Miocene forms completely match the modern great ape pattern, and this, in our opinion, makes them the only fossil hominoids that can be included in the family of great apes and humans.

There remain many divergent hypotheses about whether or not certain fossil hominoids are related to the living apes. What this diversity of opinion seems to indicate is that there is no consensus about which of the many different criteria and methods should be used for selecting characters and constructing theories. Analyses merely based on long lists of discrete characters, as demanded by cladistics[8], do not seem to offer a way out of this impasse. We agree with Steve Ward[9], who pointed out that our poor understanding of functional and developmental processes is a major hurdle that must be crossed before robust evolutionary hypotheses can be constructed.

Perhaps the time has come to reproach orthodox henningian cladistics[8] for rejecting every kind of preselection of what Cuvier called "valuable" and "valueless" features. We would argue that a return to basics is called for and that, before conducting any cladistic analysis, the usefulness of a character should be independently assessed in light of its underlying functional and structural constraints and developmental processes. Agreement on the central importance of this point may offer the first step towards forging a consensus about how to proceed. □

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River management

What's best on the banks?

David R. Montgomery

In the United States, strategies for the conservation of aquatic ecosystems emphasize the protection and restoration of streamside (riparian) forests[1,2] — that is, current official policy encourages the reversion of streamside areas to mature forest. But it has not always been thus, and throughout most of the twentieth century US government agencies have actively removed wood debris from channels to improve navigation or allow fish easier passage. These practices began to change in the 1970s, after it was recognized that the accumulation of coarse organic debris from forests leads to the greater incidence of ecologically beneficial cover, slow-water refugia and pools, and increased sediment storage[3].

Writing in *Geology*[4], Stanley Trimble has introduced a new twist into this arena. He studied four reaches of Coon Creek, in the state of Wisconsin, each of which has grassed and forested stretches. His surveys show that channels flowing through forests tend to be wider than channels flowing through grasslands, an effect he attributes to the tendency for wood debris to concentrate flow into channel banks and erode them. From differences in average channel cross-sectional area, Trimble infers that clearing of riparian forests can decrease downstream sediment loads, and thereby help to decrease the downstream effects of land management, because grass cover can protect banks against erosion and increase local sediment deposition. Although he acknowledges the danger of arguing from a single case study, Trimble warns that the restoration of riparian forests may not be good public policy.

These results and recommendations deserve close attention, as they run counter to the general understanding of the value and function of riparian forests. Indeed, another study[5] published earlier this year came to the opposite conclusion: that bank erosion in forest channels accounts for a significantly smaller percentage of the sediment yield than in comparable grassland channels.

The trouble with this topic, as exemplified by these seemingly contradictory findings, is that prediction of the response of natural water-courses to man-made or natural change is a classic under-constrained problem. Many interrelated variables are involved, which moreover are subject to complex feedback and threshold responses. These variables include the interplay of sediment supply, size and lithology; the magnitude and frequency of water discharge; the nature of bank materials; the absence, or presence and type of, vegetation on banks; and the effect of flow obstructions such as wood debris. The type of channel and its history of disturbance, and the drainage-basin context, also affect channel response. This smorgasbord of influences means that simple guidelines and blanket generalizations rarely provide a sound basis for the management of rivers and streams.

Take the highly variable influence of bank materials on bank erosion[6]. In channels with banks composed of cohesionless materials, for example, tree roots can substantially increase bank stability[5–8] (Fig. 1). Clearing of the forest to the river banks along the Tolt river, a high-energy, gravel-bed channel in the Cascade range of Washington, triggered extensive channel widening because of the loss of bank-stabilizing tree roots. This widening increased the sediment supply downstream of the affected area, which in turn caused a pulse of gravel aggradation. At a finer scale, field surveys along an undisturbed reach of the Tolt river[9] indicate that channel widening occurred only where log-jams diverted flow into banks. So scale also matters in assessing channel response; wood debris can cause local bank erosion within a channel reach in an area where the riparian forest overall maintains bank stability.

Figure 1 **The issue of whether the banks of streams and rivers are better left to revert to forest or not is a complicated one, for streamside trees can either stabilize or erode the banks on which they grow. An interlocking network of roots can increase bank strength and therefore resist erosion. But trees that fall into streams can divert flow and trigger scour and local bank erosion where they cause the water flow to converge; where they cause flow to diverge, local deposition and aggradation of sediment results. In spite of local bank erosion, the increased variability of channel widths due to wood debris in forest streams contributes to the maintenance of a more variable and complex range of habitats.**

In some forest channels, logs and log-jams trap large volumes of sediment[3,10,11] and offset sediment supplied from local bank scour. For example, channel-spanning log-jams on the Olympic peninsula, Washington state, can exceed 10 m in height, trap more than 10,000 m^3 of sediment, and significantly lower reach-scale channel slopes[11]. In these examples from channels with a mature riparian forest, the vertical storage of sediment impounded by organic debris outweighs storage lost from local channel widening. Log-jams also reduce rates of transport along the river bed by

decreasing energy gradients and increasing channel roughness[12,13]. Even if forest channels are somewhat wider than grassland channels, they may still act as net sediment sinks.

Despite conflicting reports of the effect of trees on channel width, there does seem to be one consistent observation — that bankside forests increase the variance in channel form. Variable channel width translates into a greater range of flow depth, velocity and substrate size, resulting in increased variability or complexity of habitats; all of these are features that in my experience serve as a mantra for stream ecologists. Hence, evaluation of geomorphological and ecological impacts may yield contradictory conclusions; in some cases a little extra erosion may provide a more varied, diverse and productive habitat.

Trimble's paper[4] illustrates the frustrating complexity facing those charged with managing, restoring and protecting the world's river systems. Single-recipe approaches provide a poor foundation for management of rivers and streams, in part because they often ignore connections between physical and biological processes. Moreover, coupling predictions of channel response to stream ecology and public-policy considerations further complicates an inherently challenging problem.

That leaves us with two distinct choices for ecologically orientated river management: either trust that 'natural is best' and promote restoration of riparian forests, or treat each river on a case-by-case basis. Trimble's cautionary thoughts on forest restoration would suggest the latter course of action. Unfortunately, few of those who work in this area receive the advanced training necessary to adequately understand and diagnose channel conditions. So, for now, perhaps it is wiser to favour nature's course. Continued research is needed into general models of channel response, and into the integration of fluvial geomorphology into river-system restoration and management. But the greater need is the establishment of a corps of river professionals whose expertise spans geomorphology, ecology and public policy. □

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Protein folding

The difference with prokaryotes

Mary-Jane Gething

When proteins are made, they start off as chains of polypeptides. The study of how they come to fold into their correct three-dimensional structure is a wonderfully complicated business that has been tackled in numerous ways. In their paper on page 343 of this issue[1], Netzer and Hartl explore a somewhat neglected approach — that of looking at differences in the folding pattern of nascent polypeptides in the cytoplasm of prokaryotic and eukaryotic cells. In doing so, they tell us a great deal about some basic issues to do with protein folding, but we need to step back a little to understand why.

Anfinsen's classic *in vitro* experiments on the refolding of ribonuclease[2,3] demonstrated that all of the information required to determine the final conformation of a protein can reside in the polypeptide chain itself: given the appropriate conditions, a denatured enzyme can refold into its native conformation in the absence of any other protein. Anfinsen's work was of seminal importance in establishing the central principle of self-assembly of proteins, but it probably delayed by a decade or two the initiation of investigations of protein folding *in vivo* — the trouble was we believed that the polypeptide sequence was all that there was to it. Nevertheless, over time we came to recognize that efficient folding *in vitro* is frequently limited to small, single-domain proteins and usually occurs under conditions of protein concentration, temperature, ionic strength and pH far removed from those occurring within cells.

The search for agents that support the folding of polypeptides under physiological conditions led to the characterization of a wide variety of molecular chaperones and folding catalysts that preside at the birth, maturation and death of most, if not all, proteins within cells[4,5]. These chaperones and folding catalysts do not determine the final conformation of the polypeptide substrate (Anfinsen rules OK!); rather, they increase the efficiency of folding by inhibiting off-pathway aggregation reactions or catalyse rate-limiting isomerization steps. They are members of large protein families, and are present in all cell types, from prokaryotes to humans, and in all compartments of eukaryotic cells. The high degree of conservation of the members of each family during evolution has lulled us into believing that the process of protein folding is likely to be mechanistically similar in different organisms. This is where the new work of Netzer and Hartl[1] comes in.

The original premise underlying their study was that evolution of eukaryotic proteins by gene fusion or exon shuffling demands that the newly combined domains must be able to fold independently of one another. Although this idea seems perfectly intuitive (at least in retrospect), to my knowledge its implications with respect to protein-folding mechanisms have not previously been tested. The study reveals that protein domains (which usually range from 100 to 300 amino acids in length) can indeed fold sequentially and independently when synthesized from a eukaryotic ribosome. In prokaryotes, however, folding of individual domains is delayed until the complete polypeptide chain has been synthesized. This latter situation can result in inappropriate interdomain interactions or aggregation — which are indeed often observed when complex eukaryotic proteins are synthesized in the prokaryote *Escherichia coli*.

Comparison of the protein-size profiles of different prokaryotic and eukaryotic organisms, made possible by the completion (or near completion) of sequence analyses of their genomes, reveals that prokaryotes may cope with this difficulty, at least in part, by restricting protein size and thus the complexity of protein-domain organization (see Fig. 1 of Netzer and Hartl's paper, page 343). Nevertheless, a lot of proteins in *E. coli* are more than 300 residues in length; many of them probably correspond to multifunctional proteins that have arisen by fusion of genes encoding the individual enzymatic activities or functions[6]. Given a post-translational mode of folding, such fusions would presumably have been productive only in cases where the individual domains could fold independently. In eukaryotes, however, the rapid evolution of multidomain proteins by gene fusion or exon shuffling (made possible following the development of complex genes) would not be restricted by any requirement that the component domains should not interfere with one another during the folding process.

Netzer and Hartl's work[1] also does much to resolve, intellectually if not mechanistically, a previously open question — why efficient protein folding in prokaryotes seems to rely so heavily and generally on the chaperonin GroEL, the eubacterial member of the Cpn60 (also known as Hsp60) family[5,7], whereas in the eukaryotic cytosol the chaperonin homologues (known as CCT[7,8] or TRiC[5]) appear to play a much more limited role. GroEL and its co-chaperonin GroES form a cylindrical complex that encloses a central cavity in which polypeptides can fold sequestered from the cellular environment[5]. The observation that most polypeptides synthesized in *E. coli* can associate with GroEL prior to folding (F. U. Hartl, unpublished observations) may reflect the fact that they