

composed phases around the ilmenite or perovskite grains. The peak pressure pulses may be on the order of 10^{-2} to 10^{-1} s in large-scale meteorite impacts (17), and the cooling rate will be very rapid. In such a short event, the decomposition of pyroxene into spinel + stishovite or perovskite + magnesiowüstite + stishovite would be difficult to complete in the solid state. Therefore, pyroxene probably transformed metastably into high-Fe ilmenite and perovskite without producing these other phases.

The shock event must also have affected the transformation mechanism. For the topotaxial relationship of $(100)_{\text{Cen}} // (0001)_{\text{Ilm}}$, where subscripts Cen and Ilm denote clinoenstatite and ilmenite, respectively, both planes correspond to the close-packed layers of oxygen for their respective phases (approximate cubic close-packed for clinoenstatite and hexagonal close-packed for ilmenite). Therefore, in the transition from clinoenstatite to ilmenite, the close-packed layers of oxygen are preserved, characteristic of shear transformation. Probably, the rapid transformation by the shock event favored the shear transformation mechanism for the clinoenstatite-ilmenite transition. This topotaxial relation indicates that this process may have proceeded by the displacement of the close-packed layers of oxygen on (100) plane for clinopyroxene. The intergrowth of ilmenite with clinopyroxene also suggests this mechanism. The granular ilmenite, which has no topotaxial relationship with clinoenstatite, would have formed by the nucleation and growth mechanism, probably under the slower cooling rates.

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Size Variation in Middle Pleistocene Humans

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It has been suggested that European Middle Pleistocene humans, Neandertals, and prehistoric modern humans had a greater sexual dimorphism than modern humans. Analysis of body size variation and cranial capacity variation in the large sample from the Sima de los Huesos site in Spain showed instead that the sexual dimorphism is comparable in Middle Pleistocene and modern populations.

Sexual dimorphism is potentially a major source of size variation in a population (1, 2). Most samples in the human paleontological record consist of specimens that span large chronologic and geographic ranges; consequently, interpopulational variation, directional trends, or diachronic fluctuations can contribute more to the sample variation (even if the sample is large) than sexual dimorphism.

In the Sima de los Huesos site in Sierra de Atapuerca, Spain, there is a large sample of human fossils that comes from a single Middle Pleistocene biological population, which provides an opportunity to investigate intrapopulational variation (3, 4). All skeletal elements are represented in the Sima de los Huesos human collection in large numbers, and the minimum number of individuals has been estimated at 32 on the basis of the dental sample (5). The fossils

have been directly dated by U-series and electron spin resonance to more than 200,000 years ago, and the probable age is $>300,000$ years ago (6). These dates are compatible with the faunal content of the site (7). The Sima de los Huesos hominids are attributed to *Homo heidelbergensis* and correspond to a population ancestral to Neandertals, exhibiting a mosaic of primitive traits, combined with some (in general, incipient) Neandertal-derived traits (3, 4).

Although many methods have been designed to evaluate the degree of sexual dimorphism (2), their calculations are based on individuals of known sex or skeletally diagnosed sex. A problem in paleoanthropology is that sexual dimorphism is determined on the same feature (size) used for sex diagnosis and presupposes sexual dimorphism in order to estimate itself. Some researchers have concentrated instead on a statistical approach in which the likelihood of obtaining by chance a fossil sample with a given variation is calculated (8). It is in essence a hypothesis test in which the null hypothesis is the variation of a living species analog. If none or few samples randomly generated from the extant species show a variation greater than that of the fossil sample, the null hypothesis (that is, the hypothesis that the variation of the fossil species is the same or less than that of the extant species) is rejected. Following this statistical approach we used the bootstrap method (9) to compare the intrapopulation variation between the Sima de los Huesos

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Table 1. Results of the bootstrap analysis. SH, Sima de los Huesos sample; GM, geometric mean; SD, standard deviation; ISD, index of sexual dimorphism (male mean/female mean). The values given in the last two columns are percentages of the 1000 random samples with coefficients of variation (CV) and maximum ratios (MR) above the Sima de los Huesos CVs and MRs. Variables include the following: glenoid fossa GM = (glenoid fossa height $\times$ glenoid fossa breadth)^{1/2}; humeral proximal epiphysis GM = (proximal epiphysis breadth $\times$ head vertical diameter $\times$ head transverse diameter)^{1/3}; ulnar proximal epiphysis GM = (olecranon breadth $\times$ coronoid breadth $\times$ olecranon height $\times$ trochlear anterior-posterior diameter $\times$ coronoid height)^{1/5}; lumbosacral surface GM = (transverse diameter $\times$ anteroposterior diameter)^{1/2}; subtrochanteric GM = (subtrochanteric anteroposterior diameter $\times$ subtrochanteric mediolateral diameter)^{1/2}; patellar GM = (maximum thickness $\times$ maximum height $\times$ maximum breadth)^{1/3}; talar trochlear GM = (trochlear length $\times$ trochlear breadth)^{1/2}; calcaneus GM = (maximum length $\times$ body length $\times$ sustentaculum breadth $\times$ body height)^{1/4}. We followed Martin and Saller (13) for all variable definitions except for the following: vertical diameter of the humeral head (4); ulnar olecranon height, ulnar coronoid height, and ulnar trochlear anterior-posterior diameter (14); vertical acetabular diameter (15); and calcaneus body height (16).

Skeletal part	Variable	SH <i>n</i>	Comparison samples†				CV (%)	MR (%)
			<i>n</i> *	Mean	SD	ISD		
Cranium	Cranial capacity (cm ³)	3	184‡	1336	164	1.19	-	44.7
Scapula	Glenoid fossa GM	5	160	30.3	2.8	1.16	43.9	31
Humerus	Proximal epiphysis GM	4	155	42.5	3.6	1.14	-	67.9
	Midshaft perimeter	9	155	61.1	6.2	1.15	12.5	2.5
Ulna	Biepicondylar breadth	4	155	57.1	4.9	1.14	-	69.4
	Proximal epiphysis GM	7	102¶	25.0	2.3	1.13	90	90.3
Radius	Proximal perimeter	8	102¶	51.4	6.4	1.19	85.7	70.9
	Midshaft perimeter	7	102¶	45.3	5.7	1.17	67.1	68.5
Coxal	Neck perimeter	5	424#	41.2	4.6	1.16	58.4	46
Sacrum	Vertical acetabular diameter	5	370	52.5	3.8	1.11	46	31.4
	Lumbosacral surface GM	2	142	37.6	3.5	1.11	-	30.4
Femur	Head vertical diameter	4	146	43	3.4	1.12	-	18.4
	Subtrochanteric GM	8	146	29.3	2.4	1.11	36.7	56
Patella	Midshaft perimeter	7	146	81.3	6.8	1.11	33.6	50.9
	GM	5	50‡	31.8	2.7	1.13	68.2	64.7
Tibia	Midshaft perimeter	6	114¶	75.6	7.9	1.13	30.2	42.3
Talus	Trochlear GM	8	106¶	29.2	2.3	1.11	50.7	61
Calcaneus	GM	7	156	49.7	3.3	1.10	77.4	90.9

*Sample size of the modern human samples from which 1000 random samples were generated (for each variable with a size equal to that of the SH sample). †The modern human samples of known sex (balanced sex size) come from the following collections. ‡Hamann-Todd Euro-Americans and §Hamann-Todd Afro-Americans (Cleveland Natural History Museum, Cleveland, Ohio). ||Coimbra (individuals born in the Beira Litoral region of Portugal between 1820 and 1920, kept in the Museum of Anthropology from the University of Coimbra, Portugal); ¶Palencia (individuals deceased during the last quarter of this century, kept in the Anatomical Museum from the University of Valladolid, Spain). #Raw data for the Coimbra sample from (17).

and modern humans. We simulated a large number of random samples selected with replacement from extant taxa using the same sample size as that of the fossil assemblages. Then we compared maximum ratios (MR = maximum value $\div$ minimum value) and coefficients of variations (CV = standard deviation $\times$ 100 $\div$ mean) of the simulated and the fossil samples to assess the likelihood of obtaining by chance a sample as variable as our fossil sample. Using only adult specimens we analyzed the cranial capacity and a number of postcranial variables that show sexual dimorphism in modern humans and are related, to overall robusticity and muscularity, and hence, weight. In all bootstrap simulations, we generated for each variable 1000 random samples, with each sample equal in size to the Sima de los Huesos fossil sample size (Table 1).

It has been thought (10) that crania of European Middle Pleistocene humans show more sexual dimorphism than those of mod-

ern humans, although not significantly more than those of Neandertals. In the Sima de los Huesos sample, cranial capacity can be calculated in skull 5 (1125 cm³), cranium 4 (1390 cm³), and cranium 6 (1220 cm³) (11). The Sima de los Huesos crania almost span the whole European and African Middle Pleistocene range of cranial capacities. In spite of this, the maximum ratio of the Sima de los Huesos sample is in the central part of the distribution of modern human random samples of three individuals (Table 1 and Fig. 1).

In the Sima de los Huesos collection, the postcranial skeleton also does not show an unusual size variation compared with the distribution of samples of the same size randomly generated from large samples of modern humans. Only the humeral midshaft perimeter shows an extreme maximum ratio in the Sima de los Huesos population, although it has a less exaggerated coefficient of variation (Table 1). Sexing the fossils a priori, Trinkaus

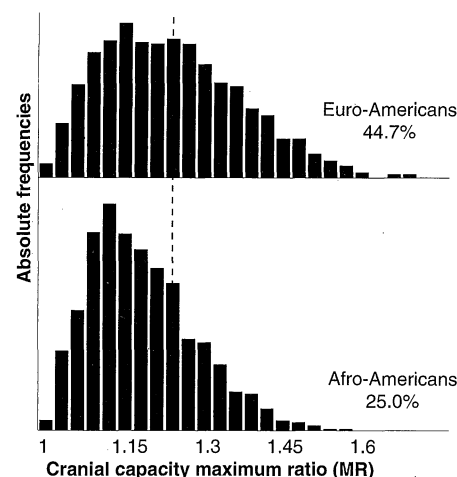


Fig. 1. Frequency histograms of cranial capacity maximum ratio calculated from 1000 random samples of Euro-Americans and Afro-Americans of the Hamann-Todd collection, and the percentage of those samples with a MR larger than that of the Sima de los Huesos sample. The cranial capacity for this collection was measured by, or under the direction of, T. Wingate Todd between 1912 and 1938 by the seed or water method (18). The vertical dashed line marks the maximum ratio (1.24) of the Sima de los Huesos sample ($n = 3$). The Afro-American sample is more homogeneous than the Euro-American sample (more diverse origin of the individuals) in the Hamann-Todd collection, and this may account for the difference between the probabilities in this figure (25% versus 44.7%).

(12) found that Neandertals exhibit sexual dimorphism in the postcranial skeleton to an extent similar to that of modern human samples. Consequently, the notion that sexual dimorphism has decreased in modern populations and that the sexual dimorphism of Middle Pleistocene hominids was greater than in modern humans is not supported by either cranial or postcranial evidence from Sima de los Huesos.

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Ecological Effects of an Insect Introduced for the Biological Control of Weeds

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Few data exist on the environmental risks of biological control. The weevil *Rhinocyllus conicus* Froeh., introduced to control exotic thistles, has exhibited an increase in host range as well as continuing geographic expansion. Between 1992 and 1996, the frequency of weevil damage to native thistles consistently increased, reaching 16 to 77 percent of flowerheads per plant. Weevils significantly reduced the seed production of native thistle flowerheads. The density of native tephritid flies was significantly lower at high weevil density. Such ecological effects need to be better addressed in future evaluation and regulation of potential biological control agents.

The perception of high economic, health, and environmental costs of chemical pest control has stimulated interest in biological control (1, 2), specifically the importation of specialized natural enemies to limit invasive coevolved pest species (3). When biocontrol is successful, pest populations are suppressed below the economic threshold by a self-sustaining interaction between the pest prey species and its introduced antagonist. Successes in the United States in-

clude biological control of insect pests, such as cottony cushion scale and red scale on citrus in southern California (4), and of weeds, such as Klamath weed (*Hypericum perforatum* L.) in northwestern rangelands (5) and alligatorweed (*Alternanthera philoxeroides*) in Florida waterways (6). However, not all biological control efforts work. Estimates of success for herbivorous insects introduced to control weeds in the United States vary, from 41% of projects with evidence of some control (2) to 20% that have exerted significant control (7). All successful programs, and many unsuccessful ones, leave nonindigenous species in the environment (8).

Biological control of invasive weeds is seen as an especially attractive option for large natural areas, such as parks, reserves, national forests, and open rangelands (1, 2, 9). However, the use of biological control

has generated controversy over the environmental risks associated with deliberate introductions of nonindigenous species. Many advocates of biological control argue that there is no evidence of significant adverse ecological effects by carefully screened insects released for weed control (10). However, the complexity of the issues (11) and the lack of data on post-release use of non-target host plants (8, 12) leave the issue unresolved. Intensive study is required to identify the role of insect herbivores in the limitation of plant growth, abundance, and distribution (13, 14), so the lack of evidence for ecological costs may simply reflect the paucity of quantitative studies after deliberate introductions (8, 12).

The flowerhead weevil, *Rhinocyllus conicus* Froeh., was the first of four insects reported as released in North America for the biological control of Eurasian thistles of the genus *Carduus* L., including musk thistle (15). After extensive prerelease screenings of host preference, oviposition, growth, and fitness of this species in Italy and Canada (16), weevils from France and Italy were released in Ontario and Saskatchewan in 1968 and were immediately redistributed to Manitoba, Quebec, and British Columbia (15). Weevils from Canada were released in the United States—in Virginia (1969), Montana (1969), California (1971), and Nebraska (1972)—and then redistributed from these sites (17, 18). Currently, *R. conicus* is also reported from Arizona, Colorado, Idaho, Iowa, Illinois, Kansas, Kentucky, Maryland, Minnesota, Missouri, New Jersey, North Dakota, Oregon, Pennsylvania, South Dakota, Tennessee, Texas, Utah, Washington, and Wyoming (15). Redistribution continues (17). The original releases were made even after initial feeding trials indicated that the weevil's host range included the native North American genera *Cirsium*, *Silybum*, and *Onopordum* (16, 18). Stronger oviposition preference for *Carduus*, plus more successful larval development on *Carduus*, were expected to limit use of native North American plants by *R. conicus* (17).

We documented the continuing expansion of host range by this weevil (19); three new host associations—with *Cirsium canescens* Nutt., *C. centaureae* (Rydb.) K. Schum., and *C. pulchellum* (Greene) Woot. & Standl.—were found. Infestation rates are given in Table 1. Three of the six native thistle species in Rocky Mountain National Park—namely *C. centaureae*, *C. tweedyi* (Rydb.) Petrak, and *C. undulatum* (Nutt.) Spreng.—had *R. conicus* developing within their flowerheads. The two lower elevation species had 43 to 70% of their flowerheads attacked (Table 1). Extensive *C. undulatum* infestation was also

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