K were determined in enamel and sediment by instrumental neutron activation analysis. We assumed a water content of 10 ± 10% and no radon loss.
40. The estimated error is simply the 1σ standard deviation of the six ages.
41. F. McDermott, R. Grun, C. B. Stringer, C. J. Hawkesworth, *Nature* **363**, 252 (1993).
42. Each quoted error is the 1σ analytical precision on one sample.
43. R. Grun, H. P. Schwarcz, J. Chadam, *Nucl. Tracks Radiat. Meas.* **14**, 237 (1988).
44. In this estimate of error, we have reduced the analytical uncertainty of the average ESR age to reflect the difference of 7 ka between the minimum EU age of 67 ka and the minimum TL age of 74 ka for the overlying stratigraphic unit.
45. G. H. Miller, P. B. Beaumont, A. T. Jull, B. Johnson, *Proc. R. Soc. London Ser. B* **337**, 149 (1992); A. S. Brooks, P. E. Hare, J. E. Kokis, *Carnegie Inst. Washington Yearb.* **92**, 95 (1993); P. E. Hare, G. A. Goodfriend, A. S. Brooks, J. E. Kokis, D. W. Von Endt, *ibid.*, pp. 80–85.
46. We thank the people and the government of the Republic of Zaire, especially the Président Délégué Général (PDG) for the Institut Zairois pour la Conservation de la Nature, Mankoto wa Mbalele, and the PDG of the Institut des Musees Nationaux, Lema Gwete, for facilitating this research. We also acknowledge the support and contributions in the field of the project co-principal investigators N. T. Boaz and J. W. K. Harris and of Kanimba Misago (archaeologist, Musees Nationaux), Mugangu Trinto Enama (Director of Graduate Studies, University of Kinshasa), and Muya wa Bitanko Kamuanga (Director, Museum de Lubumbashi). The research was supported by the National Science Foundation under grants to N. T. Boaz, J. W. K. Harris, and A.S.B. (BNS85-07891, BNS86-08269, and BNS90-14092), to W.H. and A.F. (86-02272, 89-11758, 90-47367, 91-07652, and 92-40147), and to H.S. (DBS92-10469), as well as by grants from the L. S. B. Leakey Foundation, the National Geographic Society, the George Washington University Committee on Research, Sigma Xi, Earthwatch, the Holt Family Foundation, and the Social Sciences and Humanities Council of Canada (K.S.). We are indebted to J. de Heinzelin for his work on the sections of Kt2 and Kt9 and for helpful comments on earlier drafts. The drawings were prepared by D.M.H.

18 August 1994; accepted 15 February 1995

A Middle Stone Age Worked Bone Industry from Katanda, Upper Semliki Valley, Zaire

John E. Yellen, Alison S. Brooks, Els Cornelissen, Michael J. Mehlman, Kathlyn Stewart

Three archaeological sites at Katanda on the Upper Semliki River in the Western Rift Valley of Zaire have provided evidence for a well-developed bone industry in a Middle Stone Age context. Artifacts include both barbed and unbarbed points as well as a daggerlike object. Dating by both direct and indirect means indicate an age of ~90,000 years or older. Together with abundant fish (primarily catfish) remains, the bone technology indicates that a complex subsistence specialization had developed in Africa by this time. The level of behavioral competence required is consistent with that of upper Paleolithic *Homo sapiens sapiens*. These data support an African origin of behaviorally as well as biologically modern humans.

Anatomically modern humans (*Homo sapiens sapiens*) appeared in Africa and the Levant before 90,000 years ago (ka) (*1*). By 50 ka, they had colonized Australia (*2*) and possibly east Asia (*3*). In the colder climates of Europe, central Asia, and Siberia, however, Neandertals (*Homo sapiens neandertalensis*) continued to predominate until as late as 35 ka. The middle to upper Paleolithic behavioral transition in Europe, central Asia, Siberia, and the Near East also occurred between 40 and 30 ka and is marked by the appearance of (i) new technologies, such as prismatic blade cores, specialized bone and antler tools, burins, and sophisticated hearths, (ii) more complex economic strategies, involving seasonally specific activities, storage, and long-distance procurement, (iii) larger scale social networks, reflected not only in the long-distance trade in raw materials but also in the use of personal ornaments, and (iv) an expanded use of symbols in art and daily life. Regionally specific styles of artifact manufacture in the early upper Paleolithic reflect this greater social complexity. In Europe, with a few exceptions from the transitional period (*4*), the evolutionary shifts in human morphology and behavior coincide; anatomically modern humans are associated with upper Paleolithic industries, whereas Neandertals are associated with middle Paleolithic or Mousterian industries.

J. E. Yellen, Archaeology Program, National Science Foundation, 4201 Wilson Boulevard, Arlington, VA 22230, USA.
A. S. Brooks, Department of Anthropology, George Washington University, Washington, DC 20052, USA.
E. Cornelissen, Musée Royal de l'Afrique Centrale, Section de Prehistoire, Tervuren, B-3080, Belgium.
M. J. Mehlman, Library, University of California, Santa Cruz, CA 95064, USA.
K. Stewart, Canadian Museum of Nature, Research Division, Post Office Box 3443, Station D, Ottawa, Ontario, K1P 6P4, Canada.

In Africa, however, fossils of anatomically modern humans from between 130 and ~60 ka are associated with industries grouped as Middle Stone Age (MSA), which share broad technological parallels with the Mousterian–middle Paleolithic of western Eurasia (*5*). By ~40 ka, these flake and prepared-core industries begin to be replaced, at least in some areas, by Later Stone Age (LSA) industries based primarily on microlithic technology rather than on blades (*6*). This new technology is associated with other indicators of greater behavioral complexity such as bone tools, ostrich eggshell beads, and transport of raw materials over long distances. The extent to which the MSA differs from the Mousterian in foreshadowing this complexity is uncertain (*7*).

We have recently recovered evidence for early complex behavior in the MSA from three sites at Katanda (Kt2, Kt9, and Kt16), a multisite locality in the Upper Semliki Valley of eastern Zaire, ~6 km north of Ishango, where the Semliki River exits from Lake Rutanzige (formerly Lake Edward) (*8*). The Katanda materials include a formal (*9*) bone industry, consisting of barbed bone points, unbarbed points, and a flat dagger. Bone industries from other African sites are considerably younger. Upstream at Ishango, uniserial and biserial barbed points have been dated to ~25 ka (*10, 11*). Outside Africa, formal bone points with finished bases suggestive of hafting first appear in the European Aurignacian as early as 38 to 40 ka (*12*); barbed points, however, do not occur before ~14 to 12 ka (*13*) at sites throughout Eurasia. Here we describe the artifact horizon at Kt9 with occasional reference to materials from Kt2 and Kt16. Paleoenvironmental data (*8*) suggest that all three Katanda sites were located along the valley of a southward-flowing proto-Semliki River, fringed with relatively dense gallery forest in proximity to open savannas. Sediment analyses indicate that Kt9 was the closest of the three to the proto-Semliki channel (*14*).

Excavation at Kt2 began in 1986 and continued through 1990, exposing 21 m^2 in the MSA levels. Three horizons of MSA were distinguished. The lowest, resting on the ASB paleosol, is the most comparable stratigraphically to the MSA horizons at Kt9 and Kt16. Over 2700 lithics in quartz, quartzite, and chert and 1100 faunal remains of fish and mammals were recovered from this lower horizon. The upper two MSA horizons yielded a total of 3700 lithics, predominantly in quartz, and some 75 poorly preserved faunal remains of which only 10 fragments were identifiable. Discoidal cores were the most distinctive aspect of the lithic material; formal tools were rare. In 1990, a single large fusiform bone point was recovered from the lowest MSA horizon in contact with the paleosol.

At Kt9, the MSA horizon crops out on a steep cliff face below ~8 m of horizontally stratified sand and silt, carbonate paleosols, and volcanic deposits. This overburden was intact over all but the extreme northwest and southwest corners of the excavated area at the cliff face. Removal of the overburden over an area of 35.2 m^2 revealed a dense concentration of artifacts and faunal remains (*15*).

The artifact concentration stopped abruptly on the north, east, and southeast. To the west and southwest, the original distribution had been truncated by erosion of the cliff face. The artifact horizon rested on a surface that sloped up 3° to the southeast. The thickness of the concentration averaged 5.5 cm but increased downslope to a maximum of 16 cm. The abundance of artifacts (up to 289 pieces per 400 cm^2), the abrupt edges of the concentration, and the dominance of chipped pieces over manuports or rolled quartz fragments, together with the nature of overlying cover and matrix sediments (medium to fine sands), suggest that the concentration itself is an anthropogenic feature or "pavement" (*16*).

The Kt9 concentration included over 8000 lithics, 7369 mammal and fish remains, and most remarkably, a series of 10 worked bone artifacts. This assemblage indicates the presence of a highly developed projectile technology and complex subsistence strategy. Fish remains and worked bone artifacts are rare in other MSA sites (*17–19*). The degree of abrasion and weathering on some of the lithic and faunal fragments suggests that the concentration may have been exposed for a significant period of time. Dating of the immediately overlying sands and teeth from the concentration suggests an age of 80 to 90 ka for the final burial of the site (*8*).

The lithic industry from Kt9 falls technologically and typologically within the broad range of the MSA. Local quartz and quartzites provided most of the raw material, although fragments of a nonlocal brown chert are also present. The percentage of recognizable cores, retouched pieces, and other formal artifacts in the analyzed sample of 7366 pieces is a low 8.2%. Core types were primarily discoidal but included examples with single and multiple platforms. Bipolar specimens are rare. Scrapers on retouched flakes are uncommon and do not conform to highly formalized patterns. Occasional spheroids and rubbing or grinding stones with intentionally ground flat faces are also present. The assemblage lacks formal bifacial or unifacial points or daggers, as well as hand axes, large core tools, blades, or microliths. Presence of the latter would have suggested inclusion within the LSA.

Highly formalized worked bone tools constitute the most remarkable aspect of the assemblage. These include seven well-made uniserial barbed bone points, two unbarbed points, and a large dagger-shaped object of unknown function (Table 1). All are made from rib fragments or long bone splinters of large mammals. Replication experiments and low-power microscopic examination (*20*) indicate that the shape was obtained by grinding the bone on a stone anvil or with a stone grinder. The method for barb construction on all pieces was the same: The edge was first shaped and smoothed before parallel notches, all at the same oblique angle to the long axis of the point, were cut into it. Specialized lithic artifacts such as burins were unnecessary, as the barbs could have been cut with an unmodified quartz flake. The resultant barbs are shaped like a parallelogram with three distinct edges (Fig. 1). This shape clearly distinguishes the Katanda points from later Ishangian counterparts (*21*), all of which have a triangular shape formed by the intersection of two edges.

Pieces where the butt end is preserved suggest that two hafting methods were used. Either several shallow grooves were incised around the circumference of the shaft or a series of closely spaced notches were cut into the barbed and nonbarbed edges. It is possible that the points served as harpoons, which, by definition, detach from the shaft after contact with prey, but this is unlikely because it is difficult for this grooved butt shape to hold a line against pressure from the harpooned animal. It is more likely that they were permanently fixed to a shaft.

The blunt rounded point and edges of the daggerlike object suggest that it served neither to cut nor pierce; its function is unknown. Although the two nonbarbed points probably served as weapons, their use is also uncertain. The number of clearly distinct artifact classes demonstrates that the Katanda people recognized that bone could serve as a workable plastic medium and be used for different purposes.

The barbed bone points are spatially associated with both fish and mammal re-

Table 1. Worked bone from Katanda sites. AC, almost complete; C, complete; DF, distal fragment; PF, proximal fragment.

Site	Piece number	State	Descriptive notes	Maximum width (mm)	Maximum thickness (mm)
			Barbed points		
Kt9	2	PF; tip AC; broken behind first barb	Rounded one face; medullary face flattened	19	9
Kt9	3	DF; last barb + portion of haft	Haft: two complete encircling incised grooves	17	11
Kt9	4	DF?; butt C; broken at haft incision	Markedly flattened both faces	17	8
Kt9	5	DF; butt C + five barbs	Rounded both faces; haft: three notches on barbed + three on unbarbed edge	14	7
Kt9	6	PF; tip AC + two barbs	Rounded one face; slightly flattened other	12	8
Kt9	7	AC; small fragment of tip missing; length, 142 mm.	Four barbs; slightly flattened one face; haft: three complete encircling incised grooves	19	13
Kt9	9	DF; butt C + one barb	Flattened both faces; haft: seven notches on barbed + seven on unbarbed edge	19	11
Kt16	1	AC: extreme tip and butt missing; length, 130 mm	Ten barbs; haft: nine notches barbed + nine unbarbed edge	19	9
			Unbarbed pointed pieces		
Kt9	1	Pointed end C; broken across shaft	Flattened both faces; no haft indication	14	7
Kt9	8	Pointed end AC; broken across shaft	Rounded both faces; no haft indication	11	8
Kt2	1	Butt C + shaft fragment	Rounded; no haft indication		
			"Knife"		
Kt9	10 (A, B, C, D)	Tip + portion of "blade" Tip = A + B + C D is a nonattached shaft fragment	Tip and edges rounded; flattened both faces	39	7

mains, which are present in abundance at Kt9 as well as Kt2 and Kt16. Species captured by Katanda people (8) include *Clarias* and *Synodontis*, both catfish, which constitute the majority of the assemblage. Because of *Clarias*'s much larger size (some specimens exceeded 2 m in length), this species could have provided the major meat input. *Clarias* is a bottom dweller that spawns in shallow water. The taxa represented in the samples from all three Katanda sites and the absence of individuals in juvenile size ranges are consistent with predation during spawning and suggest that the Katanda people visited the area repeatedly during limited seasons. *Clarias* and *Synodontis* spawn chiefly on floodplains in the rainy season, when they are easiest to catch (*22*).

The distribution of materials within the pavement suggests several inferences regarding behavior. Artifacts and fauna are particularly concentrated in two distinct clusters on the upslope portion of the pavement (*23*). These clusters cannot be attributed to materials settling into low points on the surface. Size sorting is evident (*24*) both overall and within each cluster, and larger pieces are located further downslope. Although the extent of abrasion on some of the bone and lithic pieces attests to extended exposure on the surface, the strong sorting by size over a short distance suggests that the deposits were redistributed slightly by low-energy transport. The effect of this was to blur the cluster edges. Although one or more edges of each cluster have been truncated by erosion of the cliff face, analysis of the remainder suggests that each exhibits bilateral symmetry and that material is concentrated in the center. On this basis, it is possible to reconstruct the original shapes and sizes of the clusters. One cluster is somewhat larger than the other (4 and 3.4 m in maximum diameter). The two clusters contain similar proportions of artifacts and faunal remains. Neither the contemporaneity nor original causality of the clusters can be proven. In terms of cluster size, distance between clusters, and similarity in both faunal and lithic remains, the pattern conforms to that of ethnographically observed debris produced by hunter-gatherer nuclear families in which production tasks are replicated by each nuclear unit (*25*).

The Kt16 site, 400 m to the north of Kt9, was discovered and excavated in 1990. From 11 m^2 of a buried MSA horizon, we recovered ~1500 lithics, 650 mammalian faunal elements, and 9700 fish remains, together with a large barbed bone point. As at Kt9 and Kt2, the assemblage consisted largely of flakes and radial cores, with rare formal tools. In contrast to the other two sites, however, Kt16 also contained several large bifacial pieces, a few blades, and two large, carefully made grindstones on dioritic, gabbroic, or amphibolite rocks. Microliths and microcores such as those associated with the late Paleolithic Ishango horizons (8) are absent at all three sites.

The Katanda sites indicate that a complex bone industry and seasonal use of aquatic resources had developed by ~90 ka. The absence of known parallels within Africa may indicate the existence at this time of a geographically limited cultural tradition, with little contact between central and southern Africa, or it may reflect inadequate exposure or exploration of the ancient margins of large tropical rivers and lakes. The presence of other, geographically limited hafted projectile traditions within the MSA, such as the Lupemban or Bambata (*26*), reflects that African hominids not only possessed considerable technological capabilities at this time but also incorporated symbolic or stylistic content into their projectile forms. The fact that other early barbed bone points, although ~55,000 to 60,000 years younger, occur only 6 km away suggests the long-term continuity of regional adaptations (*11*). The Katanda people may have been living in nuclear family units and following a specialized subsistence pattern most often associated with a terminal Pleistocene to Holocene adaptation. Their archaeological traces suggest the early presence of modern behavioral capabilities in Africa along with the evidence for anatomically modern humans.

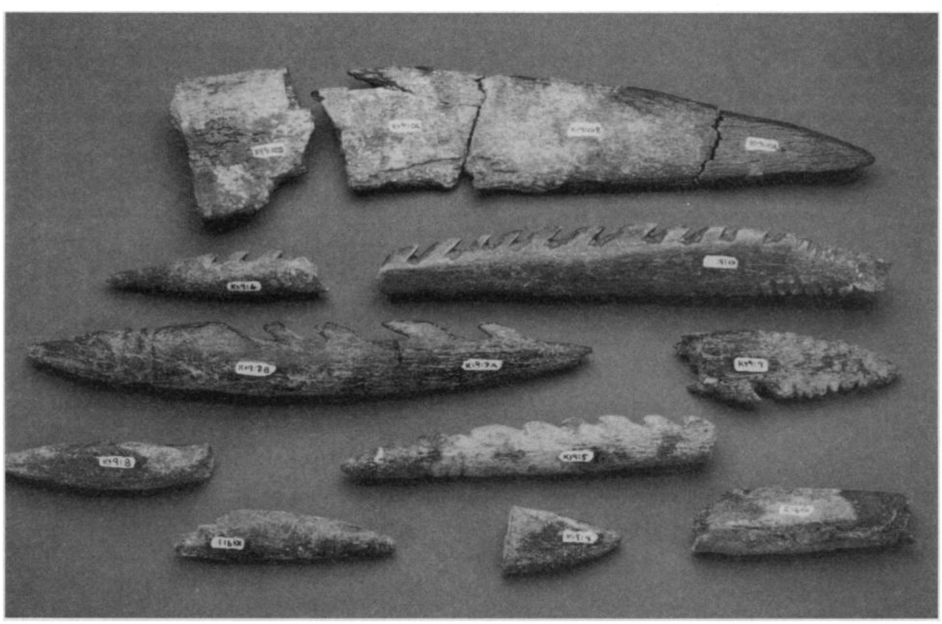

Fig. 1. Worked bone from Kt9 and Kt16. Top row: Kt9:10, D through A (left to right); second row: Kt9:6, Kt16:1; third row: Kt9:7, A and B, Kt9:9; fourth row: Kt9:8, Kt9:5; fifth row: Kt9:1, Kt9:4, Kt9:3. See Table 1 for descriptions.

REFERENCES AND NOTES

1. H. Valladas *et al.*, *Nature* **331**, 614 (1988); H. P. Schwarcz *et al.*, *J. Hum. Evol.* **17**, 733 (1988); G. H. Miller, P. B. Beaumont, A. T. Jull, B. Johnson, *Proc. R. Soc. London Ser. B* **337**, 149 (1992); A. S. Brooks, P. E. Hare, J. E. Kokis, *Carnegie Inst. Washington Yearb.* **92**, 95 (1993); P. E. Hare, G. L. Goodfriend, A. S. Brooks, J. E. Kokis, D. W. Von Endt, *ibid.*, p. 80; R. Grun and C. B. Stringer, *Archaeometry* **33**, 153 (1991).
2. R. Jones, in *The Human Revolution: Behavioral and Biological Perspectives on the Origins of Modern Humans*, P. Mellars and C. Stringer, Eds. (Edinburgh Univ. Press, Edinburgh, 1989), pp. 743–782; R. G. Roberts, R. Jones, M. A. Smith, *Nature* **345**, 153 (1990).
3. A. S. Brooks and B. Wood, *Nature* **344**, 288 (1990).
4. F. Levêque, A. M. Backer, M. Guilbaud, *Context of a Late Neandertal: Implications of Multidisciplinary Research for the Transition to Upper Paleolithic Adaptations at Saint-Césaire (Charente-Maritime) France* (Monogr. in World Prehistory 16, Prehistory Press, Madison, WI, 1993); F. H. Smith and J. Ahern, *Am. J. Phys. Anthropol.* **93**, 275 (1994).
5. Relevant sites include Klasies River Mouth, Border Cave, Die Kelders, and Equus caves in South Africa, Mumba Cave in Tanzania, and the Omo River Kibish formation in Ethiopia. Dating by various direct and indirect techniques indicate ages of ~50,000 to greater than 105,000 years [R. Grun, N. J. Shackelton, H. J. Deacon, *Curr. Anthropol.* **31**, 427 (1990); H. J. Deacon, in *The Human Revolution: Behavioral and Biological Perspectives on the Origins of Modern Humans*, P. Mellars and C. B. Stringer, Eds. (Edinburgh Univ. Press, Edinburgh, 1989), pp. 547–564; A. S. Brooks *et al.*, *Science* **248**, 60 (1990); M. J. Mehlman, *World Archaeol.* **11**, 80 (1979); *J. Archaeol. Sci.* **14**, 133 (1987); K. W. Butzer, F. H. Brown, D. L. Thurber, *Quaternaria* **11**, 15 (1969).
6. P. B. Beaumont, H. de Villiers, J. C. Vogel, *S. Afr. J. Sci.* **74**, 409 (1978); F. Van Noten, *Antiquity* **51**, 35 (1977); S. H. Ambrose, paper presented at the 11th Biennial Meeting of the Society of Africanist Archaeologists, Los Angeles, 26 to 29 March 1992; M. J. Mehlman and A. S. Brooks, paper presented at the 11th Biennial Meeting of the Society of Africanist Archaeologists, Los Angeles, 26 to 29 March 1992.
7. A. S. Brooks, in *Encyclopedia of Human Evolution and Prehistory*, I. Tattersal, E. Delson, J. Van Couvering, Eds. (Garland, New York, 1988), pp. 346–

349; S. McBrearty, *Man* **25**, 129 (1990); R. G. Klein, *The Human Career* (Univ. of Chicago Press, Chicago, 1989).
8. A. S. Brooks *et al.*, *Science* **268**, 548 (1995); See also discussion of large mammal remains in this paper.
9. Earlier bevel-shaped or pointed bone and ivory implements are known from several middle Pleistocene sites including Přezletice, Czech Republic [J. Fridrich, *Proceedings of the IXth International Union of Pre- and Proto-Historic Sciences Section VIII: Les Premieres Industries d'Europe* (Nice, France, 1976), pp. 8–23], Bilzingsleben, Germany [D. Mania and T. Weber, *Bilzingsleben III Veroffentlichungen des Landesmuseums fur Vorgeschichte in Halle* **39**, 9 (1986)], Kabwe, Zambia [J. D. Clark, in *From the Earliest Times to c. 500 BC*, vol. 1 of *The Cambridge History of Africa*, J. D. Clark, Ed. (Cambridge Univ. Press, Cambridge, 1982), pp. 248–341], and possibly the lower Pleistocene site of Swartkrans [C. K. Brain *et al.*, *S. Afr. J. Sci.* **84**, 828 (1988)], but the shaping is simple and may be due in part to use. For a summary, see (*12*).
10. A summary of research history to 1988 is provided by J. Verniers and J. de Heinzelin, in *Evolution of Environments and Hominidae in the African Western Rift Valley*, N. T. Boaz, Ed. (Virginia Museum of Natural History Mem. 1, Martinsville, VA, 1990), pp. 17–39.
11. A. S. Brooks and C. C. Smith, *Afr. Archaeol. Rev.* **5**, 65 (1987); A. S. Brooks and P. Robertshaw, in *Low Latitudes*, vol. 2 of *The World at 18 000 BP*, C. S. Gamble and O. Soffer, Eds. (Unwin Hyman, London, 1990), pp. 121–169. On the basis of both radiocarbon and amino acid racemization dating of ostrich eggshell, barbed bone points and LSA lithics at White Paintings Shelter, Tsodilo Hills, Botswana, may be associated with a date as old as or older than the barbed points from Ishango (L. H. Robbins, personal communication).
12. H. Knecht, in "Hunting and Animal Exploitation in the Later Palaeolithic and Mesolithic of Eurasia," *Archaeol. Pap. Am. Anthropol. Assoc. 4*, G. L. Peterkin, H. M. Bricker, P. Mellars, Eds. (1993), p. 33; L. G. Straus, *ibid.*, p. 83; A. S. Brooks, in *Les Fouilles Movius a Pataud*, H. M. Bricker Ed. (Centre National de la Recherche Scientifique, Paris, in press); H. Knecht, *Sci. Am.* **271** (no. 1), 82 (1994).
13. J. Troenig, *Worldwide Chronology of Fifty-Three Prehistoric Innovations* (Acta Archaeol. Lund. Ser. 8° 21, Stockholm, 1993).
14. D. Helgren, personal communication.
15. We recorded these materials within 20 cm by 20 cm squares, together with the topography of the concentration in each square. All matrix was screened through 3-mm mesh.
16. We prefer to use "pavement" rather than the more usual archaeological designation "living floor." This avoids a priori assumptions about possible aggregating agents and hominid role.
17. Site 440 located near Wadi Halfa, Sudan, contained at least six species of fish in association with a Mousterian industry [P. H. Greenwood, in *The Prehistory of Nubia*, F. Wendorf, Ed. (Southern Methodist Univ. Press, Dallas, 1968), vol. 1, pp. 100–109; J. L. Shiner, *ibid.*, vol. 2, pp. 630–650.
18. L. Robbins, paper presented at the 11th Biennial Meeting of the Society for Africanist Archaeologists, Los Angeles, 26 to 29 March 1992. Ongoing excavation at White Paintings Shelter, Tsodilo Hills, Botswana, indicates the presence of fish associated with a MSA industry.
19. Two notched bone fragments and one unbarbed bone point occur in MSA and Howieson's Poort Industries at Klasies River Mouth. Split and polished warthog or bush pig tusks have also been reported from Border Cave [R. Singer and J. Wymer, *The Middle Stone Age at Klasies River Mouth in South Africa* (Univ. of Chicago Press, Chicago, 1982); T. P. Volman, in *Southern African Prehistory and Paleoenvironments*, R. G. Klein, Ed. (Balkema, Boston, 1984), pp. 169–220]. Middle Paleolithic bone or ivory awls are known from the Khormusan industry of Egypt [A. E. Marks, in *The Prehistory of Nubia*, F. Wendorf, Ed. (Southern Methodist Univ. Press, Dallas, 1968), vol. 1, pp. 315–391] and from site Kostienki 17 on the Russian plain [M. Anikovich, *J. World Prehist.* **6**, 205 (1992)]. The complexity and formal nature of the Katanda industry, however, place it, we believe, in a cognitively distinct category.
20. C. Krupsha, thesis, George Washington University, Washington, DC (1993).
21. J. de Heinzelin, *Les Fouilles d'Ishango: Exploration du Parc National Albert, Mission J. de Heinzelin 1950*, Fasc. **2** (1957).
22. At Ishasha, south of Lake Rutanzige, in a swampy gallery forest environment similar to that implied for the Katanda MSA, large numbers of *Clarias* are taken annually by harpoon during the few days of the spawning season (T. E. Mugangu, personal communication).
23. Correlation of number of in situ lithics per square and depth of square below datum: $r^2 = 0.0370$; $n = 369$; $P = 0.01$.
24. A number of correlation analyses were conducted to examine the relation between lithic maximum length and depth below datum. These confirm that when controlled by both lithic type and raw material type, larger pieces have been displaced downslope.
25. Distance between cluster "centers," as defined by maximum lithic and faunal density, is 4.2 m. Maximum cluster diameters are 4.0 and 3.4 m. For comparative data, see J. E. Yellen, *Archaeological Approaches to the Present: Models for Reconstructing the Past* (Academic Press, New York, 1977); R. A. Gould and J. E. Yellen, *J. Anthropol. Archaeol.* **6**, 77 (1987).
26. J. D. Clark, *J. World Prehist.* **2** (no. 3), 235 (1988).
27. We thank the people and the government of Zaire for facilitating this research, which was a collaborative effort involving almost 200 individuals from more than 15 countries. This study is based on work supported by the National Science Foundation under grants to N. T. Boaz, J. W. K. Harris, and A.S.B. (BNS85-07891, BNS86-08269, and BNS90-14092). Additional financial support was provided by the George Washington University Committee on Research, the L. S. B. Leakey Foundation, the Holt Family Foundation, the National Geographic Society, the National Science Foundation, the Smithsonian Institution, the Social Sciences and Humanities Research Council of Canada, and the Musée Royal de l'Afrique Centrale. Identification of the rocks used for grind stones was made by S. Sorensen. Artifact photographs by R. E. Clark Jr. (Smithsonian Institution).

18 August 1994; accepted 15 February 1995

Crystal Structure of DCoH, a Bifunctional, Protein-Binding Transcriptional Coactivator

James A. Endrizzi, Jeff D. Cronk, Weidong Wang, Gerald R. Crabtree, Tom Alber

DCoH, the dimerization cofactor of hepatocyte nuclear factor–1, stimulates gene expression by associating with specific DNA binding proteins and also catalyzes the dehydration of the biopterin cofactor of phenylalanine hydroxylase. The x-ray crystal structure determined at 3 angstrom resolution reveals that DCoH forms a tetramer containing two saddle-shaped grooves that comprise likely macromolecule binding sites. Two equivalent enzyme active sites flank each saddle, suggesting that there is a spatial connection between the catalytic and binding activities. Structural similarities between the DCoH fold and nucleic acid–binding proteins argue that the saddle motif has evolved to bind diverse ligands or that DCoH unexpectedly may bind nucleic acids.

Transcription depends on interactions among numerous proteins, including regulatory proteins bound at specific DNA sites. Homeodomain transcription factors, for example, are recognized by protein-binding coactivators (*1*, *2*). Little is known, however, about the molecular nature of the activation signals or the structures of the interacting protein motifs. One such coactivator is DCoH, the dimerization cofactor of hepatocyte nuclear factor–1 (HNF-1) (*1*). In vertebrates, DCoH associates with the HNF-1 proteins, which regulate tissue-specific genes by binding to DNA as dimers (*3–5*). The dimerization and transcriptional activities of HNF-1α are stimulated in vitro and in vivo by DCoH, but DCoH itself contains no DNA binding activity or activation domain. These properties imply that DCoH stimulates transcription through protein-protein interactions.

J. A. Endrizzi, J. D. Cronk, T. Alber, Department of Molecular and Cell Biology, University of California, Berkeley, CA 94720-3206, USA.
W. Wang and G. R. Crabtree, Department of Developmental Biology and Howard Hughes Medical Institute, Unit in Molecular and Genetic Medicine, Stanford University School of Medicine, Stanford, CA 94305-5425, USA.

DCoH presumably binds other ligands, because it also functions in contexts devoid of HNF-1α. In *Xenopus*, for example, DCoH is maternally encoded in oocytes and localizes to cell nuclei at a time when the primary germ layers are determined during the midblastula transition (*6*). A widespread transcriptional role for DCoH was suggested by the discovery of a bacterial homolog, phhB, with ~30% identity to the rat protein (*7*). Mutations in the gene *phhB* block expression of other genes in the *phh* operon, including the gene encoding phenylalanine hydroxylase. Expression of phhB in mammalian cells facilitates activation of HNF-1–dependent genes, and mammalian DCoH complements *phhB* mutations in bacteria by supporting transcription of the *phh* operon (*8*). This complementation suggests that the mechanisms of transcriptional activa-