

fusion. The Prandtl number, the ratio of kinematic viscosity to thermal diffusivity, for liquid mercury is two orders of magnitude less than that of water. Linearized analysis of two-dimensional motions predicts that the ratio of the mean fluid velocity to the speed of the traveling thermal wave becomes large as the Prandtl number becomes small; thus the theory is not valid in the limit of Prandtl number approaching zero. Results from an extended analysis which includes nonlinear interactions between the perturbations and the mean flow are shown in Fig. 2, where the ratio of mean flow velocity to wave speed is plotted against Prandtl number. This velocity ratio, which is approximately proportional to the $15/4$ power of the inverse Prandtl number for Prandtl numbers between 1 and 0.1, is of the order of unity for Prandtl numbers of the order 10^{-1} .

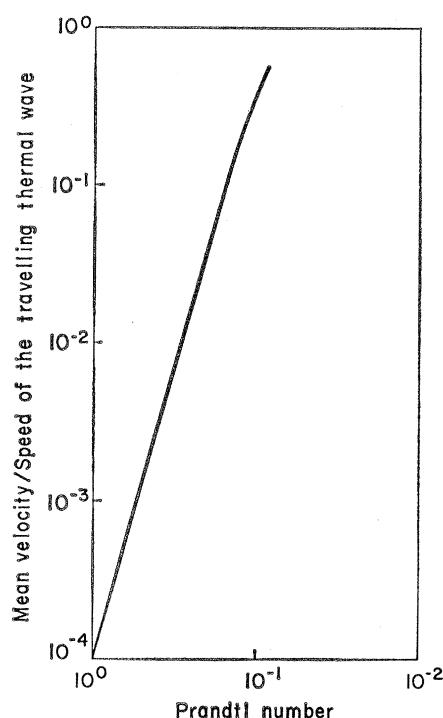


Fig. 2. Ratio of the mean velocity of the fluid to the speed of the forcing thermal wave plotted against Prandtl number. Fluid was confined within a two-dimensional channel, and temperature perturbations of the traveling wave were applied at the walls. The Boussinesq equations of motion were solved numerically for the following case: $\Delta T/T = 10^{-2}$, $\omega h^2/\kappa = 1$, $gh/U^2 = 10^4$, $kh = 10^{-2}$, where ω is the angular frequency, k is the wave number of the thermal wave, h is the channel height, κ is the thermal diffusivity, g is the acceleration of gravity, $U = \omega/k$, and $\Delta T/T$ is the relative magnitude of forced fluctuations of the wall temperature. The nonlinear interaction of the perturbations and the mean flow is included in the solution.

This experiment demonstrates that the periodic motion of a source of heat can lead to a mean fluid motion with speed several times faster than that of the source. This phenomenon may explain the relatively rapid displacements of clouds in the high atmosphere of Venus which have been observed in ultraviolet photographs (5). These observations suggest that at least the upper layers of the atmosphere of Venus are moving with speeds of 300 km/hour relative to the planet's surface. The overhead motion of the sun would provide a periodic traveling thermal source, and the zonal flow induced by this movement would be in the direction of the cloud motion, which is some 20 times faster than the overhead speed of the sun.

In the atmosphere of Venus, a near-infrared band of carbon dioxide absorbs a significant fraction of the incident solar radiation. At altitudes of tens of kilometers where pressures are of the order of an atmosphere or less (6), a kilometer of CO_2 absorbs several percent of the incident solar radiation (7). The radiative transfer would be characterized by an effective diffusion coefficient (8)

$$\kappa = 16\sigma T^3 l / 3\rho c_p$$

where σ is the Stefan-Boltzmann constant, T is the temperature, l is the mean free path of the radiation, ρ is the density, and c_p is the specific heat at constant pressure. At heights of tens of kilometers, $\kappa \approx 3l \text{ cm}^2 \text{ sec}^{-1}$, and l is at least of the order of 10^5 cm (7). Momentum transport would at best be accomplished by turbulent mixing, for which the mixing coefficient is not likely to exceed $10^4 \text{ cm}^2 \text{ sec}^{-1}$ (8). Thus it is possible that in the high atmosphere of Venus periodic heating from above occurs in a medium that can transport heat more effectively than momentum. Under such circumstances, zonal motions at high velocity could be induced in the Venus atmosphere.

G. SCHUBERT

Department of Planetary and
Space Science, University of
California, Los Angeles

J. A. WHITEHEAD

Institute of Geophysics and
Planetary Physics, University of
California, Los Angeles

References and Notes

1. E. Halley, *Phil. Trans. Roy. Soc. London Ser. A Math. Phys. Sci.* **16**, 153 (1686).
2. D. Fultz, *Meteorol. Monogr.* **4**, 36 (1959).
3. M. E. Stern, *Tellus* **11**, 175 (1959).

4. A. Davey, *J. Fluid Mech.* **29**, 137 (1967).
5. B. A. Smith, *Science* **158**, 114 (1967).
6. V. S. Avduevsky, M. Ya. Marov, M. K. Rozhdestvensky, *J. Atmos. Sci.* **25**, 537 (1968).
7. P. Fabian, T. Sasamori, A. Kasahara, in preparation.
8. R. M. Goody and A. R. Robinson, *Astrophys. J.* **146** (1966).
9. We thank W. V. R. Malkus for providing the equipment and laboratory facilities for this experiment, and P. Cox for constructing the apparatus.

5 November 1968

Species Diversity:

Benthonic Foraminifera in Western North Atlantic

Abstract. *Maximum species diversity occurs at abyssal depths of greater than 2500 meters. Other diversity peaks occur at depths of 35 to 45 meters and 100 to 200 meters. The peak at 35 to 45 meters is due to species equitability, whereas the other two peaks correspond to an increase in the number of species.*

Populations of benthonic Foraminifera exhibit species-diversity peaks at depths of 35 to 45 m, 100 to 200 m, and greater than 2500 m in the western North Atlantic. The peaks progressively increase in diversity as depth increases, the maximum diversity occurring in depths greater than 2500 m. The depths of the peaks correspond to effective wave base, the edge of the continental shelf, and the abyss. The peak in diversity at 35 to 45 m is due to species equitability rather than to an increase in the number of species, whereas the other two peaks correspond to an increase in the number of species. Data for this pattern are from 84 samples taken at depth ranges from 29 to 5001 m in the western North Atlantic (Fig. 1).

Many foraminiferal species have been recorded in abyssal depths in the Gulf of Mexico (1), off California (2), and off Panama in the eastern Pacific (3). The high foraminiferal diversities in abyssal environments closely reflect the diversity of the other groups of marine invertebrates including Mollusca, Arthropoda, and Echinodermata (4). The formerly erroneous viewpoint of very low diversity in the deep sea probably resulted from difficulty in obtaining enough individuals of larger invertebrates for an accurate estimate of the number of species (4).

The benthonic Foraminifera, being small, of high density and ubiquitous distribution, do not present many problems encountered in sampling larger organisms. Even in the abyss, hundreds

of individuals can be obtained by one core or bucket sample of 100 ml of sediment.

That the patterns reported are not local phenomena, or artifacts of Pleistocene changes, or sedimentological processes is shown by the following. Although downslope displacement may occur, the large area of high diversities precludes the possibility of sampling shallow-water or mixed assemblages. Likewise, the extent of the abyssal plain, the distance of some stations from land, and the lack of shallow-water forms in the assemblages indicate that the fauna is endemic. Most important, although the total foraminiferal fauna (living and dead) was used, an examination of living assemblages gives the same pattern.

Numerous hypotheses (5), most not mutually exclusive, attempt to explain the increase in organic diversity toward the lower latitudes. The "stability" hypothesis, of relatively uniform environment over a long period, reasonably explains the progressive increase of diversity peaks observed here. Under such conditions, biologic components become more important than physical ones. Organisms no longer need to maintain a high degree of tolerance to survive in an ever-changing environment. Entire populations are not in danger of being destroyed by extremes of weather. This lack of physiological stress may permit a higher degree of specialization with complex interactions between species to use the energy in the system more efficiently, thus more species at all trophic levels.

Although diversity is usually measured as the number of species in some sample of specified size, diversity may also be measured as the number of species and their frequencies (6, 7). The information function (7-9) effectively measures the number of species and their proportions without making any assumptions as to an underlying distribution. The function is defined as

$$H(S) = -\sum_{i=1}^S p_i \ln p_i$$

where p_i is the proportion of the i th species, and S is the number of species observed. Species with low frequencies contribute little to the value $H(S)$. For example, a species making up 30 percent of the assemblage contributes 0.36 to the value of $H(S)$, whereas a species with a frequency of 1 percent contributes only 0.05. Consequently, $H(S)$, is not as variable as

S , which is more subject to fluctuation because of the presence or absence of a rare species. The maximum value of $H(S)$ (maximum diversity) occurs when all S species have equal frequencies, in which case $H(S)$ is $\ln S$. When e , the base of the natural logarithms, is raised to the $H(S)$ power, the result is a measure of the equivalent number of equally distributed species (10). For equally distributed species $e^{H(S)} = S$, so that the ratio $e^{H(S)}/S$ is a measure of species equitability similar to some others proposed (7, 9). When the species are perfectly equally distributed the ratio = 1.

When $H(S)$ is plotted against depth (Fig. 2), the peaks in diversity occur at 35 to 45 m, 100 to 200 m, and greater than 2500 m. The highest peak occurs in waters deeper than 2500 m. Very shallow areas, less than 30 m, have values of $H(S)$ less than 1.5. In all traverses $H(S)$ increases to greater than 1.9 at about 35 to 45 m. This high is followed by a decrease to values with minima at about 70 m. Then $H(S)$ begins to increase, reaching a peak of

3.0 at 100 to 200 m. Below 200 m, the values slowly decrease down the continental slope to less than 2.0 at 2000 m. With increasing depth in the abyss, $H(S)$ rises sharply, and a maximum of 3.5 is reached at 4977 m.

Although the number of species per sample (S) is strongly correlated with $H(S)$ (Fig. 2), the $H(S)$ high at 35 to 45 m is not apparent in the species number; S usually is less than 20 in waters shallower than 70 m. Closer to the edge of the shelf, at depths of 70 to 200 m, the number of species increases to 30 to 49. As in $H(S)$, on the continental slope the number decreases to less than 30 species. At about 1000 m, the number begins to increase once more. At 2500 m, S increases to approximately 50 species, and at 4977 m (the second deepest station), 83 species, the maximum number in the study, occurs.

The ratio $e^{H(S)}/S$ has its highest set of values, 0.61 to 0.77, at the 35 to 45 m high of $H(S)$ (Fig. 2). This peak indicates that the most equitable distribution of species occurs here. A general decrease to a low of 0.22 occurs at

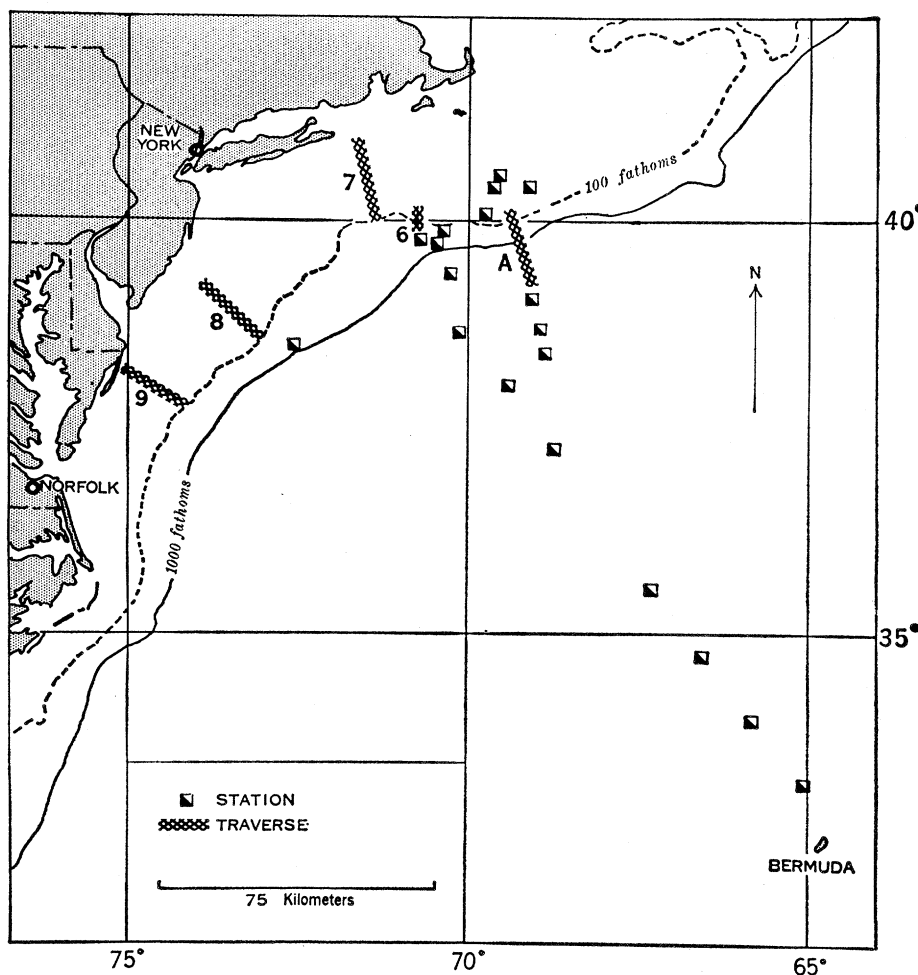


Fig. 1. Sample locations. Traverses 6 through 9 taken from Parker (14).

about 100 m. (The New Jersey traverse, however, shows a more complex pattern beyond the 35 to 45 m high, decreasing to 0.44 at 74 m, and then rising again to 0.68 at 90 m, after which the ratio decreases once more). All traverses have values usually between 0.30 and 0.50 at depths from 100 to 1000 m. Two stations at 393 and 469 m, however, have unusually high values of 0.66 and 0.68. Another low occurs at 1000 to 2000 m, with values ranging between 0.25 to 0.28. At 2000 to 5000 m the ratio again increases and ranges from 0.17 to 0.46. As Fig. 2 shows, the ratio is more variable than either S or $H(S)$.

At the successive diversity-peaks, environmental variables fluctuate progressively less. The low diversities in shallow water can be explained by the extreme physical stress placed on

organisms there. The low diversities on the continental slope may be due to environmental instability reflected in downslope movement of sediment on the slope. As mentioned earlier, the high at 35 to 45 m measured by $H(S)$ is due to species equitability rather than an increase in the number of species. The significance of this high is not yet apparent.

To achieve the complex organization and thus high diversity would require a considerable period of environmental stability. Some authors (11) suggested that the abyssal and hadal faunas are a combination of relict species and species which have migrated into the abyss since Pleistocene glaciation. If the abyssal fauna was severely affected by the Pleistocene and is relatively recent in origin, than the organic diversity reported here cannot be explained by

stability of environmental conditions over a long period.

Several lines of evidence, however, indicate that the Pleistocene glaciation was not a catastrophic event for the marine fauna. Shallow-water benthic foraminiferal faunas from the study area have undergone only slight change in the last 20 million years (12). Changes in sea level accompanying glaciation caused migration of shallow-water faunas, but with the rise in sea level, they simply repopulated the newly recovered shallow-water environments (13). If migration of shallow-water faunas into the abyss took place after the Pleistocene, species found in pre-Pleistocene shallow-water assemblages should now be found in living abyssal faunas. Comparison of Miocene and younger Tertiary shallow-water foraminiferal faunas with living abyssal faunas

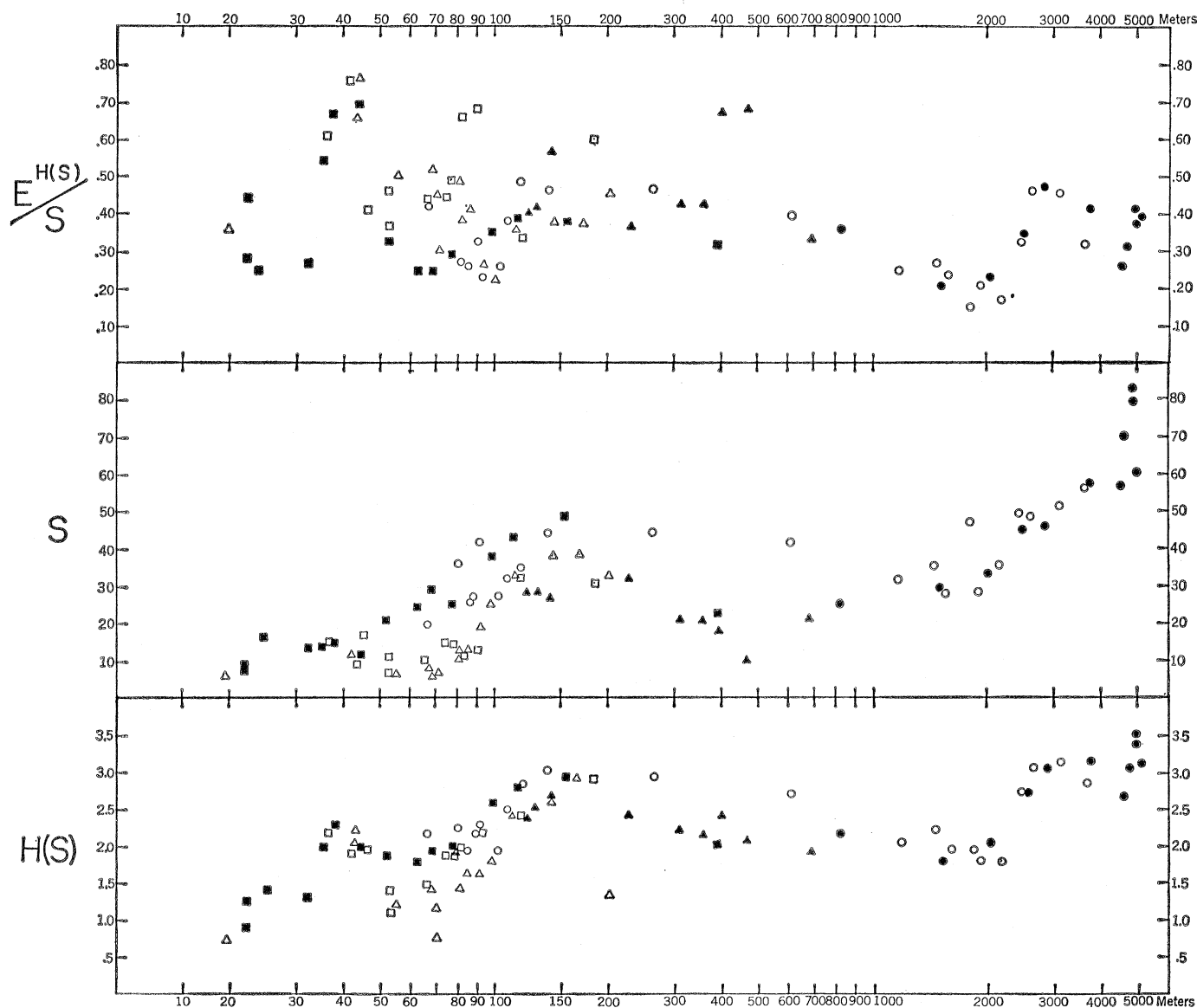


Fig. 2. Plots of species diversity and equitability with depth. Symbols: open triangle, Black Island (Parker); solid triangle, Martha's Vineyard (Parker); closed circle, Deep Sea (Gibson); open circle, Nantucket (Gibson); open square, New Jersey (Parker); closed square, Maryland (Parker).

shows this not to be the case; species found in shallow-water deposits in the Miocene and Pliocene are not presently found in abyssal depths although they still live in shallow waters. Likewise, one would expect deep-water assemblages in the Miocene and younger Tertiary to be largely or completely different from the post-Pleistocene. A sample of *Globigerina* ooze of early Miocene age was dredged at a depth of 847 m, and many of the species presently restricted to the abyssal fauna also occur only in the early Miocene deep-water assemblage. Thus, our evidence indicates that the abyssal fauna is not Recent in origin, and that time to develop the diverse faunas was available.

MARTIN A. BUZAS

Smithsonian Institution,
Washington, D.C. 20560

THOMAS G. GIBSON

U.S. Geological Survey,
Washington, D.C. 20242

References and Notes

1. F. L. Parker, *Mus. Comp. Zool. Bull.* **111**, 453 (1954).
2. O. L. Bandy, *J. Paleontol.* **27**, 161 (1953); — and R. E. Arnal, *Bull. Amer. Ass. Petrol. Geol.* **44**, 1921 (1960).
3. O. L. Bandy and R. E. Arnal, *ibid.* **41**, 2037 (1957).
4. R. R. Hessler and H. L. Sanders, *Deep-Sea Res.* **14**, 65 (1967).
5. Th. Dobzhansky, *Amer. Sci.* **38**, 209 (1950); A. G. Fischer, *Evolution* **14**, 64 (1960); P. H. Klopfer, *Amer. Natur.* **93**, 337 (1959); R. Margalef, *ibid.* **97**, 357 (1963); E. R. Pianka, *ibid.* **100**, 33 (1966); H. L. Sanders, *ibid.* **102**, 243 (1968).
6. R. A. Fisher, A. S. Corbet, C. B. Williams, *J. Anim. Ecol.* **12**, 42 (1943); F. W. Preston, *Ecology* **29**, 254 (1948); E. H. Simpson, *Nature* **163**, 688 (1949).
7. D. R. Margalef, *Gen. Syst.* **3**, 36 (1958).
8. R. H. MacArthur and J. W. MacArthur, *Ecology* **42**, 594 (1961).
9. B. B. Patten, *J. Mar. Res.* **20**, 57 (1962).
10. R. H. MacArthur, *Biol. Rev.* **40**, 510 (1965).
11. A. F. Bruun, *Nature* **177**, 1105 (1956); T. Wolff, *Deep-Sea Res.* **6**, 95 (1960).
12. T. G. Gibson, *Bull. Geol. Soc. Amer.* **78**, 631 (1967).
13. F. B. Phleger, *Mus. Comp. Zool. Bull.* **106**, 314 (1952).
14. F. L. Parker, *ibid.* **100**, 213 (1948).
15. We thank R. Beavers, R. Cifelli, J. F. Mello, J. Prioleau, and M. C. Taylor for their assistance.

10 September 1968; revised 4 November 1968 ■

Macroglobulin Structure: Homology of Mu and Gamma Heavy Chains of Human Immunoglobulins

Abstract. The amino acid sequence of fragments obtained by cyanogen bromide cleavage of the mu-chain of a human γ M-globulin is homologous to the NH_2 -terminal sequences of the gamma-chain of human and rabbit γ G-globulins and is related to that of human light chains. This supports the hypothesis that light and heavy chains evolved from a common ancestral gene.

Immunoglobulins embrace antibodies and proteins related to antibodies in having a tetrachain structure composed of a pair of heavy and a pair of light polypeptide chains, and also include Bence Jones proteins (free light chains). The three major classes of immunoglobulins, γ G, γ A, and γ M (or alternatively, IgG, IgA, and IgM), are demarcated by their heavy chains (γ , α , and μ , respectively); each class is divided into two antigenic types (K or L) based on the presence of a pair of kappa or of lambda light chains. Normal κ and λ light chains of all species are heterogeneous owing to variability in amino acid sequence of the NH_2 -terminal half (about 110 residues); in contrast, the COOH-terminal half (105 to 107 residues) is invariant in sequence except for single amino acid substitutions, some of which are apparently allelic (1). This conclusion is based on complete amino acid sequence analysis of some ten individual human κ - and λ -type Bence Jones proteins excreted by patients with multiple myeloma or macroglobulinemia (2-6) and of the κ -type Bence Jones proteins from two

mouse plasmacytoma strains (3). It is supported by partial sequence analysis of the NH_2 -terminal and COOH-terminal peptides of the κ - and λ -type light chains of many species (7). A similar bipartite structure has been proposed for heavy chains (1); the latter are composed of somewhat more than 400 amino acid residues, and can be cleaved enzymatically (8) into an NH_2 -terminal (Fd) and a COOH-terminal (Fc) fragment of approximately equal size. Although the Fd-fragment is believed to have the variable, and the Fc-fragment the constant sequence, this has not yet been established because the maximum length of sequence published comprises only the NH_2 -terminal 84 residues of one human γ -chain from a myeloma patient designated Daw (9) and the COOH-terminal 216 residues of the γ -chain from pooled, normal γ G-globulin of the rabbit (10).

We report here the complete sequence of three fragments (F1, F2, and F3) apparently comprising the first 105 residues of the NH_2 -terminal portion of a μ -chain from a pathological human γ M-macroglobulin designated Ou (Fig.

1), and also the sequence of two smaller fragments from the COOH-terminal (Fc) portion of the μ -chain (Fig. 2). When only one gap is placed in each chain, 61 residues in the first 84 (or 73 percent) are in identical positions in the human γ -chain Daw and the human μ -chain Ou, and the two chains are equally homologous to the NH_2 -terminal F1 fragment comprising the first 35 residues of the normal rabbit γ -chain (11). Evolutionary relationships of heavy and light chains are suggested by these similarities in sequence of the three heavy chains and also by similarities to κ - and λ -chains.

The μ heavy chain of the κ antigenic type γ M-globulin from patient Ou was prepared by mild reduction with dithiothreitol or β -mercaptoethanol to break the interchain disulfide bonds and subsequent alkylation with iodoacetamide. The κ light chains and the μ heavy chains were separated by gel filtration on Sephadex G-100 and three major peaks resulted. The heavy chain was cleaved by reaction with CNBr for 24 hours in 70 percent formic acid; this breaks the peptide bond on the carboxyl side of methionine and converts methionine to homoserine. The fragments formed by CNBr were fractionated with Sephadex G-100 and purified by repeated gel filtration or ion-exchange chromatography. The purified fragments were completely reduced and were aminoethylated with ethylenimine or were carboxymethylated with iodoacetamide to break intrachain disulfide bonds.

In two cases, reduction and aminoethylation yielded additional fragments. Nine fragments formed by CNBr were defined for the Ou heavy chain; altogether these accounted for the total amino acid content of the untreated μ -chain. The largest fragment was composed of about 130 amino acids (Sephadex peak 2); it accounted for the bulk of the carbohydrate in the original γ M-globulin and had a COOH-terminal homoserine residue. Two homoserine-containing units in peak 1, each composed of about 100 residues, appeared to be linked by an intrachain disulfide bond before reduction. The remaining fragments were smaller and varied in size from 4 to 50 amino acid residues. Their amino acid sequence, as determined by use of the Edman degradation method on the tryptic and chymotryptic peptides, is presented in this report. Identical fragments were also obtained by cleavage of the whole γ M-globulin with CNBr followed by