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E A C H   Y E A R, professional scientists scan thousands of titles, read hundreds of abstracts, and study a few papers in depth. Since titles are the commonest, and usually the only, form of contact between writers and potential readers in the great glut of scientific literature, catchy items are appreciated and remembered, but unfortunately rare. Every scientist has his favorite title. Mine was coined by paleontologist Albert E. Wood in 1957: "What, If Anything, Is a Rabbit?"

Wood's question may have been wry, but his conclusion was ringing: rabbits and their relatives form a coherent, well-defined order of mammals, not particularly close to rodents in evolutionary descent. I was reminded of Wood's title recently when I read a serious challenge to the integrity of a personal favorite among mammals: the zebra. Now don't get too agitated. I am not trying to turn the world of received opinion upside down. Striped horses manifestly exist. But do they form a true evolutionary unit? With "Stripes Do Not a Zebra Make"—a quite respectable title in its own right—Debra K. Bennett has forced us to extend Wood's question to another group of mammals. What, if anything, is a zebra?

Since evolutionary descent is our criterion for biological ordering, we define groups of animals by their genealogy. We do not join together two distantly related groups because their members have independently evolved some similar features. Humans and bottle-nosed dolphins, for exam-

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ple, share the pinnacle of brain size among mammals. But we do not, for this reason, establish the taxonomic group Psychozoa to house both species—for dolphins are more closely related by descent with whales, and humans with apes. We follow the same principles in our own genealogies. A boy with Down's syndrome is still his parents' son and not, by reason of his affliction, more closely related to other Down's children, no matter how long the list of similar features.

The potential dilemma for zebras is simply stated: they exist as three species, all with black-and-white stripes to be sure, but differing notably in both numbers of stripes and their patterns. (A fourth species, the quagga, became extinct early in this century; it formed stripes only on its neck and forequarters.) These three species are all members of the genus *Equus*, as are true horses, asses, and donkeys. (In this essay, I use "horse" in the generic sense to specify all members of *Equus*, including asses and zebras. When I mean Old Dobbin or Man o' War, I will write "true horses.") The integrity of zebras then hinges on the answer to a single question: Do these three species form a single evolutionary unit? Do they share a common ancestor that gave rise to them alone and to no other species of horse? Or are some zebras more closely related by descent to true horses or to asses than they are to other zebras? If this second possibility is an actuality, as Bennett suggests, then horses with black-and-white stripes arose more than once within the genus *Equus*, and there is, in an important evolutionary sense, no such thing as a zebra.

But how can we tell, since no one witnessed the origin of zebra species (or at least australopithecines weren't taking notes at the time), and the fossil record is, in this case, too inadequate to identify events at so fine a scale. During the past twenty years, a set of procedures has been codified within the science of systematics for resolving issues of this kind. The method, called cladistics, is a formalization of procedures that good taxonomists followed intuitively but did not properly express in words, leading to endless quibbling and fuzziness of concepts. A clade is a branch on an

evolutionary tree, and cladistics attempts to establish the pattern of branching for a set of related species.

Cladistics has generated a fearful jargon, and many of its leading exponents in America are among the most contentious scientists I have ever encountered. But behind the names and nastiness lies an important set of principles. Still the clear formulation of principles does not guarantee an unambiguous application in each case—as we shall see for our zebras.

I believe that we can get by with just two terms from the bounty offered by cladists. Two lineages sharing a common ancestor from which no other lineage has sprung form a *sister group*. My brother and I form a sister group (pardon the confusion of gender) because he is my only sib and neither of my parents had any other children.

Cladists attempt to construct hierarchies of sister groups in order to specify temporal order of branching in evolutionary history. For example: gorillas and chimpanzees form a sister group because no other primate species branched from their common ancestor. We may then take the chimp-gorilla sister group as a unit and ask which primate forms a sister group with it. The answer, according to most experts, is us. We now have a sister group with three species, each more closely related to its two partners than to any other species.

We may extend this process indefinitely to form a chart of
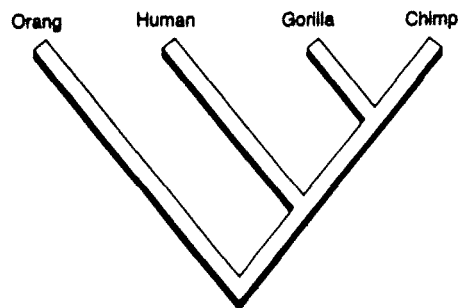
The cladistic pattern of great apes and humans. REPRINTED FROM NATURAL HISTORY. DRAWING BY JOE LE MONNIER.

branching relationships called a cladogram. But consid-
er just one more step: What primate species is the sister
group to the human-chimp-gorilla unit? Conventional wis-
dom cites the orangutan, and we add it to our cladogram.

This cladogram of "higher" primates contains an interest-
ing implication: there is no such thing as an ape, at least as
usually defined. Several species of primates may swing
through trees, eat bananas in zoos, and form good proto-
types for science fiction of various sorts. But orangs, chimps,
and gorillas (the "apes" of our vernacular) are not a genea-
logical unit because orangs are cladistically more distant
from chimps and gorillas than humans are—and we origi-
nally defined the term ape to contrast some lesser forms with
our exalted state, not to include us!

The zebra problem can also be placed in this context. If
the three species of zebras form a sister group (as humans,
chimps, and gorillas do on our cladogram), then each is
more closely related to its two partners than to any species
of horse, and zebras form a true evolutionary unit. But if
zebras are like "apes," and another species of horse lies
within the cladogram of zebras (as humans lie within the
cladogram of traditional apes), then striped horses may
share some striking similarities meriting a common vernac-
ular term (like zebra), but they are not a genealogical unit.

But how do we identify sister groups correctly? Cladists
argue that we must search for—and here comes the second
term—*shared derived characters* (technically called synapo-
morphies). Primitive characters are features present in a
distant common ancestor; they may be lost or modified
independently in several subsequent lineages. We must be
careful to avoid primitive characters in searching for com-
mon features to identify sister groups, for they spell nothing
but trouble and error. Humans and many salamanders have
five toes; horses have one. We may not therefore state that
humans are more closely related to salamanders than to
horses, and that the concept of "mammal" is therefore a
fiction. Rather, five toes is an inadmissible primitive charac-
ter. The common ancestor of all terrestrial vertebrates had
five toes. Salamanders and humans have retained the origi-

nal number. Horses—and whales and cows and snakes and a host of other vertebrates—have lost some or all of their toes.

Derived characters, on the other hand, are features present *only* in members of an immediate lineage. They are unique and newly evolved. All mammals, for example, have hair; no other vertebrate does. Hair is a derived character for the class Mammalia because it evolved but once in the common ancestor of mammals and therefore identifies a true branch on the family tree of vertebrates. Shared derived characters are held in common by two or more lineages and may be used to specify sister groups. If we wish to identify the sister group among tunas, seals, and bobcats, we may use hair as a shared derived character to unite the two mammals and to eliminate the fish.

For zebras, the question then becomes: Are stripes a shared derived character of the three species? If so, the species form a sister group and zebras are a genealogical unit. If not, as Bennett argues, then zebras are a disparate group of horses with some confusing similarities.

The method of cladistics is both simple and sensible: establish sequences of sister groups by identifying shared derived characters. Unfortunately, conceptual elegance does not guarantee ease of application. The rub, in this case, lies in determining just what is or is not a shared derived character. We have some rough guidelines, and some seat-of-the-pants feelings, but no unerring formulas. If derived characters are sufficiently "complex," for example, we begin to feel confident that they could not have evolved independently in separate lineages and that their mutual presence therefore indicates common descent.

Chimps and gorillas share a set of complex and apparently independent modifications in several of their chromosomes (mostly "inversions," literally, the turning around of part of a chromosome by breaking, flipping, and reattaching). Since these chromosomal changes are complex and do not seem to represent "easy" modifications so adaptively necessary that separate lineages might evolve them independently, we mark them as shared derived characters pre-

sent in the common ancestor of chimps and gorillas, and in no other primate. Hence they identify chimps and gorillas as a sister group.

Unfortunately, most derived characters are more ambiguous. They tend to be either easy to construct or else so advantageous that several lineages might evolve them independently by natural selection. Many mammals, for example, develop a sagittal crest—a ridge of bone running along the top of the skull from front to back and serving as an attachment site for muscles. Most primates do not have a sagittal crest, in part because large brains make the cranium bulge and leave neither room nor material for such a structure. But a general rule for scaling of the brain in mammals holds that large animals have relatively smaller brains than relatives of diminished body size (see essays in *Ever Since Darwin* and *The Panda's Thumb*). Thus, the largest primates have a sagittal crest because their relatively small brains do not impede its formation. (This argument does not apply to the great oddball *Homo sapiens*, with an enormous brain despite its large body.) The largest australopithecine, *Australopithecus boisei*, has a pronounced sagittal crest, while smaller members of the same genus do not. Gorillas also have a sagittal crest, while most smaller primates do not. We would make a great error if, using the sagittal crest as a shared derived character, we united an australopithecine with a gorilla in a sister group and linked other, smaller-bodied australopithecines with marmosets, gibbons, and rhesus monkeys. The sagittal crest is a "simple" character, probably part of the potential developmental repertoire for any primate. It comes and goes in evolution, and its mutual presence does not indicate common descent.

Bennett bases her cladistic analysis of the genus *Equus* on skeletal characters, primarily of the skull. All horses are pretty much alike under the skin, and Bennett has not found any shared derived characters as convincing as the chromosomal similarities of chimps and gorillas. Most of her characters are, by her own admission, more like the sagittal crest—hence the provisional nature of her conclusions.

Bennett argues that the genus *Equus* contains two major

cladistic groups—donkeys and asses on one side and true
horses and zebras on the other. Thus, zebras pass the first
test for consideration as a genealogical unit. Unfortunately
(or not, according to your point of view), Bennett claims
that they fail the second test. She does identify the Burchell
and Grevy zebras (*Equus burchelli* and *E. grevyi*) as a sister
group. But in her scheme, the third species, the mountain,
or Hartmann, zebra (*E. zebra*) does not join its cousins to
form a larger sister group. Instead, the sister species of the
mountain zebra is our close compatriot in farm and track,
the true horse (*E. caballus*)! Thus, mountain zebras join with
true horses before they connect with other zebras. Old Dob-
bin is inextricably intercalated within the cladogram of ze-
bras—and since he is not a zebra by any definition, then
what, if anything, is a zebra?

But Bennett's analysis is based upon only three characters,
none very secure. All are potentially simple modifications of
shape or proportion, not presences or absences of complex
structures. All, like the sagittal crest, could come and go.
Only one potential shared derived character unites true
horses with *E. zebra:* the "orientation of postorbital bars
relative to horizontal plane" (a relatively less slanted posi-
tion for a bar of bone located on the skull behind the eyes—
not exactly the stuff of which confident conclusions are
made). Only two potential shared derived characters unite

Equus burchelli (Burchell's zebra)

Equus zebra (mountain zebra)

Equus grevyi (Grevy's zebra)
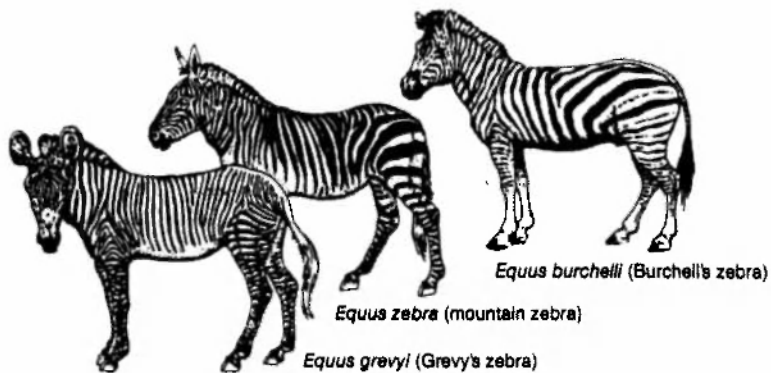
Burchell and Grevy zebras: the presence of frontal doming
(inflation of the top part of the skull) and relative skull
breadth (these two zebras have long and narrow snouts).
Unfortunately, we know that at least one of these characters
doesn't work well for Bennett's cladistic scheme because she
admits that a member of her other lineage—a horse with the
peculiar moniker of the Asiatic half-ass (*E. hemionus*)—has
independently evolved a long, narrow snout. If twice, why
not three times?

When we look for corroboration to an obvious source—
numbers of chromosomes—we are again disappointed. As I
discussed in essay 26, the various species of horses, despite
their marked similarities of form, differ greatly in number of
chromosomes. Fusion or fission of chromosomes may be a
major mechanism of speciation in mammals, and these diff-
erences may therefore have great evolutionary significance.
All zebras, and only zebras, have fewer than fifty pairs of
chromosomes (thirty-two in Hartmann's zebra to forty-six in
Grevy's zebra). All other horses have more than fifty (from
fifty-six in *Equus hemionus* to sixty-six in Przewalski's horse).
The low number of zebras might mark them as a genealogi-
cal group if the character is shared derived, and not either
primitive or evolved more than once. Bennett's hypothesis
may still be maintained by arguing either that small numbers
are primitive for all horses and that asses and true horses
acquired larger numbers by independent evolutionary
routes; or that different lineages of zebras evolved small
numbers along separate evolutionary paths. Still, since we
have no reason to associate stripes with small numbers of
chromosomes, their conjoined presence in all zebras might
best be interpreted as a sign of genealogy. The more com-
plex characters that a group shares, the more likely that the
group is genealogical—unless we have good reason to re-
gard all the characters as primitive (and we do not in this
case).

I conclude that Bennett's proposal is interesting, but very
much unproven. Suppose, however, that she is right. What
then would a zebra be? Or more specifically, how did cladis-
tically unrelated horses get black-and-white stripes? There

are two possibilities. Either the common ancestor of zebras and true horses had stripes and true horses lost them, while the three species of "zebras" passively retained them; or else, striping is an inherited developmental capacity of all horses and not so complex a character as it appears. In this case, several separate lineages could acquire stripes independently. Zebras would then be horses that have realized a potential pathway of development probably common to many or all members of the genus *Equus* (see next essay).

This particular tale of zebras may not hold, but the radical messages of cladistic ordering are secure in many cases. Some of our most common and comforting groups no longer exist if classifications must be based on cladograms. With apologies to Mr. Walton and to so many coastal compatriots in New England, I regret to report that there is surely no such thing as a fish. About 20,000 species of vertebrates have scales and fins and live in water, but they do not form a coherent cladistic group. Some—the lungfishes and the coelacanth in particular—are genealogically close to the creatures that crawled out on land to become amphibians, reptiles, birds, and mammals. In a cladistic ordering of trout, lungfish, and any bird or mammal, the lungfish must form a sister group with the sparrow or elephant, leaving the trout in its stream. The characters that form our vernacular concept of "fish" are all shared primitive and do not therefore specify cladistic groups.

At this point, many biologists rebel, and rightly I think. The cladogram of trout, lungfish, and elephant is undoubtedly true as an expression of branching order in time. But must classifications be based only on cladistic information? A coelacanth looks like a fish, tastes like a fish, acts like a fish, and therefore—in some legitimate sense beyond hidebound tradition—*is* a fish.

No debate in evolutionary biology has been more intense during the past decade than the challenge raised by cladistics against traditional schemes of classification. The problem arises from the complexity of the world, not from the fuzziness of human thought (although woolliness has made its usual contribution as well). We must recognize two rather

different components to our vernacular conception of "similarity" between organisms—and classifications are designed to reflect relative degrees of similarity. On the one hand, we must consider genealogy, or branching order. Cladistics works with branching order alone, rigorously excluding any other notion of similarity. But what about the admittedly vague and qualitative, but not therefore unimportant, notion of overall similarity in form, function, or biological role? The coelacanth, to say it again, looks and acts like a fish even if its closer cladistic relatives are mammals. Another theory of classification, called phenetics—from a Greek word for appearance—focuses on overall similarity alone and tries to escape the charge of subjectivity by insisting that phenetic classifications be based upon large suites of characters, all expressed numerically and processed by computer.

Unfortunately, these two types of information—branching order and overall similarity—do not always yield congruent results. The cladist rejects overall similarity as a snare and delusion and works with branching order alone. The pheneticist attempts to work with overall similarity alone and tries to measure it in the vain pursuit of objectivity. The traditional systematist tries to balance both kinds of information but often falls into hopeless confusion because they really do conflict. Coelacanths are like mammals by branching order and like trout by biological role. Thus, cladists buy potential objectivity at the price of ignoring biologically important information. And traditionalists curry confusion and subjectivity by trying to balance two legitimate, but often disparate, sources of information. What is to be done?

I cannot answer this question, for it raises issues of style, mores, and methodology more than demonstrable substance. But I can at least comment on the source of this bitter debate—a rather simple point that somehow got lost in the heat. In an ideal world, there would be no conflict among the three schools—cladistics, phenetics, and traditional—and all would produce the same classification for a given set of organisms. In this pipe-dream world, we would find a perfect correlation between phenetic similarity and recency of com-

mon ancestry (branching order); that is, the longer ago two groups of organisms separated from a common ancestor, the more unlike they would now be in appearance and biological role. Cladists would establish an order of branching in time by cataloging shared derived characters. Pheneticists would crunch their numerous measures of similarity in their favorite computers and find the same order because the most dissimilar creatures would have the most ancient common ancestors. Traditionalists, finding complete congruence between their two sources of information, would join the chorused harmony of agreement.

But let the reverie halt. The world is much more interesting than ideal. Phenetic similarity often correlates very poorly with recency of common ancestry. Our ideal world requires a constancy of evolutionary rate in all lineages. But rates are enormously variable. Some lineages change not at all for tens of millions of years; others undergo marked alterations in a mere thousand. When the forebears of terrestrial vertebrates first split off from a common ancestry with coelacanths, they were still unambiguously fish in appearance. But they have evolved, along numerous lines during some 250 million years, into frogs, dinosaurs, flamingos, and rhinoceroses. Coelacanths, on the other hand, are still coelacanths. By branching order, the modern coelacanth may be closer to a rhino than a tuna. But while rhinos, on a rapidly evolving line, are now markedly different from that distant common ancestor, coelacanths still look and act like fish—and we might as well say so. Cladists will put them with rhinos, pheneticists with tunas; traditionalists will hone their rhetoric to defend a necessarily subjective decision.

Nature has imposed this conflict upon science by decreeing, through the workings of evolution, such unequal rates of change among lineages and such a poor correlation between phenetic similarity and recency of common ancestry. I do not believe that nature frustrates us by design, but I rejoice in her intransigence nonetheless.