

All three also recognized two major polypeptides of 60 and 66 kD in human, cat, rat, and mouse brain extracts. These three antisera (two of which have been extensively used to map GABA-containing neurons) seem to recognize overlapping sets of epitopes. The smaller polypeptides recognized by these antisera may represent degradation products of a single 66-kD polypeptide.

The antigenicity and enzymatic activity of the fusion protein establishes the identity of the GAD cDNA. In addition, labeled GAD DNA hybridizes to a single electrophoretic component in polyadenylated RNA of cat and human brain, but not of liver or kidney, a result consistent with the expected distribution of GAD in the brain (1, 2, 17). Furthermore, the pattern of in situ hybridization with single-stranded GAD RNA probes with frozen sections of mouse brain is consistent with the immunocytochemically determined distribution of GABA-containing neurons (18).

Of particular note is the enzymatic activity of the fusion protein, which consists of 1006 amino acid residues of β -galactosidase and at least 400 amino acid residues of GAD, representing two-thirds or more of the total length of one of the brain GAD polypeptides. Apparently the attachment of

the GAD polypeptide segment to the β -galactosidase polypeptide segment is sufficiently flexible to allow the assembly not only of immunologically detectable domains but also of the active site. Direct assays of enzyme activity or ligand binding (19) may be useful for identifying other members of bacterial expression libraries.

REFERENCES AND NOTES

1. E. Roberts, T. N. Chase, D. B. Tower, Eds., *GABA in Nervous System Function* (Raven, New York, 1976).
2. L. Hertz, E. Kvamme, E. G. McGeer, A. Schouboe, Eds., *Glutamine, Glutamate and GABA in the Central Nervous System* (Liss, New York, 1983).
3. K. Saito et al., *Proc. Natl. Acad. Sci. U.S.A.* **71**, 269 (1974).
4. W. H. Oertel, D. E. Schmechel, M. L. Tappaz, I. J. Kopin, *Neuroscience* **6**, 2689 (1981).
5. W. H. Oertel, D. E. Schmechel, E. Mugnaini, M. L. Tappaz, I. J. Kopin, *ibid.*, p. 2715.
6. R. A. Young and R. W. Davis, *Proc. Natl. Acad. Sci. U.S.A.* **80**, 1194 (1983).
7. ———, *Science* **222**, 778 (1983).
8. D. L. Kaufman and A. J. Tobin, in *Molecular and Chemical Characterization of Membrane Receptors*, L. C. Harrison and J. C. Venter, Eds. (Liss, New York, 1984), pp. 241–259.
9. M. M. Harpold, P. R. Dobner, R. M. Evans, E. L. Bancroft, *Nucleic Acids Res.* **5**, 2039 (1978).
10. R. P. Ricciardi, J. S. Miller, B. E. Roberts, *Proc. Natl. Acad. Sci. U.S.A.* **76**, 4927 (1979).
11. J. E. Schwarzbauer, J. W. Tamkun, I. R. Lemischka, R. O. Hynes, *Cell* **35**, 421 (1983).
12. H. Towbin, T. Staehelin, J. Gordon, *Proc. Natl. Acad. Sci. U.S.A.* **76**, 4350 (1979).
13. N. W. Burnette, *Anal. Biochem.* **112**, 195 (1981).
14. B. A. Bidlingmeyer, S. A. Cohen, T. L. Tarvin, *J. Chromatogr.* **336**, 93 (1984).
15. J.-Y. Wu, T. Matsuda, E. Roberts, *J. Biol. Chem.* **248**, 3029 (1973).
16. J.-M. Blinderman, M. Maitre, L. Ossola, P. Mandel, *Eur. J. Biochem.* **86**, 143 (1978).
17. T. L. Wood, G. D. Frantz, J. H. Menkes, A. J. Tobin, *J. Neurosci. Res.*, in press.
18. C. W. Wuenschell, R. S. Fisher, D. L. Kaufman, A. J. Tobin, *Proc. Natl. Acad. Sci. U.S.A.*, in press.
19. For example, J. M. Sikela and W. E. Hahn, *Soc. Neurosci. Abstr.* **11**, 353 (1985).
20. M. M. Bradford, *Anal. Biochem.* **72**, 248 (1976).
21. N. R. Krieger and J. S. Heller, *J. Neurochem.* **33**, 299 (1979).
22. M. L. Tappaz, M. J. Brownstein, M. Palkovits, *Brain Res.* **108**, 371 (1976).
23. U. K. Laemmli, *Nature (London)* **227**, 680 (1970).
24. J. F. McGinnis and P. J. Leveille, *Curr. Eye Res.* **4**, 1127 (1985).
25. D. C. Spink, T. G. Porter, S. J. Wu, D. L. Martin, *Biochem. J.* **231**, 695 (1985).
26. The antiserum to GAD used in the screening was provided through the Laboratory of Clinical Science, National Institute of Mental Health, where it was developed under the supervision of I. J. Kopin, with W. Oertel, D. Schmechel, and M. Tappaz. We thank D. Martin and J. Vaughn for providing antibodies; P. Comiso for assistance in the immunoblotting experiments; Y. Kobayashi for advice on the protein purification; J. Collopy for help in manuscript preparation; and N. Buchwald, R. Fisher, A. Fowler, S. Huttner, I. Kopin, E. Roberts, E. Askanas, K. Bugra, R. Koelling, R. Scott, L. Sussman, N. Tillakaratne, D. Wandres, T. Wood, and C. Wuenschell for help and advice. Supported by a grant from the Dystonia Medical Research Foundation and NINCDS grants NS20356 and NS22256 (A.J.T.), NICHD grant HD05615 (J.F.M.), and USPHS National Research Service Award GM07185 (D.L.K.).

25 September 1985; accepted 5 February 1986

Dentochronological Separation Estimates for Pacific Rim Populations

CHRISTY G. TURNER II

Dental morphology of American Indians, Asians, and Pacific islanders is used with a multivariate statistic to estimate when genetic separation occurred between several populations. These estimates generally match independent estimates of separation. This method, called dentochronology, gives an American Indian fission date from Asians of about 13,000 \pm 3,000 years ago, which agrees with archeological data and rules out a European origin because of temporal priority. Polynesians split from Southeast Asians 5,000 \pm 2,200 years ago and are not derived from Melanesians. Ainu-Jomon originated in Sundaland 14,000 \pm 3,300 years ago. Africans have been separated from Asian-Americans 60,000 \pm 6,100 years.

MICROEVOLUTION OF DENTAL morphology was proposed for estimating the separation date of American Indians from north Asians, when the multivariate mean measure of divergence (MMD) value was chronologically calibrated with independent archeological information for both (1). The dental clock for the peopling of the New World by Paleo-Indians, set by Aleut archeological and paleoenvironmental information, indicated that the groups arrived independently in Alaska about 12,000 years ago, giving an MMD of

Aleut to northeast Asian of 0.115733 and a dental microevolution rate of 0.00964 MMD per 1000 years. Dividing the rate into the mean American Indian to northeast Asian MMD of 0.135 suggested Indian–northeast Asian separation about 14,000 years ago. This value agreed with Paleo-Indian archeological findings of Clovis culture in the American Southwest 12,000 years ago (2). A few other comparisons suggested the dentochronological method to be promising. Additional Old World and Pacific dental data were collected

in 1983–84 to further assess the method.

The teeth used here belong to 14,000 crania in 200 human skeletal samples, mostly archeological but some ethnographic or hospital preparations, mainly from the Americas, eastern Asia, and the Pacific Basin. Each sample is characterized by 28 standard crown and root traits, like incisor shoveling, molar and premolar cusp numbers, root numbers of various teeth, and others. Sexes are pooled and counts are based on individuals (3).

The MMD's were calculated for all pairs of comparisons between 85 samples. Those possessing archeological, linguistic, or physical anthropological evidence for common descent are given in Table 1. The rest are excluded for lack of relevant independent information.

Estimating the time of genetic separation between two groups is more difficult than establishing when one of the two initially colonized a new area. Helpful for reconstructing Pacific Rim population history is the 100-m rise in sea level between 16,000 to 12,000 years ago that fragmented and isolated Tasmania–Australia–New Guinea

Department of Anthropology, Arizona State University, Tempe, AZ 85287.

(Sahuland), mainland and island Southeast Asia (Sundaland), all the east Asian continental shelf islands including those of Japan, and the Americas (4). Except for 80 to 160 km of open sea between Sundaland and Sahuland, all these areas were connected by continental shelf or dry land bridges before 14,000 years ago, and afterwards were separated by variously sized sea barriers. Many comparisons in Table 1 involve populations that grew from initially small parties of "island" founders before, during, or shortly after late Pleistocene sea level changes.

Complete genetic isolation may occur later than initial regional colonization by a

fissioning group, depending on how barrier formation occurred. The "independent estimate of separation" (Table 1) assumes that gene flow between the paired comparisons has ceased or is insignificant.

The independent dates for fissioning (Table 1) are based on archeological or other evidence, or both. For example, Aleut/Eskimo separation time is based on estimated linguistic divergence supported by Aleutian carbon-14 dates. The California (and all other American groups) and north Asian separation is based on archeological findings for the colonization of Arctic northeast Siberia and the Americas. The European/A-

merican Indian comparison assumes that both populations were derived from earlier groups who had a common origin about 50,000 years ago (5). The various Sundaland and Jomon comparisons recognize that the latter had a southern origin and have been isolated in Japan more than 12,000 years (1).

There is generally good fit between the dendrochronological and independent dating estimates. Quite reasonable correspondences are the separation estimates between Aleut/Eskimo (3,888 years dental estimate; 4,000 years independent estimate), Aleut-Eskimo and north Asia [11,000 ± 3,700

Table 1. Dendrochronological estimates of human population separation.

Diverging groups	Mean MMD	SD	Rate* (MMD/1,000 years)	Dental estimate of years separated	Independent separation estimate	
					Years	Basis
Aleut/Eskimo	0.040	—	0.01029	3,888	4,000	Language, C-14 (10)
Aleut/N. Asia	0.1121	0.031	0.01026	10,929	12,000	C-14, sea level rise (11)
Eskimo/N. Asia	0.1149	0.045	0.01026	11,203	12,000	C-14, sea level rise (11)
Paleoindian/Indian	0.1437	0.024	0.0102	14,082	11,000	C-14 (2)
New World/Holland	0.5753	0.057	0.01061	52,002	50,000	First anatomical moderns (5)
New World/Denmark	0.5521	0.056	0.01061	52,016	50,000	First anatomical moderns (5)
New World/England	0.5216	0.057	0.01061	49,161	50,000	First anatomical moderns (5)
New World/N.W. Europe	0.4063	0.042	0.01061	38,294	50,000	First anatomical moderns (5)
New World/W. Africa	0.6086	0.063	0.01026	59,302	50,000	First anatomical moderns (5)
NW U.S.—Canada/N. Asia	0.1034	0.02	0.01025	10,083	15,000	C-14 Siberia and Americas (12)
E U.S.—Canada/N. Asia	0.1295	0.03	0.01025	12,631	15,000	C-14 Siberia and Americas (12)
SW U.S./N. Asia	0.1053	0.023	0.01016	10,369	15,000	C-14 Siberia and Americas (12)
California/N. Asia	0.1351	0.032	0.01016	13,297	15,000	C-14 Siberia and Americas (12)
Mesoamerica/N. Asia	0.1631	0.049	0.01016	16,053	15,000	C-14 Siberia and Americas (12)
S. America/N. Asia	0.1326	0.038	0.01016	13,054	15,000	C-14 Siberia and Americas (12)
Archaic Canada/N. Indian	0.029	0.008	0.01006	2,882	4,000	C-14 (13)
Hiogo Japan/China	0.0282	0.028	0.00986	2,860	2,500	Yayoi stratigraphy, C-14 (14)
Japan/China	0.0178	0.014	0.00986	1,805	2,500	Yayoi stratigraphy, C-14 (14)
Recent Japan/China	0.0428	0.04	0.00986	4,341	2,500	Yayoi stratigraphy, C-14 (14)
Kanto Japan/China	0.0364	0.042	0.00986	3,692	2,500	Yayoi stratigraphy, C-14 (14)
Kamakura Japan/China	0.039	0.038	0.00986	3,955	2,500	Yayoi stratigraphy, C-14 (14)
Early Thailand/Jomon	0.121	0.044	0.00993	12,185	10,000	Obsidian, C-14, sea level rise (15)
Early Malay/Jomon	0.1188	0.089	0.00965	12,305	10,000	Obsidian, C-14, sea level rise (15)
Leang Tjang/Jomon	0.1188	0.041	0.00981	12,559	10,000	Obsidian, C-14, sea level rise (15)
Sundaland/Jomon	0.0956	0.027	0.00968	9,877	15,000	Obsidian, C-14, sea level rise (15)
Sundaland/Tsukumo Jomon	0.0875	0.034	0.00968	9,040	14,000	Obsidian, C-14, sea level rise (15)
Sundaland/Hokkaido Jomon	0.1501	0.024	0.00968	15,507	14,000	Obsidian, C-14, sea level rise (15)
Sundaland/Yoshiko Jomon	0.1785	0.038	0.00968	18,481	14,000	Obsidian, C-14, sea level rise (15)
Sundaland/S.W. Jomon	0.178	0.037	0.00968	18,390	14,000	Obsidian, C-14, sea level rise (15)
Early Thailand/S.E. Asia	0.0307	0.028	0.00991	3,099	3,500	C-14 (16)
Early Laos-Vietnam/S.E. Asia	0.0018	0.004	0.00991	182	4,000	C-14 (16)
Early Malay Archipelago/S.E. Asia	0.1122	0.053	0.00991	11,326	6,000	Typological extrapolation, C-14 (17)
Leang Tjadang/S.E. Asia	0.0655	0.043	0.00991	6,612	5,000	Typological extrapolation, C-14 (17)
New Britain/S.E. Asia	0.1644	0.045	0.00991	16,596	15,000	Sea level rise (18)
New Guinea/S.E. Asia	0.1649	0.031	0.00991	16,646	15,000	Sea level rise (18)
Solomons/S.E. Asia	0.1531	0.030	0.00991	15,455	15,000	Sea level rise (18)
Malay-Java/Polynesia	0.0496	0.022	0.00999	4,964	4,000	C-14 (19)
New Britain/Polynesia	0.1068	0.057	0.01002	10,659	15,000	Sea level rise (18, 20)
New Guinea/Polynesia	0.1329	0.043	0.01002	13,264	15,000	Sea level rise (18, 20)
Solomons/Polynesia	0.1688	0.089	0.0100	16,816	15,000	Sea level rise (18, 20)
Australia/Melanesia	0.14	0.092	0.0100	13,967	20,000	C-14, sea level rise (18, 20)
Australia/Tasmania	0.282		0.01001	28,183	20,000	C-14, sea level rise (18, 20)
Ceylon/Europe	0.0487	0.015	0.01024	4,757	10,000	Language (21)
Danish Neolithic/Europe	0.0247	0.019	0.01024	2,413	4,000	C-14 (22)
Early Nubia/Egypt	0.021		0.01021	2,056	11,000	C-14, hieroglyphs (23)

*The rate is based on the average of all groups excluding the comparative pair wherever they are combined or alone. Between 27 and 44 MMD's are involved in each rate value.

(1 SD) years dental; 12,000 years independent], all American Indian–north Asian combinations (13,000 ± 3,000 years dental; 15,000 years independent), Japan/China (3,300 ± 3,300 years dental; 2,500 years independent), southeast Asia/Jomon (12,300 ± 6,000 years dental; 10,000 years independent), Sundaland/Jomon (14,000 ± 3,300 years dental; 14,000 years independent), and the various combinations involving Melanesia, Australia, and Polynesia.

A few groups' dentochronological separation estimates differ considerably from their respective independent estimates. The New World–northwest Europe comparison is one such. The dental separation date is about 10,000 years less than the dates between the New World and the other European series. The explanation for the northwest Europe deviation is that these people's ancestors had mixed with Neolithic and later west Siberian Mongoloids (6) and are dentally a bit more like New World Mongoloids than are unadmixed Europeans. Another deviant finding is that for early Laos-Vietnam/southeast Asia. This is apparently a sampling error since the early Thailand/southeast Asia dental date is well in line with the independent estimate of separation. The early Malay Archipelago/southwest Asia dental date is much older than the independent estimate, but this is attributable in part to archeological problems in dating the skeletons. It is also possible that the early Malay archipelago people were not genetically close to mainland southeast Asians, as this region is near the border of Howells' (7) proposed "Old Melanesia" and "Hoabinhia" of 50,000 years ago. Finally, the early Nubia/Egyptian dental date for separation differs widely from the archeological findings. Both dental sampling and archeological dating may be contributing to the deviation.

Despite the few unexplained deviations, there is generally solid correspondence between the dental and independent assessments for separation. Further support of the dentochronological method exists with four comparisons between Ainu and Jomonese samples that are not included in Table 1. The Jomonese were the prehistoric people of Japan. Their living descendants are the linguistically isolated Ainu. Today's Austro-Tai-speaking Japanese are descended from mainland Asian immigrants who began arriving in large numbers during Yayoi times (2,200 years ago). Genetic studies of modern Ainu show them to be markedly admixed with Japanese (8). Instead of showing a dental date of about 2,000 years of separation, the Ainu/Jomon value is 10,500 years. Admixture with Japanese has accelerated dental microevolution in the Ainu by a factor of 5. Possibly a similar admixture or

population replacement event underlies the early Malay Archipelago/southeast Asia and early Nubia/Egypt deviations.

Given that the dentochronological method usually produces dates close to expectation, it is important that no comparison suggests that the Americas were colonized much before 15,000 years ago. This estimate weighed against that for New World–European divergence (50,000 to 60,000 years ago) provides priority for an Asian rather than a European origin of American Indians. Suggestions for occupation of Australia in excess of 30,000 years are supported by the 28,000-year separation date between Australians and Tasmanians. Dentally, the long-standing controversy about Polynesian origins is resolved; at least the possibility that Polynesians originated primarily in Melanesia is eliminated. The greatest dental separation date from these skeletal samples is 60,000 ± 6,100 years, between west African and New World populations. This value is in line with recent antiquity estimates for anatomically modern humans (*Homo sapiens sapiens*) of 50,000 to 100,000 years ago (9).

How dental microevolution occurs is not clear, but it is seemingly quite regular. Where it provides dates markedly different from independent dating estimates there is a chance that the latter are incorrect.

In summary, dentochronological estimates for genetic separation between numerous skeletal samples have strong correspondence with independent branching estimates. The major exceptions can be explained by subsequent admixture in one of the branch pairs. The average world dental microevolution rate of 0.01003 ± 0.004 MMD per 1,000 years may help in estimating the antiquity of other skeletal population samples.

REFERENCES AND NOTES

1. C. G. Turner II, in *Out of Asia: Peopling the Americas and the Pacific*, R. Kirk and E. Szathmary, Eds. (Journal of Pacific History, Canberra, 1985), pp. 31–78. MMD is a well-known multivariate statistic developed by C. A. B. Smith [see A. C. Berry and R. J. Berry, *J. Anat.* **101**, 361 (1967)].
2. C. V. Haynes, in *Quaternary Extinctions. A Prehistoric Revolution*, P. S. Martin and R. G. Klein, Eds. (Univ. of Arizona Press, Tucson, 1984), pp. 345–353; F. H. West, *The Archaeology of Beringia* (Columbia Univ. Press, New York, 1981); R. C. Owen, in *The Origins of Modern Humans. A World Survey of the Fossil Evidence*, F. H. Smith and F. Spencer, Eds. (Liss, New York, 1984), pp. 517–563.
3. See C. G. Turner in (1) for more details.
4. D. M. Hopkins, in *The First Americans: Origins, Affinities, and Adaptations*, W. S. Laughlin and A. B. Harper, Eds. (Fischer, New York, 1979), pp. 15–41; J. Chappell and B. G. Thom, in *Sunda and Sahul: Prehistoric Studies in Southeast Asia, Melanesia and Australia*, J. Allen, J. Golson, R. Jones, Eds. (Academic Press, New York, 1977), pp. 275–291.
5. W. W. Howells, *Evolution of the Genus Homo* (Addison-Wesley, Reading, MA, 1973).
6. A. A. Zubov and N. E. Khaldeyeva, Eds., *Ethnic Odontology of U.S.S.R.* (Science Press, Moscow, 1979), in Russian.

7. W. Howells, *The Pacific Islanders* (Scribner's, New York, 1973).
8. C. G. Turner II, in *Late Pleistocene and Early Holocene Cultural Connections of Asia and America*, R. S. Vasilievsky, Ed. (USSR Academy of Sciences, Siberian Branch, Novosibirsk, 1983), pp. 72–76, in Russian; H. Suzuki, *Univ. Mus. Univ. Tokyo Bull.* **19** (1982), pp. 7–49; S. Misawa, Y. Hayashida et al., in *JIBP Synthesis: Anthropological and Genetic Studies on the Japanese*, S. Watanabe, S. Kondo, E. Matsunaga, Eds. (Univ. of Tokyo Press, Tokyo, 1975), pp. 265–307; K. Hanihara, T. Masuda, T. Tanaka, M. Tamada, *ibid.*, pp. 256–262.
9. G. Brauer, in *The Origins of Modern Humans. A World Survey of the Fossil Evidence*, F. H. Smith and F. Spencer, Eds. (Liss, New York, 1984), pp. 327–410.
10. W. S. Laughlin, *Aleuts: Survivors of the Bering Land Bridge* (Holt, Rinehart & Winston, New York, 1980).
11. W. S. Laughlin, *Science* **142**, 633 (1963).
12. N. N. Dikov, *Ancient Cultures of Northeastern Asia: Asia Joining America in Ancient Times* (Nauka, Moscow, 1979), in Russian; D. E. Dumond, *Science* **209**, 984 (1980); R. E. Ackerman, in *Late Pleistocene and Early Holocene Cultural Connections of Asia and America*, R. S. Vasilievsky, Ed. (USSR Academy of Science, Siberian Branch, Novosibirsk, 1983), pp. 49–56, in Russian.
13. C. C. Kennedy, *Natl. Mus. Can. Bull.* **206** (1966), p. 100; J. F. V. Miller, H. Epp, T. W. Foster, J. S. Wilson, G. Adams, *Na-Pa-O* **3**, 13 (1972).
14. C. G. Turner II, *Science* **193**, 911 (1976); K. Hanihara, in *Out of Asia: Peopling the Americas and the Pacific*, R. Kirk and E. Szathmary (Journal of Pacific History, Canberra, 1985), pp. 105–112.
15. T. Akazawa, in *Rec. Prog. Nat. Sci. Jpn.* **8**, 1 (1983); K. H. Chen, H. Cann, T. C. Chen, B. Van West, L. Cavalli-Sforza, *Am. J. Phys. Anthropol.* **66**, 327 (1985); D. Bayard, *Pac. Aff.* **53**, 89 (1980); N. N. Cheboksarov, *The Ethnic Anthropology of the Eastern Asia* (Nauka, Moscow, 1966); F. Ikawa-Smith, *Am. Sci.* **68**, 134 (1980); W. G. Solheim II, *Asian Perspect.* **23**, 9 (1983); C. G. Turner II, *Q. Rev. Archaeol.* **4**, 11 (1983); *Am. J. Phys. Anthropol.* **51**, 619 (1979); *J. Hong Kong Archaeol. Soc.* **10**, 80 (1984).
16. M. Pietruszewsky, *Homo* **32**, 1 (1981); C. Higham, *Am. Sci.* **67**, 670 (1979).
17. T. Jacob, *Some Problems Pertaining to the Racial History of the Indonesian Region* (Necrlandia, Utrecht, 1967).
18. J. P. White, and J. Allen, *Science* **207**, 728 (1980); P. Bellwood, *Man's Conquest of the Pacific: The Prehistory of Southeast Asia and Oceania* (Oxford Univ. Press, New York, 1979).
19. R. Shutler, Jr., and M. E. Shutler, *Oceanic Prehistory* (Cummings, Menlo Park, CA, 1975).
20. J. B. Birdsall, *Sunda and Sahul: Prehistoric Studies in Southeast Asia, Melanesia and Australia*, J. Allen, J. Golson, R. Jones, Eds. (Addison-Wesley, Reading, MA, 1977), pp. 113–167; J. Flood, *Archaeology of the Dreamtime* (Univ. of Hawaii Press, Honolulu, 1983); A. G. Thorne and M. H. Wolpoff, *Am. J. Phys. Anthropol.* **55**, 337 (1981); J. P. White and J. F. O'Connell, *Science* **203**, 21 (1979); *A Prehistory of Australia, New Guinea, and Sahul* (Academic Press, New York, 1983).
21. M. Ruhlen, *A Guide to the Languages of the World* (Language Universals Project, Stanford University, Palo Alto, CA 1975). I extended Indo-European 4,000 additional years from its dated origin near the Black Sea to allow for spread into western Europe. Apparently this was not necessary.
22. K. Broste, J. B. Jorgensen, C. J. Becken, J. Brondsted, *Prehistoric Man in Denmark* (Munksgaard, Copenhagen, 1956).
23. A. M. Lythgoe, *The Predynastic Cemetery N 7000 Naga-ed-der*, D. Dunham, Ed. (Univ. of California Press, Berkeley, 1965), part 4; F. Wendorf, *Prehistory of Nubia* (Southern Methodist Univ. Press, Dallas, 1968).
24. Supported by the NSF grant 8303786, the National Geographic Society, the International Research and Exchanges Board, U.S.S.R. Academy of Sciences, and Arizona State University Research Council. I thank L. Nuss for data processing, J. Turner and K. D. Turner for help in collecting much of the Asian data. Contribution 23 to my Peopling of the Pacific Basin and Adjoining Areas series.

12 August 1985; accepted 6 March 1986