

is productive. In the event studied by Kleinfield *et al.*<sup>2</sup>, the  $V_{H1}$  of a productive  $V_{H1}DJ_{H1}$  rearrangement is exchanged with an upstream  $V_{H1}$  segment to produce a novel productive rearrangement, indicating that the recombinase is still active in cells with a productive  $V_{H1}DJ_{H1}$ . This finding may, at first glance, seem inconsistent with an allelic exclusion mechanism regulating  $V_{H1}$  to  $DJ_{H1}$  rearrangement. However, current evidence suggests that joining is prevented in cells with a productive  $V_{H1}DJ_{H1}$  rearrangement by limiting access of the recombinase to  $V_{H1}$  gene segments rather than by turning off recombinase activity<sup>3</sup>. Recombinase is thought to lose access because transcription of germ-line  $V_{H1}$  segments stops in cells that produce complete heavy chains<sup>4</sup>.

Notably, the described  $V_{H1}$  to  $V_{H1}DJ_{H1}$  recombinations seem to involve proximal  $V_{H1}$  segments and it has been shown that the activity of the heavy-chain enhancer in the  $J_{H1}$  to  $D_{H1}$  intron allows transcription of the proximal unrearranged  $V_{H1}$  segment<sup>5</sup>; perhaps by providing access to recombinase. Because allelic exclusion appears to occur in nearly 100 per cent of normal B cells, it seems that  $V_{H1}$  to  $V_{H1}DJ_{H1}$  joining does not frequently activate expression of both heavy-chain alleles.

$V_{H1}$  to  $V_{H1}DJ_{H1}$  joining may also prevent bias in the development of the heavy-chain  $V$ -region repertoire. Differentiating B cells use the  $V_{H1}$  segments nearest the  $J_{H1}$  elements at high frequency to form  $V_{H1}DJ_{H1}$  rearrangements<sup>6</sup>, which limits the spontaneously generated heavy-chain repertoire. But the repertoire of mature peripheral B cells appears to involve all  $V$  segments equally<sup>7</sup>. How this occurs is not known, although cellular selection mechanisms have been implicated. Kleinfield *et al.* suggest that  $V_{H1}$  to  $V_{H1}DJ_{H1}$  joining may be a means of successively replacing rearranged 3'  $V$  segments with more 5'  $V$  segments. However, if replacement involves nearest neighbours, as suggested from the data of Reth *et al.*, it is difficult to imagine successive recombination events between hundreds of  $V$  genes playing a major role in the process. Final understanding awaits further elucidation of the mechanism and frequency of this process. □

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## Animal behaviour

# How great white sharks, sabretoothed cats and soldiers kill

from Jared M. Diamond

PREDATORS that attack large prey endowed with formidable defensive weapons face a dilemma. If the victim is not incapacitated by the first blow and the predator must continue to engage the victim in order to kill it, the predator itself risks injury. For example, lions are occasionally crippled or killed by zebra, giraffe or rhinoceros prey. Recent studies suggest that two quite different large predators — the great white shark<sup>1,2</sup> and the extinct sabretoothed cats<sup>3</sup> — independently evolved the same solution to this dilemma.

Adult great white sharks (*Carcharodon carcharias*), the largest living marine fish capable of preying on vertebrates, often feed on seals, whales and other sharks. Common victims in Californian waters are elephant seals, which have formidable teeth combined with a maximum size exceeding that of the shark. The seal is more agile than the shark and is therefore most efficiently hunted by surprise. Timothy Tricas and John McCosker<sup>1,2</sup> reconstructed the shark's strategy from observations of attacks; scars on seals that got away; and underwater observations (while protected within steel cages) of sharks approaching bait. Bite scars on surviving seals indicate a single massive bite on the underside of the body. Apparently a shark cruising underwater sees above it the silhouette of a seal basking at the surface, rises undetected towards the seal from behind and below, quickly bites out a large chunk of the seal (the entire biting takes only 1 second), and rapidly retreats to avoid injury. The shark then waits for the seal to go into shock or to haemorrhage before closing in to complete the kill and to feed.

This reconstructed sequence helps one to understand what happens to human victims of great white sharks. Most survivors never saw the shark that attacked them: they merely

felt themselves lifted into the air and then dropped after suffering a single haemorrhaging bite. Victims usually die from loss of blood, not of limbs or vital organs.

A similar strategy appears to have been practised on land by extinct sabretoothed cats of the genera *Smilodon* and *Homotherium*<sup>3</sup>. These lion-sized predators take their name from their very long upper canines (exposed tooth up to 15 cm long in *Smilodon*). How these weapons were used to kill has been in dispute. The prevalent view until recently was that the upper canines were used to stab or slash the victim while the lower jaw was merely drawn down out of the way. However, closer examination casts doubt on the usefulness of the blunt sabres for stabbing and slashing: they are round-tipped, oval rather than knife-like in cross-section, and barely clear the lower jaw.

Our most detailed information about the preferred prey of sabretooths comes from a probable den, Friesenhahn Cave in Texas, where remains of adult plus very small juvenile *Homotherium* co-occur with scores of baby mammoths, presumably killed by the adult cats and dragged to the den to feed the kittens. Even a baby mammoth could hardly have been killed by the cat at a single blow. Yet it would

IMAGE  
UNAVAILABLE  
FOR  
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REASONS

How *Smilodon* used its peculiar anatomy to rip a large piece of flesh out of its prey. Propping its mandible on the prey (a), the cat used its powerful head-depressing muscles to drive in the upper canines (b), rotate the head until the jaws closed (c, d) and pull out a fold of flesh. (Drawing by Mark Hallett. From ref. 3, courtesy of the Los Angeles County Museum of Natural History.)

have been suicidal for the cat to continue to grip the baby, as the mother would then have time to crush or impale the cat.

A solution to this dilemma is suggested by William Akersten's anatomical studies<sup>3</sup> of remains of *Smilodon* trapped in the famous La Brea tar pits of Los Angeles. Muscle scars on *Smilodon* bones show that the muscles for closing the jaws were not especially strong but that the muscles to depress the head by rotating it downwards around the joint with the first neck vertebra were massive (see figures). The chin was flanged, and the jaws opened to the enormous gape angle of 95° to permit the same clearance between the long upper and lower canines as does the 65° gape of modern cats. Akersten suggests the following sequence. A cat ambushes a baby mammoth straying from its mother and uses its powerful fore-limbs to pull down the baby, exposing the abdomen. The cat opens its jaws wide, catches a large fold of flesh between the upper and lower



(From ref. 3.)

Cranium and mandible of *Smilodon*.

canines, wedges the lower jaw firmly against the prey by the chin flanges, and then completes the bite by the head-depressing muscles. It then flees from the approaching mother mammoth and waits for the baby to haemorrhage, die, and be abandoned by its mother.

Yet one more predator has independently evolved a similar solution to the problem posed by a formidable victim. The most dangerous prey of all is an armed man, routinely hunted only by other armed men. Inexperienced soldiers aim for the head or heart, but these small targets are easily missed. "Always aim for the stomach when you shoot" was the advice of an experienced African bush fighter — "it is just as good, because no man can live long after his intestines have been shot away"<sup>4</sup>. Nor could an elephant seal or baby mammoth. □

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## Anthropology

# The longest human record

from John E. Yellen

THE recent conference\* to honour J. Desmond Clark for his contributions to African pre-history provided a unique opportunity to review current ideas about the archaeological record of this continent. African palaeoanthropology is most clearly distinguished by its quest for the first uniquely hominid antecedent: the earliest known hominid fossils derive from the Eastern Rift Valley in Kenya. Evidence for the first million years of cultural development, in the form of stone tools, butchered animal remains and possibly the controlled use of fire, are also limited to the African continent. The first modern humans, *Homo sapiens sapiens*, were widely distributed in Africa well before their appearance in Europe and the near East and the development of complex societies, in relative independence from those in other parts of the Old World.

Excavations this past summer near Ishango, eastern Zaire, produced stone artefacts associated with faunal remains that are just over two million years old (Jack Harris, University of Wisconsin; Noel Boaz, Virginia Museum of Natural History). In conjunction with stone-tool assemblages from Ethiopia of about the same age, systematic lithic modification must have appeared more than two million years ago. Unfortunately, these artefacts cannot be assigned to specific species.

Arguments were presented that *Homo habilis* was capable of speech (Dean Falk, University of Puerto Rico; Philip Tobias, University of the Witwatersrand). This species had a larger brain than australopithecine forms with prominent enlargement of Broca's and Wernicke's areas, both associated with language in modern humans. These advances appeared at about the same time as the first stone tools.

Whereas most palaeoanthropologists agree that by the mid-Pleistocene *Homo erectus* had controlled use of fire, there has been no evidence for earlier occurrences. Because charcoal decomposes in tropical environments, African evidence is extremely difficult to obtain. Recently discovered patches of reddened earth in East African sites dates between 1.5 and 1.7 million years ago and which are associated with cultural remains were suggested to indicate much earlier human use of fire (Desmond Clark, University of California; Jack Harris, University of Wisconsin). But palaeomagnetic and thermoluminescent analyses failed to provide unequivocal evidence of sediment heating.

The question of early hominid hunting reflects on cognitive ability and social organization. Although animal bones with stone-tool cutmarks provide evidence of carcass use by humans earlier than 1.5 million years ago, it is uncertain whether these remains were acquired by hunting or by scavenging from carnivore kills. If hominids were primarily scavengers, they would be left with the less-choice body parts, which would be reflected in the skeletal elements recovered and the way they were treated to remove remaining scraps of meat. Using such criteria, faunal remains from both Olduvai and Koobi Fora can be interpreted to indicate hunting as cutmarks appear on the primary meat-bearing bones of small bovids which would be unlikely to survive the attention of large carnivores (Henry Bunn, University of Wisconsin).

Also at issue was a large sample of excavated cattle and sheep bones from the Neolithic site of Ngamuriak in southern Kenya. In this butchered assemblage the larger and smaller species are processed differently and a similar pattern is evident in early hominid material (Fiona Marshall, University of California). On the other hand, analysis of the Olduvai Bed I fauna shows 13 cases of overlapping stone-tool and carnivore tooth marks. In eight of these the tool mark overrules that made by tooth, indicating human scavenging (Pat Shipman, Johns Hopkins University).

Recent work on the eastern margin of the Kalahari Desert shows a pattern of increasing complexity and hierarchical organization which, in effect, set the stage for the emergence of the Zimbabwe culture (James Denbow, National Museum of Botswana). The Venda, who are among the lineal descendants of Zimbabwe people, use variation in motifs on compound walls to denote status. Direct counterparts exist in Zimbabwe period stone-walled structures and, by application of Venda data, it has been possible to reconstruct a five-level hierarchy which extended from heads of individual households to the divine national leader (Thomas Huffman, University of the Witwatersrand). Because the gradual evolution of this system can be traced through time it is highly unlikely that the final structure was a direct result of outside stimulus (trade with Indian Ocean powers) but more probably derived from indigenous roots. □

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