

affinity. These changes in FGF might easily activate nearby satellite cells to divide and form new muscle fibers and could explain persistent regeneration observed in the dystrophic mouse. The mechanisms by which mdx mouse skeletal muscle escapes lethal phenotypes seen in Duchenne patients who have the identical mutation should provide clues to understanding and treating the human disease.

REFERENCES AND NOTES

1. A. Mauro, *J. Biophys. Biochem. Cytol.* **9**, 493 (1961); R. E. Allen, P. K. McAllister, K. C. Masak, *Mech. Ageing Dev.* **13**, 105 (1980); B. H. Lipton and E. Schultz, *Science* **205**, 1292 (1981).
2. F. P. Moss and C. P. LeBlond, *Anat. Rec.* **170**, 421 (1970); R. Bischoff, *Dev. Biol.* **115**, 129 (1986); U. Konigsberg, B. Lipton, I. R. Konigsberg, *ibid.* **45**, 260 (1975).
3. B. Olwin and S. Hauschka, *Biochemistry* **25**, 3487 (1986); R. E. Allen, M. V. Dodson, L. S. Luiten, *Exp. Cell Res.* **152**, 154 (1984); D. Gospodarowicz, J. Weseman, J. S. Moran, J. Lindstrom, *J. Cell Biol.* **70**, 395 (1976); B. K. Lathrop, E. N. Olson, L. Glaser, *ibid.* **100**, 1540 (1985).
4. D. Z. Ewton and J. R. Florini, *Endocrinology* **106**, 577 (1980); J. R. Florini, *Muscle & Nerve* **10**, 577 (1987); E. Jennische, A. Skottner, A. Hannson, *Acta Physiol. Scand.* **129**, 9 (1987); T. A. Linkhardt, C. H. Clegg, S. Hauschka, *Dev. Biol.* **86**, 19 (1981).
5. E. Kardami, D. Spector, R. C. Strohman, *Dev. Biol.* **112**, 353 (1985); *Proc. Natl. Acad. Sci. U.S.A.* **82**, 8044 (1985); R. Bischoff, *Dev. Biol.* **115**, 140 (1986).
6. D. Gospodarowicz, J. Cheng, G. Lui, A. Baird, P. Bohlent, *Proc. Natl. Acad. Sci. U.S.A.* **81**, 6963 (1984); Y. Shing *et al.*, *Science* **223**, 1296 (1984); T. Maciag, T. Mehlman, R. Friesel, A. B. Schreiber, *ibid.* **225**, 932 (1984).
7. E. Kardami, D. Spector, R. C. Strohman, *Dev. Biol.* **126**, 19 (1988).
8. R. C. Strohman and E. Kardami, in *Cellular Endocrinology: Hormonal Control of Embryonic and Cellular Differentiation*, G. Serrero and J. Hayashi, Eds. (Liss, New York, 1986), pp. 287-296.
9. G. Bulfield, W. G. Siller, P. A. L. Wright, K. J. Moore, *Proc. Natl. Acad. Sci. U.S.A.* **81**, 1189 (1984).
10. J. Dangain and G. Vrbova, *Muscle & Nerve* **7**, 700 (1984); Y. Tanabe, K. Esaki, T. Nomura, *Acta Neuropathol.* **69**, 91 (1986); L. F. B. Torres and L. W. Duchon, *Brain* **110**, 269 (1987).
11. M. Koenig, E. P. Hoffman, A. P. Monaco, C. Feener, L. M. Kunkel, *Cell* **50**, 509 (1987); E. P. Hoffman, A. P. Monaco, C. C. Feener, L. M. Kunkel, *Science* **238**, 347 (1987).
12. E. P. Hoffman, R. H. Brown, L. M. Kunkel, *Cell* **51**, 919 (1987).
13. A. G. Engel, in *Myology*, A. G. Engel and B. Q. Banker, Eds. (McGraw-Hill, New York, 1986), pp. 1185-1202.
14. J. Folkman *et al.*, *Am. J. Pathol.* **130**, 393 (1988).
15. A. Baird and N. Ling, *Biochem. Biophys. Res. Commun.* **142**, 428 (1987); I. Vlodavsky *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **84**, 2292 (1987).
16. Y. Naparstek, I. R. Cohen, Z. Fuks, I. Vlodavsky, *Nature* **310**, 241 (1984).
17. N. Buffinger and R. C. Strohman, unpublished results.
18. Width differences between lanes of Fig. 1A and Fig. 1B are due to use of a Miniblotter 16 (Immunetics, Cambridge, MA) in the immunoblot, which restricts antibody solutions to narrow strips along the length of the nitrocellulose membrane.
19. Human recombinant bFGF was provided by S. Hauschka and G. McKnight. Supported by NIH grant R01 AG02832 and a grant from the Muscular Dystrophy Association.

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Corn and Culture in Central Andean Prehistory

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The prehistoric development and spread of domesticated maize varieties in the highlands of Peru, unlike the drier coastal deserts, is little known because ancient maize remains in this area survive mainly as fragments, kernels, and cob parts. An analysis of fragmented charred maize from prehistoric households (A.D. 450 to 1500) in the Mantaro Valley reveals a developmental sequence of maize varieties for Highland Peru. The evidence indicates an adoption of large-kernelled maize varieties beginning in the Late Intermediate (A.D. 1000). This is centuries later than a similar change in maize, associated with the Wari expansion, that occurred in coastal areas, and indicates minimal Wari impact in the Mantaro Valley.

DOMESTICATED MAIZE AND THE human groups that use it are interdependent. The hundreds of existing maize varieties are cultural artifacts created, maintained, used, changed, and moved by human groups (1, 2). The study of

prehistoric maize varieties is valuable to understanding the evolution of both maize itself and of the associated cultures.

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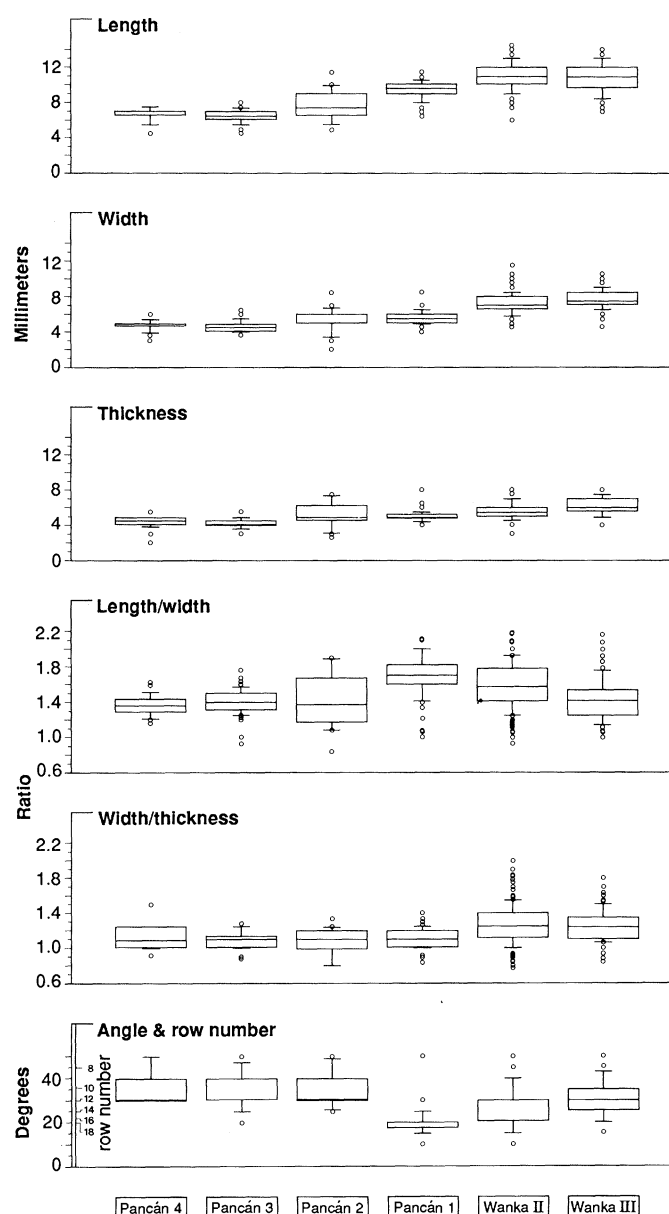


Fig. 1. Trends in kernel size, shape, and row number, showing distributions of kernel measurement values for six variables through time. The five lines in the percentile box plots mark the 10th, 25th, and 50th (median), 75th, and 90th percentiles. The small circles mark the <10th and >90th percentiles.

Maize in Peru is extremely variable and has had a long evolution shaped by cultural developments and change (2, 3). This evolution has been studied for coastal Peru, where arid conditions allow excellent preservation of ancient maize cobs, ears, and plant parts (3-8). However, in the wetter highlands, only maize charred in antiquity survives and generally is recovered only in the form of kernels, indurated cob parts (cupules), and fragments. This fragmentary material precludes measurements such as ear shape and cob diameter used to classify more complete specimens (2, 9-12). In this case in the highlands, by analysis of charred maize kernels, we examined the changes in maize and maize use associated with 1000 years of culture history (A.D. 450 to 1500) in the upper Mantaro Valley in the central Andes. An increase in kernel size and in maize type diversity took place after the Middle Horizon (A.D. 700 to 1000).

Archeological research by the Upper Mantaro Archaeological Research Project and others has documented many prehistoric sites in this high Andean Valley (elevation range for sites, 3400 to 4100 m) (13-17). Plant remains systematically recovered through flotation and fine-screening (18) include an abundant record of maize use. The maize remains consist almost completely of separate kernels and cupules, most of which are broken. For this study, measurable kernels from six time periods were compared.

The maize from the earlier time periods is from houses, middens, and patios in four strata at the site of Pancán (15). The two lowest levels, Pancán 4 and Pancán 3, both date to the Early Intermediate (A.D. 450 to 700). Pancán 3 is Middle Horizon (A.D. 700 to 1000), and Pancán 1 is early Late Intermediate (A.D. 1000 to 1300). The material from the two later time periods, Wanka II (late Late Intermediate, A.D. 1300 to 1460) and Wanka III (Inca period, A.D. 1460 to 1532), was recovered from households in two large town sites, Umpamalca and Hatunmarca, respectively (14).

Measurable kernels (a total of 536) were removed from over 200 flotation and screen samples taken from the four levels of Pancán and from the Wanka II and Wanka III households. The following attributes were recorded for each kernel: length, width, thickness, angle, and cap type. Length, width, and thickness reflect the general dimensions of the kernel. The angle formed by the two long sides gives an estimate of the row number of the ear from which the kernel came (19, 20). Cap type was recorded as square, round, or beaked. Ratios of length to width and width to thickness were calculated to give relative indices of the

shape of the kernels from the front and the top.

The kernels show great overall variability and a pattern in time (Fig. 1). There is a general increase in kernel length, width, and thickness. The kernels become relatively flatter in cross section. The kernel angles found in Pancán 4, 3, and 2 are similar and large, (probably from 10- and 12-row ears). In

Pancán 1, small kernel angles probably reflect 16- to 18-row ears. The much larger kernels of the subsequent Wanka II and Wanka III periods gradually become rounder in shape, and the median row number decreases, as angles reflecting 12- and 14-row ears become most common.

In order to understand how the variation in the maize assemblages changed over time,

Table 1. Upper Mantaro Valley data summary for ten kernel types. The kernel types were derived by a cluster analysis. The seven variables included in the analysis were length, width, thickness, angle, cap type, width to length (w/l) ratio, and width to thickness (w/t) ratio.

Type	n	Mean length (mm)	Mean width (mm)	Mean thickness (mm)	Mean l/w ratio	Mean w/t ratio	Mean angle* (day)	Cap types† (%)		
								S	R	B
A	60	13.0	7.9	6.2	1.67	1.30	26	42	27	31
B	37	10.4	7.0	6.7	1.51	1.05	26	6	33	61
C	56	9.2	5.3	4.9	1.75	1.08	20	13	11	76
D	90	11.2	6.2	5.2	1.81	1.21	20	55	26	19
E	67	11.3	7.7	5.7	1.46	1.38	29	80	20	0
F	88	6.3	4.5	4.2	1.42	1.10	36	22	19	59
G	51	7.9	6.3	5.4	1.27	1.17	31	14	27	59
H	13	12.2	10.0	7.0	1.23	1.43	37	36	45	18
I	36	8.9	7.7	6.6	1.17	1.17	44	26	40	34
J	38	11.0	8.3	6.0	1.33	1.39	39	19	53	28

*For 8-row, 45°; 10-row, 36°; 12-row, 30°; 14-row, 26°; 16-row, 22°; and 18-row, 20°. †S, square; R, round; B, beaked.

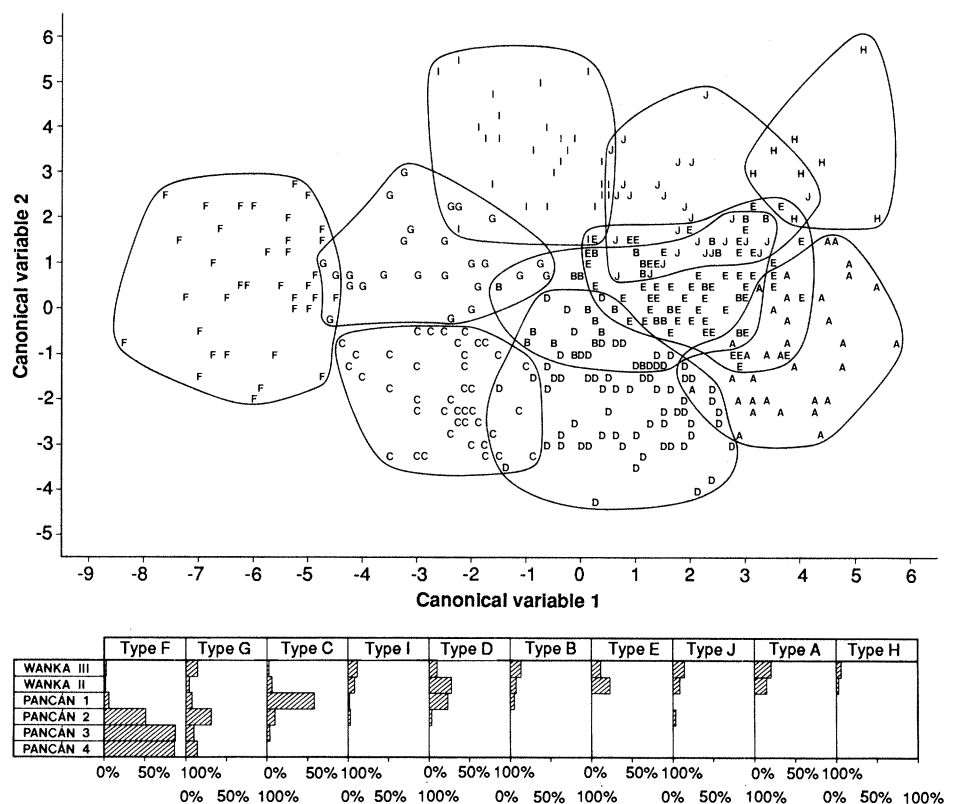


Fig. 2. Relations of the ten kernel types. Scatterplot of the first and second variates from a canonical analysis of the ten kernel groups. The bar graphs below the scatterplot show the percentage composition of the kernel types from each time period. The types are arranged in the relative order of their values on the first canonical variate (compare to the scatterplot). The standardized canonical coefficients are (for canonical variable 1 and canonical variable 2) angle, -0.2128 and 0.8511; width, 0.6037 and 0.4123; length, 1.4202 and -0.4032; thickness, 1.0681 and 0.3841; cap type, -0.2335 and 0.0417; width to length, -0.3825 and 0.6856; and width to thickness, 0.8220 and 0.1265.

the kernels were classified into types by a cluster analysis method and use of nearest centroid sorting. To select the best number of groups, the cluster analysis was run four times specifying different numbers of clusters (6, 8, 10, and 12). Ten clusters corresponded most closely to the types perceived subjectively. The attributes of the ten types are given in Table 1. These archeological types should not be understood as representing actual races of maize; they are rather an initial classification for assessing the relative variation through time.

Types C, F, and G are small, mostly beaked kernels that fall in the size range of the modern Andean popcorn races (2, 3). Type I is a short, thick type with a low row number (8-row). Types A, D, and E are larger, long in proportion to their width, with quite high row (12- to 18-row) numbers and many square-capped kernels. Types H and J are large broad kernels, with rounded caps, flat cross sections, and low row (8- and 10-row) numbers.

The relation among the ten types can be seen in a plot of the first and second canonical variables, which together account for 86% of the variability in the assemblage (Fig. 2). The first canonical variable (increasing width, length, and relative flatness) is associated with time, as is shown in the bar graphs below the scatterplot in Fig. 1. The two earliest assemblages are dominated by small type F. The Pancán 2 assemblage appears to be more varied, although the sample size is small. Greater variation and domination by a new type (type C, a high row number beaked type) is evident in level 1 of Pancán. Diversity in types is greatest in Wanka II and Wanka III, each phase with kernels of all ten types, though in different proportions. Two unusually large type H kernels found in Wanka II contexts approach the size and shape of the Cuzco races, suggesting that large-kerneled, low-row number varieties were grown in the Mantaro before Inca times, rather than being spread with Inca hegemony as has been suggested (2).

On the coast of Peru researchers have noted, after a long and rather stable period dominated by popcorns, a sudden change toward new flint and flour maize types from the highlands (2, 3). They postulate that this change is associated with the Wari expansion out of the Ayacucho region (Middle Horizon, about A.D. 550 to 850). The Mantaro Valley data indicate that an influx of new flint and flour types there is not associated with Middle Horizon, but rather with the Late Intermediate (after A.D. 1000). This maize evidence parallels the lack of Middle Horizon Wari architecture and the scarcity of Wari sherds in the area in

indicating that the people of the upper Mantaro received little direct Wari influence.

At the close of the Middle Horizon in the Mantaro area a number of changes in ways of growing, preparing, and eating food are associated with the new use of large-kerneled maize types. Stone hoes become more common (15), as do the actual remains of corn and other crops (15, 21). Large grinding stones and manos become more common in relation to mortars and pestles (15), perhaps reflecting grinding of the new floury maize types. Bowls become larger in Wanka I times, with new vessel types appearing in Wanka II and in Inca times (15). This may reflect new foods suitable to floury maize, such as *chicha* (maize beer), *mote* (hominy), *kancha* (toasted maize), and *sanco* (fine cornmeal cakes). Maize in Inca times, and probably earlier, was a high-prestige and ceremonial food (22).

Comparison of charred maize kernels from six time periods has helped in understanding changes in maize use and associated culture in the Mantaro Valley over a millenium. The data show (i) a continuity in use of small-sized maize into and through the Middle Horizon, indicating a lack of Wari influence there as compared to the coast, and (ii) a florescence of large-kerneled flint and flour types occurring in the Late Intermediate, associated with new cultural dimensions in farming, crops, and eating.

REFERENCES AND NOTES

1. B. F. Benz, thesis, University of Wisconsin, Madison (1986).

2. R. McK. Bird, thesis, University of California, Berkeley (1970).
3. A. Grobman, W. Salhuana, R. Sevilla, *Races of Maize in Peru*, National Research Council Publ. 915 (1961).
4. R. McK. Bird, *Maize Genet. Coop. News Lett.* **52**, 90 (1978).
5. ——— and J. B. Bird, *Am. Antiq.* **45**, 325 (1980).
6. D. Bonavía, *Precerámico peruano: los Gavilanes: mar, desierto y oasis en la historia del hombre* (Editorial Ausonia-Tallerer Graphics S.A., Lima, 1982).
7. A. Grobman, D. Bonavía, D. H. Kelley, with P. C. Mangelsdorf and J. Cámara-Hernández, *Bot. Mus. Leaf. Harv. Univ.* **25**, 221 (1977).
8. M. A. Towle, *The Ethnobotany of Pre-Columbian Peru* (Aldine, Chicago, 1961).
9. R. McK. Bird and M. M. Goodman, *Econ. Bot.* **31**, 471 (1978).
10. M. M. Goodman and E. Paterniani, *ibid.* **23**, 265 (1969).
11. F. B. King, thesis, University of Illinois, Urbana (1987).
12. N. H. Nickerson, *Ann. Mo. Bot. Gard.* **40**, 79 (1953).
13. D. Browman, thesis, Harvard University, Cambridge, MA (1970).
14. T. K. Earle et al., *Univ. Calif. Los Angeles Inst. Archaeol. Monogr.* **28** (1987).
15. C. A. Hastorf, T. K. Earle, H. E. Wright Jr., L. J. LeCount, G. S. Russell, E. Sandefur, *Andean Past* (in press).
16. R. Matos Mendieta, *Revta Mus. Nac. Lima* **37**, 41 (1971).
17. J. Parsons and C. Hastings, *Peruvian Prehistory*, R. Keatings, Ed. (Cambridge Univ. Press, Cambridge, 1988), pp. 190–229.
18. C. A. Hastorf, thesis, University of California, Los Angeles (1983).
19. H. C. Cutler and L. W. Blake, *Univ. Ill. Urbana Bull. Archaeol. Surv.* **7** (1973).
20. D. M. Pearsall, *Econ. Bot.* **34**, 344 (1980).
21. C. A. Hastorf and M. J. DeNiro, *Nature* **315**, 489 (1985).
22. J. V. Murra, *Culture in History*, S. Diamond, Ed. (Columbia Univ. Press, New York, 1960), pp. 393–407.
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Stereochemical Course of Catalysis by the *Tetrahymena* Ribozyme

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The group I intron from *Tetrahymena* catalyzes phosphodiester transfer reactions on various RNA substrates. A modified RNA substrate with a phosphorothioate group in one stereoisomeric form at the site of reaction was synthesized in order to determine the stereochemical course of an RNA-catalyzed reaction. The reaction product was digested with a stereospecific nuclease to determine the configuration of the product phosphorothioate. The reaction occurs with inversion of configuration at phosphorus, implying an in-line pathway for the reaction.

THE GROUP I SELF-SPLICING RIBOSOMAL RNA intron from *Tetrahymena* catalyzes its excision from the primary RNA transcript and exon ligation to form the mature transcript (1, 2). In vitro, the free intron can function as a site-specific ribonuclease, a terminal transferase, a phosphotransferase, and an acid phosphatase, depending on the RNA substrate provided

and the conditions of the reaction (3–5). This RNA is a true catalyst in that it can mediate multiple turnovers of some reactions (3, 6).

Whether the ribozyme catalyzes transesterification reactions stereospecifically has

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