distinction between the two kinds of duplication—contiguous and discrete—is an important one. In the first case, the result is a larger protein fashioned at the expense of the preexisting gene product. Many examples of this phenomenon are recognizable in existing protein sequences (2), and there is little doubt that this process has been the major route to larger proteins. In the second case, two independent gene products result, for one of which there ought to be a relaxation of the evolutionary restraints imposed by natural selection. As such, it is free to mutate, most often to random oblivion, but occasionally to a form

adapted to some new role. The mutations that lead to divergence are mostly single base substitutions that engender individual amino acid replacements, although other events leading to deletions or insertions also occur.

Examples of creating a new protein with a new function by this route suggest that the new protein usually retains many of its preexisting features, the structural adaptations for new roles often being quite subtle, such as the sundry polypeptide chains that constitute the vertebrate hemoglobin system (3). The general shapes and folding patterns of these proteins are similar, and they all bind heme in essentially the same way. But small differences in their structures affect their interactions and their oxygen-binding properties. Similarly, examination of the deep-rooted phylogenetic tree of serine proteases reveals that the fundamental catalytic machinery is virtually identical for all these enzymes, but differences in the substrate binding region allow for an elegant selectivity of action for the diverse gene products that have descended from a host of duplications in the past (4). Even when the function of the “new” protein changes radically, as in the case of haptoglobin, a vertebrate transport protein clearly descended from serine protease stock (5), key structural features are retained. In this case the protein, whose present role is the salvaging of spent globins, has sharpened its ability to bind specific polypeptides but has lost its capability for hydrolyzing them (6, 7). Similarly, α -lactalbumin, a cofactor in the lactose synthetase system that has evolved from the polysaccharide-splitting enzyme lysozyme, has retained its ability to bind a saccharide component but has lost its hydrolytic capability (8). By comparison, it ought to be much more difficult to fashion a new protein with a specific function de novo. In the case of enzymes, the likelihood of assembling a stable constellation of amino acids that

The author is a professor in the Department of Chemistry, University of California, San Diego, La Jolla 92093.