senting cells. Contributions from Gleichmann's laboratory have provided another dimension for this approach by examining lymphoproliferative responses to different xenobiotics in vivo. This work complements our studies because it demonstrated that immune reactivity was not against the administered compound, but a metabolite of higher oxidation state; we showed how such products could be produced within a lymphoid compartment.

In order to account for the autoimmune side effects of drugs, Gleichmann and colleagues adopt a variant of the conventional explanation of drug-altered self-proteins as the initiating event. Other recent proposals include direct activation of lymphocytes through redox cycling or inhibition of DNA methylation reactions. However, the features of drug-induced lupus and the nature of SLE suggest that ultimate understanding might require an explanation for which there is currently no precedent.

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Thumbs, Tools, and Early Humans

By comparative functional analysis of thumb morphology, the report by Randall L. Susman (*1*) tackles the key question of which extinct hominids used tools. He contrasts living apes and their short, thin, weak thumbs and resulting power grasps with living humans and their long, stout, strong thumbs and refined precision grasps. The latter is said in the report to be correlated with tool behavior of extinct hominids; it is proposed, for example, that *Australopithecus afarensis* with its ape-like thumb was not a toolmaker, but *Paranthropus robustus* with its human-like thumb was.

Even with their inferior thumbs, however, apes engage in dextrous manipulation of objects by precision grasping and make and use a variety of tools (*2*). Most of these tools are made from vegetation and so will not endure in any future archaeological record, but this is beside the point. Some of the tools of wild chimpanzees are of stone and show characteristic wear patterns (*3*). To deny tool behavior to hominids older than 3 million years ago on the basis of their ape-like thumbs is thus unfounded. One could say that a particular kind of hominid technology, flaked stone, has not yet been seen in wild apes, although it has been shown in captive ones (*4*). More fruitful might be detailed studies of living apes and humans in terms of which types of grasps are associated with which types of tool-using and -making, especially in terms of task demands and raw materials.

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Randall L. Susman (*1*) makes a significant contribution towards our understanding the appearance of toolmaking capabilities in early hominids. He (*1*) proposes a test that "relies on a single thumb element and one that is well represented in the fossil record" to "help resolve the question of which Plio-Pleistocene hominids were responsible for the earliest tool assemblages" (*1*, p. 1572). The inference of behavior from morphology in fossil taxa is warranted if (i) there is some living species that bears the morphological trait, (ii) the trait is used for the same behavior in all living taxa that possess it, (iii) there is a clear functional linkage between the behavior and the trait, and (iv) there is no evidence that the trait arose in the living species before the behavior was adopted (*2*). Given these rules of comparative analysis, we reassess the evidence presented by Susman (*1*) for tool use among fossil hominids with the use of our data on gorilla thumb morphology.

Susman (*1*) describes several thumb muscles present in humans, but absent in apes, which he states are required for using a precision grasp. Noting that large transarticular forces are produced at the human metacarpophalangeal joint by these muscles, Susman (*1*) explains the relatively expanded human metacarpal head as an adaptation to reduce joint stress. He concludes that "humans have broader metacarpal heads than apes" (*1*, p. 1571) and, using a ratio of metacarpal head breadth to metacarpal length, shows that "values for African apes and modern humans do not overlap" (*1*, p. 1571). Susman (*1*) then uses this ratio as a criterion to separate modern toolmakers from non-toolmakers and to infer toolmaking capabilities in fossil hominids.

We tested this hypothesis by measuring pollical metacarpal head breadth and metacarpal length in adult humans, bonobos, and chimpanzees, and expanded the sample to include gorillas (*3*). When these data are plotted along with those of adult humans, following Susman (*1*), metacarpal head breadth of gorillas exceeds that of chimpanzees and overlaps markedly the range of variation shown for humans (Fig. 1A). Applying the ratio used by Susman (*1*), the range of values for mountain gorillas overlaps that of humans more than it does that of chimpanzees (Fig. 1B). The majority of fossil taxa for which tool use is implied by Susman (*1*) fall well within the range of variation observed for gorillas (Fig. 1B) (*4*). Susman also noted "great apes have relatively shorter thumbs than do humans, with metacarpals that are reduced in relative length" (*1*, p. 1571). Plots of thumb metacarpal length against body size (*5*) in adult apes and humans demonstrate that, at comparable body sizes, adult gorillas have first metacarpals that do not differ significantly in length from those of humans (*6*).

The presence of a wide metacarpal head relative to metacarpal length is proposed by Susman (*1*) as a reliable test for human-like precision grasping and tool use in fossil hominids. However, gorillas possess a wide metacarpal head (Fig. 1), but do not use a precision grip and do not manufacture stone tools. Thus, not all living taxa which possess the trait use it for the same behavior, (contrary to ii). Our results (*6*) also demonstrate that the proposed (*1*) functional link between metacarpal length and precision grasping is problematic. The gorilla-human pattern could be interpreted as primitive for African apes and humans, with *Pan* possessing the derived (*6*) morphology as a specialization for arboreal life. Thus (iv) is also violated in light of evidence suggesting the metacarpal proportions of *Homo sapiens* could have evolved before the adoption of tool use.

These conclusions then beg the question of what might be a robust morphological correlate of precision grasping and tool use in fossil hominids. As Napier (*7*) noted, "precision grip . . . is not an essential requisite at this [Oldowan] level of craftsman-

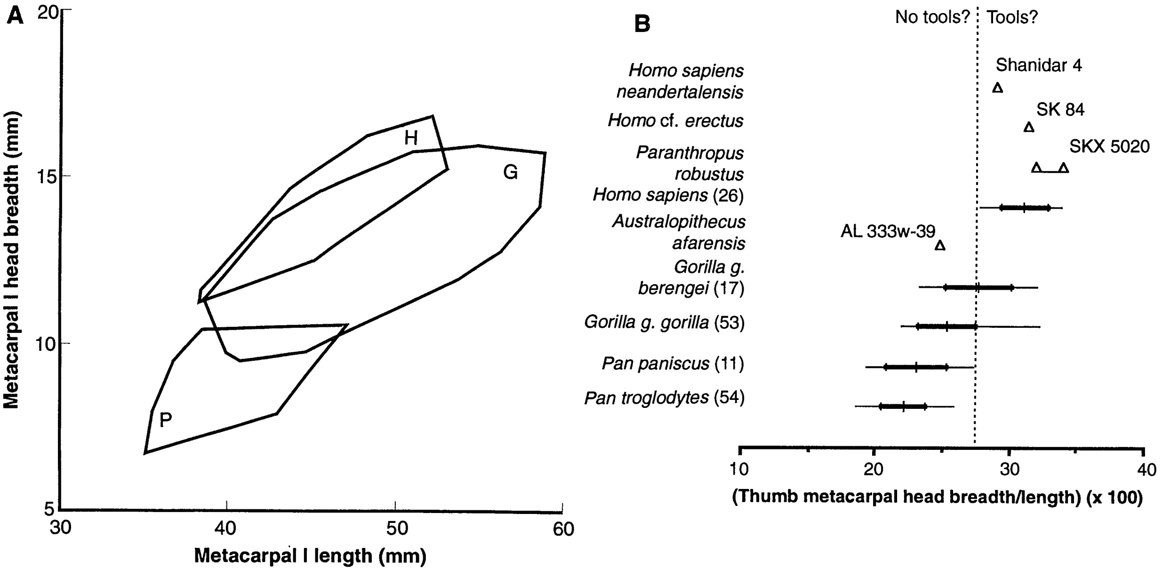

Fig. 1. (**A**) Plot of metacarpal I length versus metacarpal I head breadth in modern humans (H), gorillas (G), and bonobos and chimpanzees (P). Polygons illustrate the range of values for each genus. Fifty percent of the human sample overlaps the gorilla range. (**B**) Plot of metacarpal I head ratio in the above human and ape sample, along with values for the fossil hominid metacarpals included for analysis by Susman (*1*). The sample includes gorillas. Values for apes and modern humans overlap considerably, and each fossil hominid falls within the range of variation observed for gorillas. Thin vertical black lines are sample means; thick horizontal bars represent one standard deviation from the sample mean; long bars represent the range of sample values. Sample sizes are in parentheses.

ship" (*7*, p. 411). That is, a precision grip is not required to manufacture Oldowan stone tools. Consequently, the absence of certain precision grasping specializations in the hand of *Australopithecus afarensis* does not preclude the use of tools by this species. The search for morphological features related to tool use might instead be redirected towards examining precision and non-precision tool grips and their morphological correlates. Inferences regarding hand function in fossil hominids are limited by either fragmentary or unassociated material (*1*). However, accurate behavioral reconstructions depend on an extensive set of hand features (*8*) rather than single thumb elements that happen to be common in the fossil record.

We may agree with Susman's body of work on this subject (*9*), but with regard to a single-trait test we concur with his earlier view that morphologists should "heed the advice of those who espouse consideration of the total morphological pattern than to make claims for the extraordinary significance of any particular trait" (*10*, p. 100).

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1. R. L. Susman, *Science* **265**, 1570 (1994).
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3. Our gorilla sample includes 26 male and 27 female *Gorilla gorilla gorilla* and 8 male and 9 female *Gorilla gorilla berengei* housed at the Powell Cotton Museum and Musée Royale de l'Afrique Centrale. Our first metacarpal measurements follow those presented by Susman [figure 1A in (*1*)].
4. The mean values for mountain gorillas and humans (Fig. 1B) differ significantly (ANOVA, $P < 0.05$). However a fossil specimen represents a single individual, not a mean value, for an extinct population. Therefore, the difference between the sample ranges, not their means, is the most important statistic for determining whether or not a fossil specimen can be reliably allocated to one particular extant population over another.
5. Actual body weights are unavailable for most of the individuals included in our sample. For the purpose of bivariate allometric comparisons, we used a skeletal surrogate of body mass to estimate body size. The size variable used for these bivariate comparisons is a composite measure calculated as the mean of humeral diaphyseal length, humeral midshaft diameter, pubic length, and femoral diaphyseal length for each individual.
6. Plots of thumb metacarpal length versus estimated body size in adult African apes and humans demonstrate that metacarpal length in chimpanzees, unlike that in humans and gorillas, has a higher slope (ANCOVA slope test, $P = 0.037$). Relative to body size, metacarpal length of gorillas does not differ significantly from that of humans in slope (ANCOVA slope test, $P = 0.506$) or in position (ANCOVA y-intercept test, $P = 0.452$). Susman (*1*) also suggests apes, as compared with humans, have a narrow, parallel-sided metacarpal shaft, and apes possess a small metacarpal base. However Susman (*1*) does not provide quantitative data to support these observations, and does not describe the functional link between these features and precision grasping.
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The "African ape" sample in the report by Susman (*1*) included pygmy and common chimpanzees (p. 1571) but did not include gorilla data (note 19, p. 1573). We have examined a wider range of hominoid variation (Table 1).

Our comparison of chimpanzee and human data replicated Susman's (*1*) findings with high fidelity (Fig. 1A). However, when we added the other hominoids to the sample, our results were not as simple (Table 1 and Figs. 1B and 2). Susman's (*1*) test, applied to the larger sample, classified 62% of gorillas as possessing "humanlike precision grasping." Because chimpanzees make tools and Susman (*1*) did not include gorilla data, this raises questions about the test's diagnostic value.

Susman (*1*) essentially measured relative robusticity of the pollical metacarpophalangeal joint, and proposed that this reflects "humanlike precision grasping." However, this measure reflects at least two other parameters. First, within apes there is a body size relationship to this joint (Figs. 1B and 2B) that was not explored by Susman (*1*). This relationship partially explains why gorilla and human data overlap in the ratio of the first metacarpal head breadth to metacarpal length, and argues for the addition of some independent control for body size to Susman's (*1*) test. However, even this may not be sufficient given that a body size relation within hominids is unknown, and human and gorilla data overlap in *both* body mass (*4*, *5*) and metacarpal ratio. Thus, Susman's (*1*) measure on a single bone apparently does not supplant Napier's (*6*) morphological criteria for toolmaking behavior. Second, bone and joint morphologies are primarily a product of their loading histories (*7*–*11*), so the relatively robust human thumb (*12*) likely indicates an adaptation to relatively greater loads than those experienced by ape thumbs. Napier (*13*) defined the precision and power grips,

Table 1. Mean (± standard deviation; range) metrics for Metacarpal I.

Species	Sample size Male	Sample size Female	Head breadth (mm)	Length (mm)	Breadth/length (× 100)
*Hylobates lar**	8	10	5.59 (±0.28; 6.2–5.1)	34.56 (±1.81; 37.5–29.9)	16.19 (±0.73; 17.3–14.7)
Hylobates syndactylus†	2	3	6.10 (±0.31; 6.4–5.7)	35.70 (±1.78; 38.0–34.0)	17.11 (±1.04; 18.8–16.2)
Pongo pygmaeus‡	11	23	10.39 (±1.31; 12.8–8.5)	45.78 (±5.07; 56.6–34.2)	22.72 (±1.87; 26.6–19.4)
*Pan troglodytes**	20	20	9.37 (±0.70; 10.6–8.1)	41.26 (±2.70; 47.6–34.6)	22.74 (±1.75; 26.4–19.1)
Gorilla gorilla§	22	23	12.81 (±1.67; 15.9–9.7)	48.51 (±6.04; 60.6–38.7)	26.45 (±2.05; 33.3–22.5)
A.L. 333w-39			10.1‖ 10.13 (±0.10; 10.0–10.2)¶	39.5‖ 39.48 (±0.33; 39.0–39.7)¶	25.57 25.65 (±0.32; 25.19–25.82)¶
Homo sapiens‖	30	30	13.49 (±1.31; 16.2–11.0)	44.09 (±3.84; 53.8–34.1)	30.65 (±2.11; 35.6–26.5)
SK 84**			10.7	34.6	30.92
Shanidar 4††			14.2	44	32.27

*From Cleveland Museum of Natural History (CMNH). †From National Museum of Natural History (NMNH). ‡Four females and one male from CMNH; 19 females and 10 males from NMNH. §19 females and 18 males from CMNH; four females and four males of *G. g. beringei* from NMNH. ‖Breadth and length measurements from Bush *et al.* (*2*). ¶Based on four measurements obtained by four different individuals on the record cast housed at CMNH. #20 African Americans and 20 European Americans from CMNH: 20 Amerindians from Late Archaic Ward site. **Breadth and length measured from a cast at CMNH. ††Breadth and length measurements from Trinkaus (*3*).

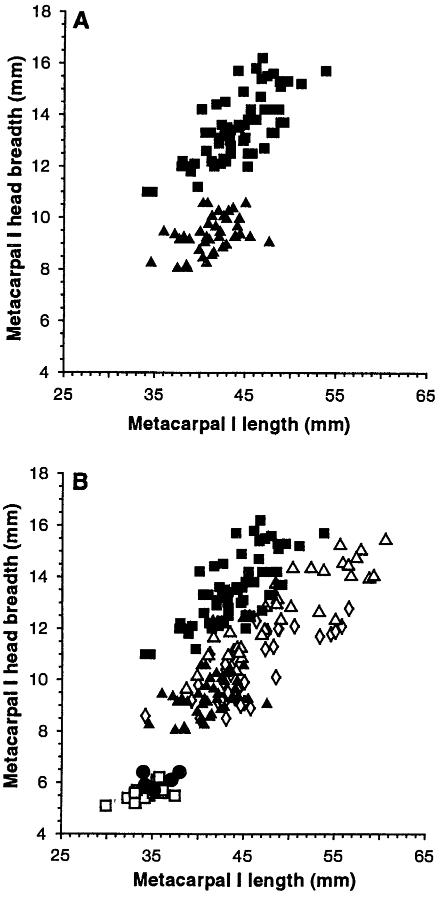

Fig. 1. (**A**) Plot of metacarpal I length versus metacarpal I head breadth in *Homo sapiens* (■), and *Pan troglodytes* (▲). (**B**) Same plot, but adds *Gorilla gorilla* (△), *Hylobates lar* (☐), *Hylobates syndactylus* (●), and *Pongo pygmaeus* (◇). Sample defined in Table 1.

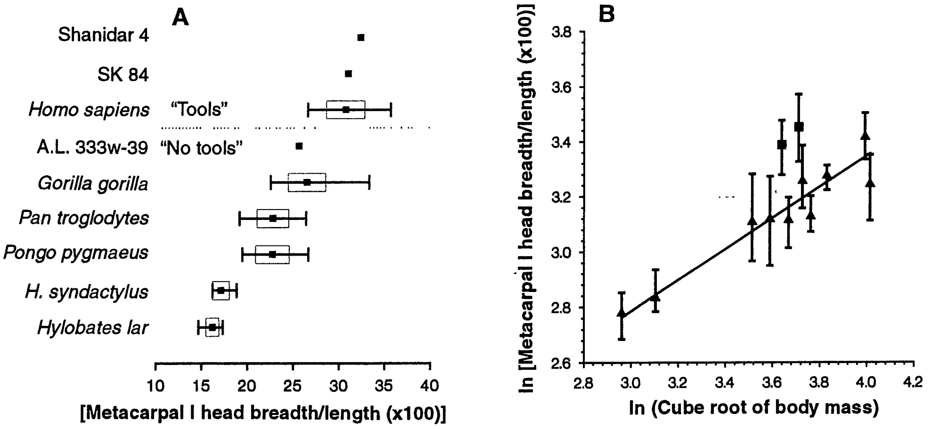

Fig. 2. (**A**) Plot of the mean (■), one standard deviation (☐) and range (—) for the metacarpal I head breadth and length index in hominoids. Sample defined in Table 1. (**B**) Plot of natural logarithm of metacarpal I head breadth over length (×100) versus natural logarithm of the cube root of body mass. For both, mean values (▲, ■) are shown, while for the former ranges (—) are also provided. Body masses are from Jungers (*5*). Apes (▲) are from left to right: *Hylobates lar* (mean of four subspecies, 7182.5 g); *Hylobates syndactylus* (11,050 g); female *Pongo pygmaeus* (means of two subspecies, 37,750 g); female *Pan troglodytes* (47,400 g); male *Pan troglodytes* (60,000 g); female *Gorilla gorilla* (71,500 g); male *Pongo pygmaeus* (mean of two subspecies, 79,600 g); female *Gorilla gorilla beringei* (97,700 g); male *Gorilla gorilla beringei* (159,200 g); male *Gorilla gorilla* (169,500 g). *Homo sapiens* (■) are from left to right: female 55,000 g); male (68,230 g). Reduced major axis regression shown for the apes only (r = 0.952; slope = 0.563; y intercept = 1.095).

and Marzke (*14*) showed the latter to be "unique today to humans" (p. 297). Dramatically greater forces are imposed during the power grip than the precision grip (*15*). Therefore, instead of Susman's (*1*) suggestion of a precision grip adaptation, a more likely functional interpretation is that the relatively robust human thumb is an adaptation that reflects its dominant role in the fully pentadactyl human power grip.

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Response: The issues raised by McGrew reflect more a difference in our perspectives than in the data and thesis of my report (*1*). I do not deny that apes engage in tool use as do birds, monkeys, and many other mammals (*2*). In it, I acknowledged that chimpanzees at Tai use wood and stone hammer and anvil technology at certain times of the year to exploit hard nuts. However, chimpanzees do not grip tools in the way that humans do (*3*). Chimpanzee tool use and the worn hammers it leaves behind, fall short of toolmaking of the kind we see in the residues of the Oldowan Industrial Complex as left by *Paranthropus* and early *Homo*. The rudimentary type of tool use we observe in chimpanzees leaves no imprint on their thumb (or other) anatomy. Where McGrew and I part conceptual company is in my conviction that unless the type of tool behavior that an animal engages in leaves traces on it's anatomy, it does not exist for the paleoanthropologist. If behavioral change preceeds morphological change in evolution, then we should not expect to spot the very *first* tool users in the fossil record. One might speculate that *Australopithecus afarensis* (which had a chimpanzee-like thumb) used sticks to hammer and threaten, stems to fish for termites, leaves as sponges or umbrellas, or even rocks to hammer and hurl, as seen in wild chimpanzees today. This could well represent the initial stage of tool use in the early hominid career. But because neither tools (including those of either bone or stone) nor anatomical evidence of tool behavior are associated with *A. afarensis*, there is no firm basis for projecting this behavior on these early hominids. I see no way to falsify such an inference. As such, it does not appear to be a testable hypothesis.

McGrew calls for studies of apes and humans in order to link grasps with task demands and raw materials. Much of the work on precision handling, sufficient for interpreting the morphology of the hand in living apes and humans, has been already done (*3*, *4*). There, indeed, may be some fertile ground yet to be explored in the study of hand use in wild, tool-using chimpanzees but the question of which species of early hominids made the Oldowan tools can only be answered by (i) the recovery of appropriate fossils and (ii) comparison of the fossils to counterparts in living apes and humans in which the links between morphology and behavior have been clearly established.

Hamrick and Ionuye state (their figure 1B) that two populations of gorillas extend into the "tool" portion of the plot. Data from the larger sample of lowland gorillas, however, reveal a large range that is skewed and seems to be driven by outliers on the high end. When I compute the ratio of metacarpal length to head breadth, the mean value in gorillas (males and females, mountain and lowland) is 24.2 (n = 30, SD = 1.97, range = 20.5 to 31.9). This range extends into the "tool using" range (figure 1 of their comment). The largest, and only value I obtain for thumb articular head breadth to thumb length that encroaches on the "tool" makers is 31.9 in a single female (Cleveland Museum No. 1756) (figure 1 of the comment). Hamrick and Inouye's data place a greater number of individuals in the "tool" range. The problem with gorillas is that, although figure 2 in my report (*1*) reveals a close morphological affinity of *Pan* and *Australopithecus*, gorillas are morphologically distinct from early hominids. On this basis one might question their appropriateness in this comparative context before reaching the question of "tool" versus "nontool" values on the index in question.

Hamrick and Inouye are mistaken in their statement that gorillas have thumbs that do not differ in length from those of humans. They use a size variable (denominator) that is driven by the relatively short femur in gorillas (*5*). Because the other elements in their size surrogate are humerus length [which does not differ in extant hominoids (*6*)], pubis length, and humeral midshaft diameter (both of which make only a relatively small contribution to the mean), the ratio is highly biased by the negative scaling of gorilla femur length. There are other better, less idiosyncratic, measures of relative thumb length than the one proposed by Hamrick and Inouye. For example, as we are considering the effectiveness of precision grasping, we can use the measures proposed by Napier (*7*) and used by many others to compare thumb length to overall finger length (the "hand length index" of Napier), index finger length (the "opposability index" of Napier), or other measures of hand length. What is the point of compairing thumb length to body mass (or a questionable surrogate thereof) when we are addressing the question of how the thumb opposes the fingers? The length of the thumb relative to the fingers is the most appropriate comparison. It reveals, as I state (*1*), that great apes have relatively short thumbs. Humans have relatively long thumbs.

Finally, we might suspect (although there is no evidence of either tools or anatomy) that the earliest hominids used tools in an apelike fashion (as I illustrate, *A. afarensis* has a chimpanzee-like thumb). But without tools and without any anatomical traces, we can only speculate about tool behavior at this early point in the human career. I suggest that until tool behavior leaves traces on the hand (or elsewhere in the anatomy), the issue is moot for the paleoanthropologist. As a result, we probably will not be identifying the first tool users in the human career just as we probably will not detect the very first hominids who spent most of their days walking on two limbs instead of four. (Nonetheless, it seems reasonable to assume that at some point facultative bipedality was frequent enough to reach an "anatomical threshold.") Tool behavior (precision grasping or handling) does become evident in the hominid hand around 2.0 million years ago, 500,000 years after the appearence of stone tools. I have studied the total morphological pattern of the most extensive set of hand bones, O.H. 7, from Olduvai Gorge (*8*). But that is the single, exceptional case of a "set" of hand bones (numbering only four complete bones of a possible 30 bones in a human hand). The hominid fossils recovered from the limestone caves of South Africa are broken, dissociated remains of carnivore meals. It behooves us to search for ways to extract information on single elements. That is what I have attempted to do. I do not find a compelling reason to abandon or alter this strategy at this time.

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