A NEW AGE OF DISCOVERY[1]

Michael J. Donoghue[2] *and William S. Alverson*[2,3]

ABSTRACT

Whereas past ages of discovery have been associated with the exploration of new continents, the current episode is marked by exploration at smaller spatial scales and in more extreme habitats, some of which are surprisingly close at hand. This new age of discovery is richer and more illuminating by virtue of the attention being paid to phylogenetic relationships and geographic ranges. Although it is difficult to quantify progress in understanding the tree of life or biogeographic patterns, a series of examples illustrates that the magnitude and significance of recent discoveries are unquestionably great. Extraordinary discoveries provide an obvious, yet underutilized, mechanism to capture the imagination of the scientific community and the public at large.

Key words: age of discovery, biodiversity, biogeography, exploration, new species, phylogeny.

We tend to regard "the age of discovery" as something long since past. Whether the phrase refers to the colonization of North America by trans-Beringian migrants, arrival of the Moa Hunters and Maoris in New Zealand, or (most likely) the forays of European explorers into the New World from the 15th century onward, depends on one's sense of history and focus. However, there may be general attributes of all previous epochs with which we can evaluate whether any particular period really qualifies as an age of discovery. We will argue that the present era most certainly deserves this title.

Briefly consider the most recent of these ages of discovery, which began in the late 1400s. European exploration of the Americas, Australia, Africa, and the South Pacific brought to light an extraordinary number of new species. Even more importantly, these were species quite unlike any known before: the rhinocerous (Fig. 1), the kangaroo, and the dodo, to name only a few. David Quammen (1996) helps us imagine what it must have been like to hear about or see such animals for the first time:

> ". . . the first report of a hummingbird, . . . of a toucan, . . . of giant anteaters and sloths and vicunas . . . first report of the American bison, a giant-headed animal almost too majestic to be real. Imagine how these prod-

igies must have unnerved a complacently pious sixteenth-century European."

How can the present day possibly compare either in terms of the number of novelties being discovered or their "surprisingness"?

NEW SPECIES

In most major lineages the number of new species being described is not falling off. Instead, the numbers have actually been rising over the last decade to levels comparable to those of the mid-18th to late 19th century (before which comparisons are difficult, since formal rules for naming species had not been developed). Surprisingly, perhaps, this includes the groups that we tend to think of as being the best known. For example, the description of new mammal species is on the rise (Wilson & Reeder, 1993), and this is not, as one might initially suppose, primarily due to the splitting of known species as a consequence of using molecular markers. Instead, it appears to be directly correlated with serious exploration of new areas (Morell, 1996). For instance, fieldwork over the last decade in the Annamite mountains on the border of central Vietnam and Laos has brought to light several large
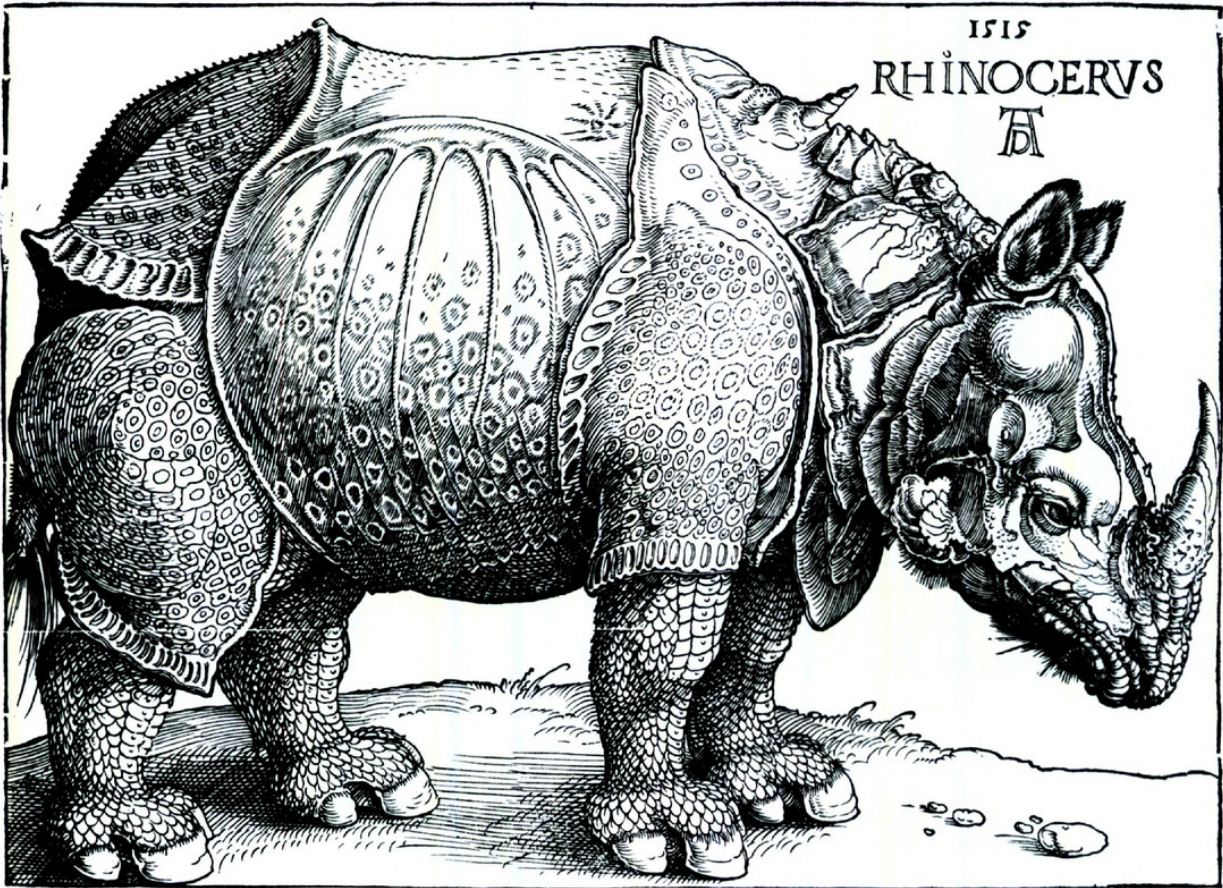
Men vintſe te coope by Hendrick Hondius Plaetſnijder in s'Gravenhage.

Figure 1.   The fantastic rhinoceros, as conceived by Albrecht Dürer at the time these animals were first discovered by Europeans. [Reprinted, with permission, from an original print at the Agnes Mongan Center, Fogg Art Museum, Harvard University Art Museums.] Nearly two centuries later, upon seeing a rhinocerous, John Evelyn remarked, "It more ressembled a huge enormous Swine, than any other Beast amongst us ... but in my opinion nothing was so extravagant as the Skin of the beast, which hung downe on her ha[u]nches ... loose like so much Coach leather ... and these lappets of stiff skin, began to be studdied with impenetrable Scales, like a Target of coate of maile, loricated like Armor.... T'was certainly a very wonderful creature, of immense strength in the neck and nose especially" (Evelyn, 1684).

mammals—a species of bovid, *Pseudoryx nghetin-hensis* (Dung et al., 1993), and at least three species of muntjac deer (Schaller & Vrba, 1996; Giao et al., 1998; MacKinnon, 2000 this issue). Moreover, the rate of description of new mammal species has risen despite decreased attention to taxonomy and a documented increase in the time between discovery and description (Patterson, 1994).

Amphibians provide another well-documented example of the rising rate of species description (Glaw & Köhler, 1998; see Fig. 2). Again, this reflects, to a considerable extent, the discovery of novelties in the wild, rather than the application of molecular methods or changes in species concepts. Hanken (1999) documented this point, citing David Wake's (1996) discovery of a new lungless salamander from the San Gabriel mountains, less than 30 miles from Los Angeles, as well as species de-

scribed in 1998 from Brazil, Mexico, Nepal, and New Zealand.

The same trends in discovery (if not formal naming) doubtlessly apply in less well studied groups, such as plants, fishes, insects, mites, nematodes, and especially Bacteria (eubacteria) and Archaea (archaebacteria, e.g., Pace, 1997; Fuhrman & Campbell, 1998; Madigan, 2000 this issue), although reliable estimates are harder to come by (e.g., see Gaston, 1991, on insects; Prance et al., 2000 this issue, on vascular plants). If there were more taxonomists, and if the lag time between the discovery and naming of new taxa were shorter, then the rate of description would surely be far higher. Many new species have already been collected, or are already known to be new, but remain undescribed simply for lack of expertise and time. Plant monographers, for example, can show any cu-
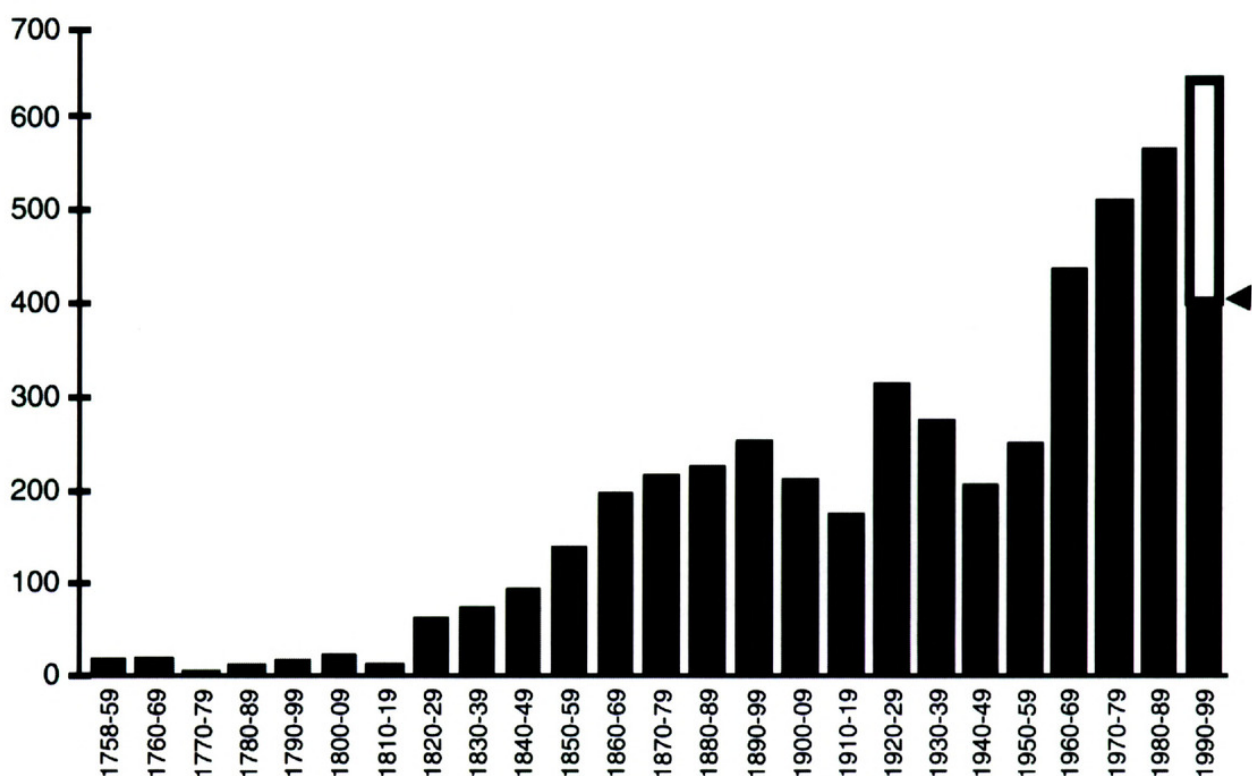
Figure 2. Amphibian species descriptions since 1758 (synonyms not included), clustered by decade, from Glaw and Köhler (1998). The arrow indicates the end of 1995; descriptions for the period 1996–1999 were extrapolated.

rious visitor a nearby specimen cabinet containing undescribed species.

By the criterion of the number of new species being described, we believe that the present compares favorably with any time since the mid-1700s. But how surprising are the new species that are being discovered in the late 20th century? Are we finding anything significantly different, or are we just filling gaps in an already well-known range of variation? John Horgan, author of *The End of Science* (published by Helix Books, in 1996), presents the latter view:

"We are down to the details now. Every now and then something interesting will turn up. We will find a new species of lemur in Madagascar, or weird bacteria living in deep-sea vents. But at this point we are unlikely to discover something really surprising . . ." (J. Horgan, 1998).

This will sound absurd to those actively engaged in the discovery of new life forms, but such a "dotting the i's and crossing the t's" assessment of the situation is widespread both within the scientific community and the public at large.

To counter Horgan's naive but evidently persuasive claim, we need to consider criteria whereby a new species would qualify as "really surprising." Perhaps the primary criterion should be whether a new species fundamentally expands the way we

think about the diversity and evolution of life. Unfortunately, this is much harder to quantify than counting the number of published descriptions of new species.

NEW PHYLA, ETC.

One possible indicator of the distinctiveness of newly discovered life forms, or perhaps of their informativeness with respect to our understanding of evolution, is the rate of description of new higher taxa. As Brusca (2000 this issue) shows, the description of new animal phyla does not appear to have diminished in recent years. Species are still being discovered that are considered by the relevant taxonomic communities to be as distinct as the familiar phyla are from one another. The major difference is that these new organisms are, on the whole, smaller, which means we are having to look more closely. Sometimes, as in the case of *Nanaloricus mysticus* of the recently described metazoan phylum Loricifera (Kristensen, 1983), this has entailed careful scrutiny of an obscure (though certainly widespread!) habitat—between sand grains on the ocean floor. In other cases new life forms have been found more or less right under our noses. *Symbion pandora*, a metazoan animal referred to the new Cycliophora, was described in 1995 from

a specimen collected on the mandible of a Norwegian lobster (Funch & Kristensen, 1995).

New "classes" of animals, sometimes with enormous significance for our understanding of major lineages, are also still being described at a regular pace. Examples include the Remipedia within Crustacea, discovered in a marine cave in the Bahamas (Yager, 1981), and the Concentricycloidea within echinoderms, found on waterlogged wood in deep waters off the coast of New Zealand (Baker et al., 1986).

In angiosperms there are excellent examples, mainly in the form of new families erected to accommodate extraordinary new species. For example, recall the excitement generated by *Ticodendron incognitum* Gómez-Laur. and L. D. Gómez (Ticodendraceae) from Costa Rica (Gómez-Laurito & Gómez P., 1989, 1991), and the subsequent realization that these trees occupy wet montane forests from southern Mexico to central Panama (Hammel & Burger, 1991). But the most spectacular case is probably *Lacandonia schismatica* E. Martínez and Ramos. This species of Triuridaceae-like monocot was described in 1989 in the new family Lacandoniaceae from material collected in the Lacandon region of Chiapas, Mexico (Martínez & Ramos, 1989). Astonishingly, its stamens are on the very inside of the flower (at the apex of the receptacle), surrounded by the carpels (Márquez-Guzmán et al., 1989; see Fig. 3a). This discovery, only a few years ago, came as a complete surprise—nothing about the other ca. 250,000 species of angiosperms predicted this brand new flower architecture. It also provides a unique opportunity to test the "ABC model" for genetic determination of flower organ identity (Coen & Meyerowitz, 1991; Vergara et al., 1999).

NOT PHYLA, ETC.

If the description of higher taxa were our only means of assessing the surprisingness of recent discoveries, we would miss many of the most exciting finds. The several examples below highlight radically new life forms (as different, we believe, as those discussed above), which were described only as new genera or as species within existing genera. These cases provide a dramatic reminder of the arbitrary nature and inadequacy of the Linnaean ranks—even in gauging the degree of disparity, which ranks are most often thought to represent.

In 1995, with very little fanfare, Dennis Desjardin and his colleagues described "an unusual psychrophilic aquatic agaric from Argentina" within the existing fungal genus *Gloiocephala* (Tricholom-

ataceae). This remarkable new species, *G. aquatica*, develops its fruiting bodies and spores underwater, often beneath a layer of ice covering lakes in a zone between the Patagonian steppes and the Andes. As it appears to be the only known agaric to sporulate underwater, the term "unusual" is clearly an understatement—this is a brand-new way of being a mushroom. A similar discovery was also made in gastromycetes. In 1976, Escobar et al. described the genus *Limnoperdon* to accommodate the only known "aquatic" (actually, floating) puffball, which they found in marshes adjacent to the University of Washington in Seattle.

Amphibians also provide excellent examples of recently discovered lifestyles. In 1973, a new genus and species of leptodactylid frog, *Rheobatrachus silus*, was described on the basis of animals found in streams near Brisbane, Australia (Liem, 1973). Shortly thereafter, Corben et al. (1974) documented that *Rheobatrachus* exhibited a unique form of parental care. Brooding of the embryos and young takes place inside the stomach until the tadpoles or juvenile frogs are eventually (some eight weeks after ingestion) "propulsively ejected" through the mouth. This brooding mechanism is otherwise completely unknown in vertebrates. Furthermore, it requires special physiological mechanisms to turn off the secretion of gastric juices, which otherwise would kill the young. In 1983, Tyler et al. reported that prostaglandin secreted by the larvae inhibit acid production in the female's stomach "in a manner not seen elsewhere in the Animal Kingdom." Despite the potential medical significance of this remarkable phenomenon, further study will not be possible. *Rheobatrachus silus* appears to be extinct in the wild (Laurance et al., 1996).

In 1996, Nussbaum and Wilkinson described a new species and genus of caecilian (Amphibia: Gymnophiona), *Atretochoana eiselti*. As they documented (also see Wilkinson & Nussbaum, 1997), this is the largest lungless terapod, by far! It is 74–80 cm in length, while the next largest, a plethodontid salamander, is about ⅓ this size, at around 28 cm. The mouth is not connected to the nasal cavity in this animal, and its many other weird cranial features allow an exceptionally wide gape (see Fig. 4). These modifications are presumably associated with a novel feeding mechanism, but the natural history of these organisms is completely unknown. In fact, this extraordinary beast was "discovered" in a museum in Vienna and was known from only a single specimen collected from an unknown South American locality sometime in the last century. Now, another specimen has been located, this time in a jar in a Brazilian collection

Figure 3. Counterclockwise, from upper left. —a. Flower of *Lacandonia schismatica* (Lacandoniaceae, Triuridales), with three centrally positioned stamens surrounded and partially obscured by many papillose carpels. Photo courtesy of R. E. Alvarez-Buylla, E. Meyerowitz, and F. Vergara. —b. *Chrysaora achlyos* off the coast of northern Baja California, Mexico, in July 1989. The bell diameter is ca. 1 m and the combined oral arms, extending beyond the frame of photograph, are approximately 6 m long. Photo used with permission of J. Martin and Howard Hall Productions. —c. *Squamanita contortipes* parasitizing a host mushroom, probably *Galerina cerina*. Photo by S. A. Redhead.

(Wilkinson et al., 1998). Ironically, it, too, lacks a specific collection locality.

Other newly discovered species highlight how much we still have to learn. From Bacteria, consider *Prochlorococcus*, discovered only about a decade ago. Of great interest owing to the presence of both chlorophyll a and b (as in green plants), it is known now to be a major component of the phytoplankton in tropical and subtropical seas, and among the world's most important primary producers (see Fuhrman & Campbell, 1998). Moreover, the ability of *Prochlorococcus* to thrive in a wide range of light conditions seems to be explained by the existence of closely related but quite distinct species, living at different depths (Moore et al., 1998). Also of potentially huge ecological significance are new disease-causing bateria. For example, a newly discovered species of proteobacterium (related to

Figure 4. Lateral view of the head of the lungless caecilian *Atretochoana eiselti*. Its odd skull shape may reflect relaxed constraints on aspects of skull architecture involved with respiration and selection for increased gape size for prey capture. Photo by R. Nussbaum, from Wilkinson and Nussbaum (1997).

Sphingomonas) seems to be causing massive coral die-offs in Florida's reef communities (Richardson et al., 1998).

One of our favorite metazoan examples is the scyphozoan jellyfish *Chrysaora achlyos* (see Fig. 3b). This species was described by Joel Martin and colleagues in 1997, based on four specimens collected off the coast of southern California in the fall of 1989, and some photographs from northern Baja California (Martin et al., 1997). One of several species in this genus, *C. achlyos* is remarkable by virtue of being enormous. In fact, with a bell measuring over 1 m in diameter, this is the largest invertebrate described in this century, rivaled in size only by the giant squid and an arctic jellyfish described in the 1800s (J. Martin, pers. comm.). Although thousands washed ashore in 1989, it has not been seen since.

From vertebrates comes the story of the salamander *Eurycea sosorum*. This species was described in 1993 from specimens collected in the Barton Springs Aquifer, within the city of Austin, Texas (Chippendale et al., 1993). Known only from a single popular swimming spot, and therefore in

grave danger of extinction, this species continues to attract considerable attention in Austin. Subsequent exploration of nearby springs, some located within Austin housing developments, has turned up dozens of new species (D. Hillis, pers. comm.). Description of these species, from a relatively small area well endowed with herpetologists, will increase the number of described salamanders of the world by about seven percent!

Just as numerous new amphibians are coming to light, so, too, are novel pathogens that prey upon them (Hanken, 1999). A new genus and species of chytrid fungus, *Batrachochytrium dendrobatidis*, described very recently (Longcore et al., 1999), appears to be a major proximate cause of mass mortality events in frogs around the world (Berger et al., 1998; Morell, 1999). Being the only chytrid known to prey on vertebrates, this new species also greatly expands our understanding of a major and ubiquitous fungal group (Longcore et al., 1999; Pessier et al., 1999).

Seed plants also provide fine examples. *Wollemia nobilis* W. G. Jones, K. D. Hill & J. M. Allen, the sister group of *Agathis* (Gilmore & Hill, 1997) or

possibly all other Araucariaceae (Setoguchi et al., 1998), and closely resembling a fossil known from the Cretaceous through the Oligocene, was discovered in 1994 growing in the Wollemi National Park, ca. 200 km northwest of Sydney, Australia (Jones et al., 1995; Briggs, 2000 this issue). How could a large tree, with such distinctive architecture, growing near the largest city in Australia, have escaped detection until 1994?

At about the same time, Andrew Douglas and colleagues were realizing that collections of an odd proteaceous tree made in the 1960s and 1980s from northeastern Queensland represented a new species, *Eidothea zoexylocarya* A. W. Douglas & B. Hyland. These 40-m-tall plants, seemingly endemic to rainforests in the Bloomfield River watershed, are the sole representatives of an apparently basal lineage of Proteaceae, the Eidotheoideae (Douglas, 1995; Douglas & Hyland, 1995). Its fruits are nearly identical to 60-million-year-old fossils of *Xylocaryon lockii* F. Muell. (Holden, 1995).

Neviusia cliftonii Shevock, Ertter & D. Taylor (Rosaceae, Kerrieae) provides a similar example (Ertter, 2000 this issue). This species was described in 1992 from material collected south of Mount Shasta in northern California (Shevock et al., 1992). Although it is a rather conspicuous and locally abundant shrub and grows at several localities in an area where the vegetation had previously been mapped, it seems never to have been collected before 1992. As the authors speculated, the abundance of poison-oak in the vicinity may have been enough to discourage thorough exploration. Judging by its resemblance to an Eocene fossil from British Columbia, *N. cliftonii* is probably a relict in this area (Shevock et al., 1992). Its closest living relative, *Neviusia alabamensis* A. Gray, is known from only a few localities in Alabama and Arkansas.

ATTENTION TO PHYLOGENY

The ongoing age of discovery differs importantly from earlier episodes by virtue of the attention being paid to phylogeny. The phylogenetic notion of relationship was nonexistent before the mid-1800s, and not until recently have new methods and sources of evidence allowed rigorous and (we trust) increasingly accurate phylogenetic inferences. Although biodiversity is still commonly equated with the enumeration of species (and genetic diversity within species), the idea has now expanded. Biodiversity is not just about species, at the tips of the tree, but about the whole tree of life. Thus, finding any branch of the tree, external or internal, consti-

tutes a genuine act of discovery. Viewed in this light, it is counterproductive to draw too strong a boundary between discovering species and discovering clades. These activities are pieces of the same underlying project, namely, understanding the entire tree of life.

Addition of this phylogenetic dimension makes the ongoing age of discovery far richer, and certainly far more powerful in connection with practical problems such as, for example, the choice and design of nature reserves and the search for useful natural products. In general, knowledge of phylogenetic relationships brings with it the power of prediction. Phylogenetic research should therefore be viewed as a welcome addition to, rather than a competitor with, the study of species diversity.

Consequently, it is of great interest to consider, as we have for species, both the rate of discovery of new clades and the surprisingness of these new discoveries. Unfortunately, we know of no straightforward way to quantify these things. There is little baseline information regarding the rate of discovery, and databases such as TreeBASE (http://phylogeny.harvard.edu/treebase), which could eventually be a ready source of such information, have grown too unevenly to provide an accurate measure of clade discovery. Nevertheless, the rate appears to be growing exponentially, and shows no signs of tapering off (Sanderson et al., 1993). At least this is the case if the number of clades being discovered grows in proportion to the rapidly increasing number of phylogenetic analyses being published, which we have no reason to doubt.

In theory, one might approximate the rate of discovery by tallying new names applied to clades, but at present this information is not being databased consistently enough. However, it is important to appreciate that even if this were now possible, the number of clades actually being named is far less than the number of clades being discovered, or even the number of clades identified with great confidence. Reluctance to formally name clades stems in part from the traditional Linnaean nomenclatural system's emphasis on the assignment of taxonomic rank, and the potential consequences of such assignments on the application of names at other levels (Baum et al., 1998; Hibbett & Donoghue, 1998). Related to this is the realization that there are not enough familiar ranks in the Linnaean system to do justice to the many nested clades being discovered even in average-sized phylogenetic analyses. In practice, the current nomenclatural codes (e.g., Greuter et al., 1994) encourage formally naming clades only after relationships throughout the group in question have been rather well estab-

lished, as opposed to encouraging the naming of well-supported new clades as they are discovered, usually one or a few at a time (Hibbett & Donoghue, 1998).

The surprisingness of recent discoveries is also hard to judge because prior views on relatedness have often not been expressed unambiguously enough. Nevertheless, it is clear that many entirely unexpected discoveries have been made. We now appreciate, for example, that "prokaryotes" are not a single branch, but two (or more) major branches, with lineages of Archaea probably more closely related to eukaryotes than they are to Bacteria (e.g., Pace, 1997). Likewise, we can say with growing confidence that animals and fungi (Baldauf & Palmer, 1993; Wainright et al., 1993), and possibly also slime molds (Baldauf & Doolittle, 1997), are more closely related to one another than they are to plants or any other eukaryotes.

While these are obviously major advances in our understanding of life, such discoveries may not seem terribly surprising since relationships of the major lines of life have always seemed obscure. What about within metazoan animals and green plants, where phylogenetic theories have been better developed—have any really surprising results emerged from recent studies?

The answer is an unambiguous yes! Relationships among major metazoan lineages have come into much sharper focus, and a number of traditional views have been overturned. For example, whereas it has long been assumed that annelids are more closely related to arthropods than they are to molluscs (as evidenced by segmentation and the existence of seemingly intermediate onycophorans), much recent evidence points instead to the existence of a euthrocozoan or lophotrochozoan clade, which includes annelids and molluscs, to the exclusion of arthropods (Eernisse et al., 1992; Halanych et al., 1995).

More astonishing, perhaps, is the possibility of an ecdysozoan clade, which includes all of the molting animals, and therefore unites arthropods with such groups as onycophorans, tardigrades, and even nematodes (Aguinaldo et al., 1997; Giribet & Ribera, 1998; Knoll & Carroll, 1999). And within arthropods (Fortey & Thomas, 1997; Brusca, 2000), there is mounting evidence for the union of crustacea and insects and even the paraphyly of crustacea with respect to insects (and possibly the other major arthropod groups as well). Among other things, this implies convergent evolution of adaptations to life on land (tracheal systems, Malpighian tubules, etc.) in hexapods and myriopods (traditionally the Atelocerata).

Even within mammals, where one supposes that many relationships have long since been established with certainty, there have been some major surprises in the last few years (de Jong, 1998). Our favorite case concerns the position of elephant shrews and golden moles. Once considered insectivores, these are now seen to be united with aardvarks, hyraxes, sea cows, and elephants, which implies extraordinary morphological radiation within a basically African clade (Springer et al., 1997; Stanhope et al., 1998).

Within green plants, molecular phylogenetic studies have tended to confirm earlier suggestions based on morphology (Donoghue, 1994), but there are also some very surprising results, of which we mention only a few (see Doyle, 1998, for others). The whisk-ferns, Psilotaceae, now appear to be related to Ophioglossales (e.g., Hasebe et al., 1995; Manhart, 1995; Wolf, 1997), as opposed to being remnant rhyniophytes or related to some group of leptosporangiate ferns, as suggested previously. Within ferns, the aquatic and heterosporous Salviniaceae and Marsileaceae, long viewed as unrelated, now appear to be directly linked (e.g., Pryer et al., 1995; Wolf et al., 1999), a connection also supported by fossil evidence (Rothwell & Stockey, 1994). Within angiosperms, the tricolpate or eudicot clade, recognized first in morphological analyses (Donoghue & Doyle, 1989; Doyle & Hotton, 1991), has been rather consistently upheld in molecular studies (e.g., Chase et al., 1993; Rice et al., 1997; Soltis et al., 1998; and even the highly unresolved parsimony jackknife analysis of Källersjö et al., 1998). This represents a real departure from the traditional view that caryophylids, hamamelids, and other major lineages were derived independently from magnoliids (e.g., Cronquist, 1988). Other surprises include Drosera and Nepenthes being related to caryophillids (Albert et al., 1992), a clade including almost all plants with mustard oils (Rodman et al., 1996), and a connection of woody Hamamelidaceae and Cercidophyllum with herbaceous Saxifragaceae and relatives (Soltis & Soltis, 1997).

Some of the most interesting early results, such as the basal position of Ceratophyllum within angiosperms in rbcL analyses (e.g., Chase et al., 1993), have not been consistently recovered as additional data have been brought to bear. But other seemingly weird results have been upheld. Of these, we are most excited about the possibility that Proteaceae, Platanaceae, and Nelumbo are positioned near the base of eudicots, and may form a clade (Chase et al., 1993; Rice et al., 1997; Soltis et al., 1997; Hoot et al., 1999). Based on outward

appearances, one would never guess that these plants are closely related, and a direct relationship of the three had never been suggested. On closer consideration, this arrangement is not illogical from a morphological standpoint, though it has proven quite difficult to identify any morphological synapomorphies (Hoot et al., 1999; A. Douglas, pers. comm.).

Although many phylogenetic problems have been convincingly resolved in recent years, the relationships of many groups remain unclear. In most cases, this reflects nothing more than limited attention, and we can expect straightforward solutions. Yet, in some other cases, relationships remain unresolved despite considerable attention. For example, it is fair to say that relationships among major mammal lineages are still up in the air (de Jong, 1998). Likewise, relationships among major seed plant groups have still not been satisfactorily resolved (Doyle, 1998; Hansen et al., 1999; Winter et al., 1999). Within flowering plants, perhaps the most remarkable confusion surrounds Rafflesiales. While the position of most of the other parasitic groups has fallen into place, the relationships of Rafflesiales remain highly uncertain, despite great efforts on the part of Nickrent and colleagues (Nickrent et al., 1998). In fact, at this stage it is still unclear whether Rafflesiales are eudicots, or are instead more closely related to one or another monosulcate group (as Hydnoraceae now appear to be related to Aristolochiales/Piperales). A remarkably accelerated rate of evolution of the nuclear ribosomal genes of these plants may be creating artifacts in phylogenetic analyses (e.g., placement of Rafflesiales at the very base of angiosperms; Nickrent & Starr, 1994; Nickrent & Duff, 1996).

What can we expect in the near future? First, and most obviously, the discovery of clades is still in its infancy, and many more breakthroughs are on the horizon. We expect that even the most recalcitrant problems, including those just highlighted, will eventually yield to more data and better methods of analysis.

Second, we trust that more attention will be paid to the naming of newly discovered clades, so as to facilitate communication about exciting results as rapidly, unambiguously, and with as little nomenclatural disruption as possible. For this purpose we believe that a new phylogenetically oriented code of nomenclature is needed (see above). Fortunately, such a phylogenetic code is being developed as a result of a workshop held at the Harvard Herbaria in August 1998. This will soon be available via the internet for evaluation and, subsequently, for formal use. In this system there are no categorical ranks, and names are applied to clades by means of phylogenetic definitions (e.g., a "node-based" definition, such as "the least inclusive clade that contains species X and species Y"; de Queiroz & Gauthier, 1992, 1994). This, we believe, represents a major and very positive shift away from arbitrary decisions about rank and the need to appeal to authority (e.g., Cronquist, 1988; APG, 1998) concerning the circumscription of taxa. One would immediately know, for example, whether or not "Bombacoideae" is included in "Malvaceae," if both names were given phylogenetic definitions and if a particular phylogenetic hypothesis were accepted (Baum et al., 1998; Alverson et al., 1999); without phylogenetic definitions, botanical authorities could and probably would disagree about this, even if they accepted the same underlying phylogeny for their nomenclatural decisions.

Finally, as emphasis shifts toward phylogenetic knowledge, the need to database such information will become increasingly obvious, both to track progress and to render phylogenetic discoveries accessible to a very wide variety of potential users. Several complementary efforts have been initiated to keep track of and synthesize this information, including TreeBASE (see above) and the Tree of Life project (http://phylogeny.arizona.edu/tree/phylogeny.html). However, owing to the exponential increase in phylogenetic research, and limited support for these projects, they have not been able to keep pace and are therefore still inadequate for many purposes. We hope that this situation will improve as journals move toward electronic submission of phylogenetic data sets as a co-requisite of publication (see, e.g., *Mycologia*), perhaps also linked with the registration of clade names. In any case, this is a problem that the systematics community will need to address in order to capitalize on the major investments being made in phylogenetic research.

ATTENTION TO GEOGRAPHY

The present age of discovery also differs in the attention being given to geographic ranges. Collection localities were barely a consideration until quite recently. Recall, for example, Darwin's difficulties in reconstructing (after the fact) the islands from which his Galápagos finches were actually collected (Sulloway, 1982). In contrast, we now place great value on detailed, accurate specimen labels and on databasing geographic information. Many of the most important questions about the organization of biodiversity depend heavily on such information, such as the distribution and relative "hotness" of
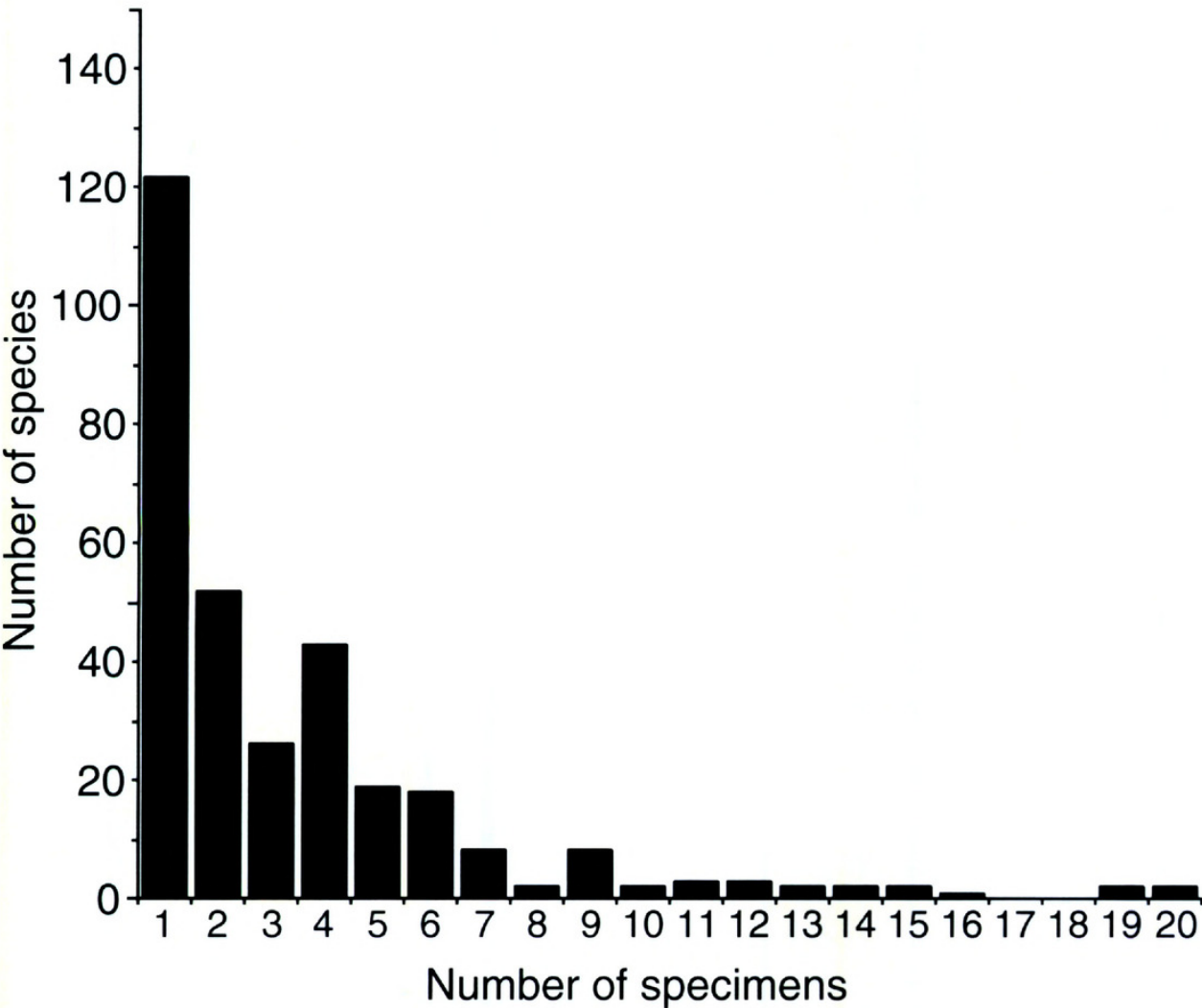
Figure 5.   Number of specimens for species of woody tropical plants. The data represented in this graph were obtained by Madriñán-Restrepo (1996) from recent monographs of neotropical plants: 317 species were scored in 15 genera from 8 families: *Rollinia* (Annonaceae), *Licania* (Chrysobalanceae), *Agarista, Gaultheria* (Ericaceae), *Aiouea, Aniba, Mezilaurus, Nectandra, Pleurothyrium, Rhodostmonodaphne* (Lauraceae), *Eschweilera, Gustavia* (Lecythidaceae), *Guarea* (Meliaceae), *Pouteria* (Sapotaceae), and *Arytera* (Sapindaceae).

diversity hotspots (Reid, 1998), or the existence of refugia in Amazonia (Nelson et al., 1990). Moreover, many critical practical applications of taxonomic knowledge, such as estimating the impact of human disturbance on species loss (e.g., Pimm et al., 1995), are impossible without reasonable knowledge of geographic distributions.

Where, then, do we stand in our knowledge of geographic ranges? This question is difficult to answer, since baseline data have not been compiled in an appropriate fashion. However, there are several reasons to believe we are still very far from having an accurate picture. One clear indication is the fact that many species are known from one or a few museum collections, and these are often old and lack sufficiently detailed locality data. The lungless caecilian, *Atretochoana eiselti*, which we highlighted above, provides a striking example:

neither of the two collections of this remarkable species provides locality data more specific than "South America."

Data collected by Madriñán-Restrepo (1996) from monographic treatments of 15 tropical plant genera (Fig. 5) illustrate a situation that is undoubtedly common. Of the 317 species he considered, 122 (38.5%) were known from just one specimen, 52 (16.4%) from two specimens, and 26 (8.2%) from three specimens. That is, more than half were represented only by one or two specimens, and almost two-thirds by three or fewer. Few of the species he scored were known from more than 10 specimens, and none from more than 20. In such cases there are simply insufficient data to draw reasonable inferences about geographic range.

It is possible, of course, that species known from one or two specimens or localities are truly very

restricted in occurrence. However, in most cases subsequent fieldwork indicates otherwise. Detailed data on this point have not been assembled, but we know that in most groups of organisms every field trip yields range extensions, sometimes major ones. A good example is provided by recent fieldwork in a small corner of Qinghai, China's fourth largest province, with an area of around 720,000 km² (about 6% larger than the state of Texas). Before an expedition in 1995, only four bryophyte species were reported in the literature for all of Qinghai. Three weeks of moss collecting by Benito Tan in Yushu Prefecture alone yielded 57 genera and 109 species (Tan & Yu, 1997). Two of these species were new to science, three were previously unknown in China, and ten collections represented major range extensions within China.

Even in groups of organisms and in places that have been better collected, key elements have often been overlooked. In 1998, our colleague in the Harvard Herbaria, Gustavo Romero, collected *Erisma japura* Spruce ex Warm. (Vochysiaceae) from the Isthmus of Pimichin (between the Orinoco and Amazon basins) in Venezuela. The first collection of this species from Venezuela had been made only the year before, from the same area; previously, it was known from a few collections along the Rio Negro in Colombia and from Brazil. What makes this remarkable is that Alexander von Humbolt and Aimé Bonpland, Richard Spruce, Alfred Wallace, Llewelyn Williams, Julian Steyermark, Bassett Maguire, and others, all worked here, but none of them collected *Erisma japura*, despite the fact that it appears to be the dominant tree in the non-flooded forests of the area. Individuals range to 35 m in height and over 1 m in diameter, and have conspicuous winged fruits that are used as a source of starch by local people (G. Romero, pers. comm.).

Two other discoveries, also of large neotropical trees, emphasize that our knowledge of the distribution of many clades is still rudimentary. *Ruptiliocarpon caracolito* Hammel & N. Zamora was described in 1993, primarily on the basis of collections from Costa Rica's Osa Peninsula (Hammel & Zamora, 1993). Its closest relative appears to be *Lepidobotrys* (Lepidobotryaceae) of the Gabon-Cameroon region of Africa. In a similar case, *Pseudomonotes tropenbosii* A. C. Londoño, E. Alvarez & Forero was described in 1995 from the Colombian Amazon (Londoño et al., 1995). This is only the second New World species of the otherwise Old World Dipterocarpaceae, which dominate the tropical forests of Asia. The other neotropical species, *Pakaraimaea dipterocarpacea* Maguire & Ash-

ton, was discovered less than 20 years earlier (Maguire & Ashton, 1977).

Examples like these are surely common, but are they really very surprising? After all, one could argue that these are not organisms about which we thought we had good knowledge to begin with. Have we learned anything really new about the distributions of organisms that we thought we knew well, organisms of great enough interest that conscious efforts had been made to find them and establish their ranges?

Again, the answer is a definitive yes! The most striking recent case concerns the coelacanth, *Latimeria chalumnae*. Thought to have been extinct since the Upper Cretaceous, and of great evolutionary interest from the standpoint of the origin of tetrapods, a specimen was caught off the coast of South Africa in 1938. After an intensive search, a second specimen was found in 1952 near the Comoro Islands, northwest of Madagascar (Thomson, 1989). Since then, more than 100 additional specimens have been taken of the now endangered fish in the vicinity of the Comoro Archipelago, but nowhere else. It therefore came as a great shock when, on the 30th of July, 1998, a coelacanth was caught in a gill-net off the coast of north Sulawesi, Indonesia, almost 10,000 km away from the Comoros (Erdmann et al., 1998; see note p. 126). Other populations may exist between the two sites, but in any case this discovery reminds us how little we know about the distributions of even large and well-publicized marine organisms.

Similar lessons are provided by the rediscovery of species thought to have become extinct in recent time. Botanists will be aware, for example, of the rediscovery of *Takhtajania perrieri* (Capuron) Baranova & J-F. Leroy in northeastern Madagascar, about 150 km east of the spot where the original and only collection was made 85 years earlier (Schatz et al., 1998). Being of great interest from the standpoint of angiosperm evolution (as the only modern African-Madagascar representative of the vessselless Winteraceae), botanists from the Missouri Botanical Garden and their Malagasy colleagues had tried in vain since 1974 to relocate *Takhtajania*. A Malagasy collector stumbled upon a population of over 250 adults while doing inventory work in 1994, and study material has been made available to botanists around the world. Molecular phylogenetic analyses now suggest that *Takhtajania* is the sister group of the rest of the Winteraceae (E. Zimmer, pers. comm.).

Even better known rediscoveries involve vertebrates, especially mammals. Again from Madagascar comes the story of the rediscovery of the greater

bamboo lemur, *Hapalemur simus* (Wright, 1988), which was thought to have become extinct in 1900. A living animal was purchased in a market in 1964, but soon escaped from captivity; not until 1972 was a small population found in the wild. In 1986, two expeditions, one led by Patricia Wright from the United States and the other by Bernhard Meier of Germany, were successful in locating it again. This set the stage for detailed studies of behavior and ecology, which led in turn to the realization that there were actually two separate species involved. The new species, which they called the golden bamboo lemur, *H. aureus* (Meier et al., 1987), apparently specializes on new shoots of the bamboo plant, exceptionally rich in the poison cyanide.

Two fungal examples further emphasize the potentially great importance of such discoveries. The mushroom *Squamanita contortipes*, first described in 1957 (in the genus *Cystoderma*), was rediscovered in 1992 during the course of systematically sampling the macrofungi of old-growth spruce-hemlock forests on the Olympic Peninsula of Washington (Redhead et al., 1994). As shown in Figure 3c, *S. contortipes* fruit bodies were found growing from the cap of another agaric, a species of *Galerina*. This observation provided the crucial clue to the interpretation of the lifestyle and morphology of an entire group of fungi. *Squaminita* species were initially described as having "protocarpic tubers," sometimes mysteriously resembling the tissues of distantly related mushrooms. Owing to the Olympic Peninsula specimens, these structures are now understood to be deformed hosts, and *Squaminita* is now recognized to be only the second agaric genus in which all species are obligate parasites of other basidiomycetes.

In 1994, a group of Cornell students taking a field mycology course in upstate New York encountered unusual fruiting bodies growing out of the backs of dead beetle larvae. These turned out to be the ascomycete *Cordyceps subsessilis*. Propagation of this material in the laboratory revealed it to be the formerly unknown sexual stage (teleomorph) of the mold *Tolypocladium inflatum*, which produces the immunosuppresive compound cyclosporin, a billion-dollar drug used in preventing the rejection of transplanted organs (Hodge et al., 1996). This knowledge makes possible, for the first time, the search for other pharmaceutically important chemicals (possibly of use in treatment of autoimmune diseases) in related *Cordyceps* species.

What developments do we anticipate with respect to geographic ranges? Most obviously, it will be critical to continue databasing geographic information associated with museum specimens and making this accessible to potential users. This will give a much better picture of the distributions of species and clades, but will still be insufficient for many purposes, both for lack of collections, and because, as several of our examples illustrate, a set of collection localities is not the same as a range, and may even be a poor approximation of the entire distribution. A critical step will, therefore, be the development and application of models for estimating real geographic ranges from sets of collection sites. Fortunately, great strides have been made in this area with the development of Geographic Information Systems (GIS) and models such as those underlying BIOCLIM/BIOMAP, for example (see Austin, 1998; Scott & Jennings, 1998).

Another exciting prospect entails improved connections between geographic and phylogenetic information. This would not only revolutionize the study of historical biogeography, but would also provide a genuinely new perspective on the distribution of diversity as this relates to conservation and management issues (e.g., Vane Wright et al., 1991). Already there are concrete examples, involving a range of organisms and spatial scales. For instance, phylogenetic analyses point to Papua New Guinea as a hotspot of genetic diversity in shiitake mushrooms, and therefore a conservation priority (Hibbett & Donoghue, 1996). Analyses in Asteraceae and curculionid beetles highlight the significance of southern temperate regions in relation to global biodiversity (Morrone et al., 1996). Similarly, in the north temperate zone the Pacific Northwest harbors a variety of species of tremendous phylogenetic significance (D. Wake, pers. comm.), such as *Ascaphus truei*, the sister group of all modern frogs (Ford & Cannatella, 1993). Ultimately, we envision a concatenation of databased geographic information (especially predicted ranges along the lines of BIOCLIM/BIOMAP) with databased phylogenetic information (along the lines of TreeBASE). Among many other things, this would enable the wide-scale application of phylogenetic measures of diversity (e.g., Williams et al., 1991; Faith, 1992).

CONCLUDING THOUGHTS

To systematists, it is probably already clear that we live in an age of discovery and that this one is richer and more profound by virtue of the attention being paid to both phylogeny and geography. Yet, this is not at all obvious to much of the scientific community or to the general public, who tend to regard the discovery of diversity as a tedious filling-

in of minor gaps in our already comprehensive knowledge. Whether or not we have failed, ourselves, to fully appreciate the number and significance of recent discoveries is debatable. What is not debatable is that we have failed to effectively deliver news of these stunning discoveries to those outside of our community. As we have suggested, there are a variety of reasons for this, including our limited ability to compile information on the number of newly discovered species and clades, or to convey the surprisingness of new discoveries. We also are limited by a system of nomenclature that tends to discourage rather than facilitate a full elaboration of the tree of life. These issues need to be confronted directly, and soon.

In the meantime, there are several avenues along which we can advance public awareness and appreciation of biodiversity. Perhaps most obviously, we can highlight exactly how it is that understanding and protecting biodiversity is in our own best interest, even economically. It is hard to imagine a more compelling statement of this connection than the "Teaming with Life" document prepared recently by the Biodiversity and Ecosystems Panel of the President's Committee of Advisors on Science and Technology (PCAST; Raven et al., 1998). Big and bold new biodiversity discovery projects are another mechanism to capture the public's imagination. For example, we see enormous educational potential in the All Taxa Biodiversity Inventory (ATBI) being undertaken by the Great Smoky Mountains National Park (www.discoverlife.org). Several of the projects to be sponsored as part of the DIVERSITAS International Biodiversity Observation Year (IBOY) in 2001 (www.icsu.org/diversitas) have similar potential: for example, retracing key voyages of past ages of discovery (by Darwin, Banks, von Humboldt, and Wallace), or assembling an enormous tree of life and somehow physically displaying its grandeur to the public, or launching major international expeditions to assess diversity in little known regions or in extreme environments.

New discoveries of the sorts we have highlighted have enormous potential to inspire commitment to the project of discovering the diversity of life. However, to fully capitalize on this potential, we will need to pay more attention to specific mechanisms for awakening wonder. Is it possible to induce the sense of awe, amusement, and even befuddlement that remarkable new organisms inspired during the last great age of discovery? What is it that inspires wonder in six-year-old children visiting a natural history museum for the first time? Along these lines we are encouraged by several recent developments.

In a fine analysis of the aesthetics of biological diversity, Kiester (1997) drew attention to the existence of a wide range of biodiversity experiences, contrasting those centered on the immediate, tangible beauty (or bizzareness) of individual organisms with those invoking a sense of the vastness or power of nature (what Immanuel Kant called "sublime" experiences). If we pay closer attention to such distinctions, the range of experiences triggered by biodiversity discoveries could surely be expanded, and their impact could be far greater on the public's perception of nature and the discovery process itself.

In view of this, we should renew our attention to how new discoveries are brought forward in natural history museums and elsewhere. We are delighted by recent experimentation with museum exhibits, especially those inspired by the "wonder cabinets" of the past (Hutchinson, 1965; Weschler, 1995). These collections of rarities—natural objects often commingled with works of art and assembled in seemingly haphazard fashion—help put the observer slightly, but very constructively, off balance. Perhaps the premier modern experiment of this type is David Wilson's Museum of Jurassic Technology in Los Angeles, California (Weschler, 1995). By playfully straddling the dynamic boundary between reality and fiction, Wilson seems to have hit upon an unusually successful way of stimulating doubt and wonder. Today's natural history museums, which sometimes convey an unwarranted certainty or finality about our knowledge of the world, would benefit from careful scrutiny of the Wilson model. There is great power, we believe, in the mystery and strangeness of life, and in deeply appreciating how little we still know about it. The torrent of biological novelties now coming to light may provide the very best way to tap that power.

Literature Cited

Aguinaldo, A. M. A., J. M. Turbeville, L. S. Linford, M. C. Rivera, J. R. Garey, R. A. Raff & J. A. Lake. 1997. Evidence for a clade of nematodes, arthropods, and other moulting animals. Nature 387: 489–493.

Albert, V. A., S. E. Williams & M. W. Chase. 1992. Carnivorous plants: Phylogeny and structural evolution. Science 257: 1491–1495.

Alverson, W. S., B. A. Whitlock, R. Nyffeler, C. Bayer & D. A. Baum. 1999. Phylogeny of the core Malvales: Evidence from *ndh*F sequence data. Amer. J. Bot. 86: 1459–1471.

APG (Angiosperm Phylogeny Group). 1998. An ordinal classification for the families of flowering plants. Ann. Missouri Bot. Gard. 85: 531–543.

Austin, M. P. 1998. An ecological perspective on biodiversity investigations: Examples from Australian eucalypt forests. Ann. Missouri Bot. Gard. 85: 2–17.

Baker, A. N., F. W. E. Rowe & H. E. S. Clark. 1986. A

new class of Echinodermata from New Zealand. Nature 321: 862–864.

Baldauf, S. L. & W. F. Doolittle. 1997. Origin and evolution of the slime molds (Mycetozoa). Proc. Natl. Acad. Sci. U.S.A. 94: 12007–12012.

——— & J. D. Palmer. 1993. Animals and fungi are each other's closest relatives: Congruent evidence from multiple proteins. Proc. Natl. Acad. Sci. U.S.A. 90: 11558–11562.

Baum, D. A., W. S. Alverson & R. Nyffeler. 1998. A durian by any other name: Taxonomy and nomenclature of the core Malvales. Harvard Pap. Bot. 3: 315–330.

Berger, L., R. Speare, P. Daszak, D. E. Green, A. A. Cunningham, C. L. Goggin, R. Slocombe, M. A. Ragan, A. D. Hyatt, K. R. McDonald, H. B. Hines, K. R. Lips, G. Marantelli & H. Parkes. 1998. Chytridiomycosis causes amphibian mortality associated with population declines in the rain forests of Australia and Central America. Proc. Natl. Acad. Sci. U.S.A. 95: 9031–9036.

Briggs, B. G. 2000. What is significant—The Wollemi pine or the southern rushes? Ann. Missouri Bot. Gard. 87: 72–80.

Brusca, R. C. 2000. Unraveling the history of arthropod biodiversification. Ann. Missouri Bot. Gard. 87: 13–25.

Chase, M. W., D. E. Soltis, R. G. Olmstead, D. Morgan, D. H. Les, B. D. Mishler, M. R. Duvall, R. A. Price, H. G. Hills, Y-L. Qiu, K. A. Kron, J. H. Rettig, E. Conti, J. D. Palmer, J. R. Manhart, K. J. Sytsma, H. J. Michaels, W. J. Kress, K. G. Karol, W. D. Clark, M. Hedrén, B. S. Gaut, R. K. Jansen, K-J. Kim, C. F. Wimpee, J. F. Smith, G. R. Furnier, S. H. Strauss, Q-Y. Xiang, G. M. Plunkett, P. S. Soltis, S. M. Swensen, S. E. Williams, P. A. Gadek, C. J. Quinn, L. E. Eguiarte, E. Golenberg, G. H. Learn, Jr., S. W. Graham, S. C. H. Barrett, S. Dayanandan & V. A. Albert. 1993. Phylogenetics of seed plants: An analysis of nucleotide sequences from the plastid gene rbcL. Ann. Missouri Bot. Gard. 80: 528–580.

Chippindale, P. T., A. H. Price & D. M. Hillis. 1993. A new species of perennibranchiate salamander (Eurycea: Plethodontidae) from Austin, Texas. Herpetologica 49: 248–259.

Coen, E. S. & E. M. Meyerowitz. 1991. The war of the whorls: Genetic interactions controlling flower development. Nature 353: 31–37.

Corben, C. J., G. J. Ingram & M. J. Tyler. 1974. Gastric brooding: Unique form of parental care in an Australian frog. Science 186: 946–947.

Cronquist, A. 1988. The Evolution and Classification of Flowering Plants. New York Botanical Garden, Bronx, New York.

Desjardin, D. E., L. Martinez-Peck & M. Rajchenberg. 1995. An unusual psychrophilic aquatic agaric from Argentina. Mycologia 87: 547–550.

Donoghue, M. J. 1994. Progress and prospects in reconstructing plant phylogeny. Ann. Missouri Bot. Gard. 81: 405–418.

——— & J. A. Doyle. 1989. Phylogenetic analysis of angiosperms and the relationships of Hamamelidae. Pp. 17–45 in P. Crane & S. Blackmore (editors), Evolution, Systematics and Fossil History of the Hamamelidae, Vol. 1. Clarendon Press, Oxford.

Douglas, A. W. 1995. Proteaceae, Affinities. Flora of Australia 16 (Eleagnaceae, Proteaceae 1): 6–10.

——— & B. P. M. Hyland. 1995. Proteaceae, Eidotheoideae. In: Flora of Australia 16: 127–129. CSIRO Australia, Melbourne.

Doyle, J. A. 1998. Phylogeny of vascular plants. Annual Rev. Ecol. Syst. 29: 567–599.

——— & C. L. Hotton. 1991. Diversification of early angiosperm pollen in a cladistic context. Pp. 169–195 in S. Blackmore & S. H. Barnes (editors), Pollen and Spores. Clarendon Press, Oxford.

Dung, V. V., P. M. Giao, N. N. Chin, D. Tuoc, P. Arctander & J. MacKinnon. 1993. A new species of living bovid from Vietnam. Nature 363: 443–445.

Eernisse, D. J., J. S. Albert & F. E. Anderson. 1992. Annelida and Arthropoda are not sister taxa: A phylogenetic analysis of spiralian metazoan morphology. Syst. Biol. 41: 305–330.

Erdmann, M. V., R. L. Caldwell & M. K. Moosa. 1998. Indonesian "king of the sea" discovered. Nature 395: 335.

Ertter, B. 2000. Floristic surprises in North America north of Mexico. Ann. Missouri Bot. Gard. 87: 81–109.

Escobar, G. A., D. E. McCabe & C. W. Harpel. 1976. Limnoperdon, a floating gastromycete isolated from marshes. Mycologia 68: 874–880.

Evelyn, J. 1684. Diary of John Evelyn, Vol. IV. Pp. 389–390, 22 October; quote from K. Whittaker, 1996, The culture of curiosity. Pp. 75–90 in N. Jardine, J. A. Secord & E. C. Spary (editors), Cultures of Natural History. Cambridge Univ. Press, Cambridge.

Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. Biol. Conservation 61: 1–10.

Ford, L. S. & D. C. Cannatella. 1993. The major clades of frogs. Herp. Monogr. 7: 94–117.

Fortey, R. A. & R. H. Thomas (editors). 1997. Arthropod Relationships. Chapman and Hall, London.

Fuhrman, J. D. & L. Campbell. 1998. Microbial microdiversity. Nature 393: 410–411.

Funch, P. & R. M. Kristensen. 1995. Cycliophora is a new phylum with affinites to Entoprocta and Ectoprocta. Nature 378: 711–714.

Gaston, K. J. 1991. The magnitude of global insect species richness. Conservation Biol. 5: 283–296.

Giao, P. M., D. Tuoc, V. V. Dung, E. D. Wikramanayake, G. Amato, P. Arctander & J. R. MacKinnon. 1998. Description of Muntiacus truongsonensis, a new species of muntjac (Artiodactyla: Muntiacidae) from central Vietnam, and implications for conservation. Animal Conservation 1: 61–68.

Gilmore, S. & K. D. Hill. 1997. Relationships of the Wollemi pine (Wollemia nobilis) and a molecular phylogeny of the Araucariaceae. Telopia 7: 275–291.

Giribet, G. & C. Ribera. 1998. The position of arthropods in the animal kingdom: A search for a reliable outgroup for internal arthropod phylogeny. Molec. Phylogenetics & Evol. 9: 481–488.

Glaw, F. & J. Köhler. 1998. Amphibian species diversity exceeds that of mammals. Herpetological Rev. 29: 11–12.

Gómez-Laurito, J. & L. D. Gómez P. 1989. Ticodendron: A new tree from Central America. Ann. Missouri Bot. Gard. 76: 1148–1151.

——— & ———. 1991. Ticodendraceae: A new family of flowering plants. Ann. Missouri Bot. Gard. 78: 87–88.

Greuter, W., F. R. Barrie, H. M. Burdet, W. G. Chaloner, V. Demoulin, D. L. Hawksworth, P. M. Jørgensen, D. H. Nicolson, P. C. Silva, P. Trehane & J. McNeill. 1994. International Code of Botanical Nomenclature (Tokyo Code). Regnum Veg. 131.

Halanych, K. M., J. D. Bacheller, A. M. A. Aguinaldo, S.

M. Liva, D. M. Hillis & J. A. Lake. 1995. Evidence from 18S ribosomal DNA that the lophophorates are protostome animals. Science 267: 1641–1643.

Hammel, B. & W. G. Burger. 1991. Neither oak nor alder, but nearly: The history of Ticodendraceae. Ann. Missouri Bot. Gard. 78: 89–95.

———— & N. A. Zamora. 1993. *Ruptiliocarpon* (Lepidobotryaceae): A new arborescent genus and tropical American link to Africa, with a reconsideration of the family. Novon 3: 408–417.

Hanken, J. 1999. Why are there so many new amphibian species when amphibians are declining? Trends Ecol. Evol. 14: 7–8.

Hansen, A., S. Hansmann, T. Samigullin, A. Antonov & W. Martin. 1999. *Gnetum* and the angiosperms: Molecular evidence that their shared morphological characters are convergent, rather than homologous. Molec. Biol. Evol. 16: 1006–1009.

Hasebe, M., P. G. Wolf, K. M. Pryer, K. Ueda, M. Ito, R. Sano, G. J. Gastony, J. Yokoyama, J. R. Manhart, N. Murakami, E. H. Crane, C. H. Haufler & W. D. Hauk. 1995. Fern phylogeny based on *rbc*L nucleotide sequences. Amer. Fern J. 85: 134–181.

Hibbett, D. S. & M. J. Donoghue. 1996. Implications of phylogenetic studies for conservation of genetic diversity in shiitake mushrooms. Conservation Biol. 10: 1321–1327.

———— & ————. 1998. Integrating phylogenetic analysis and classification in fungi. Mycologia 90: 347–356.

Hodge, K. T., S. B. Krasnoff & R. A. Humber. 1996. *Tolypocladium inflatum* is the anamorph of *Cordyceps subsessilis*. Mycologia 88: 715–719.

Holden, C. 1995. Ancient trees down under. Science 267: 334.

Hoot, S. B., S. Magallon & P. B. Crane. 1999. Phylogeny of basal eudicots based on three molecular data sets: *atp*B, *rbc*L, and 18S nuclear ribosomal DNA sequences. Ann. Missouri Bot. Gard. 86: 1–32.

Horgan, J. 1998. Quoted in "Resolved: science is at an end. Or is it?" by D. Overbye (editor), The New York Times, 10 Nov. 1998.

Hutchinson, G. E. 1965. The Ecological Theater and the Evolutionary Play. Yale Univ. Press, New Haven.

Jones, W. G., K. D. Hill & J. M. Allen. 1995. *Wollemia nobilis*, a new living Australian genus and species in the Araucariaceae. Telopea 6: 173–176.

Jong, W. W. de 1998. Molecules remodel the mammalian tree. Trends Ecol. Evol. 13: 270–275.

Källersjö, M., J. S. Farris, M. W. Chase, B. Bremer, M. F. Fay, C. J. Humphries, G. Petersen, O. Seberg & K. Bremer. 1998. Simultaneous parsimony jackknife analysis of 2538 *rbc*L sequences reveals support for major clades of green plants, land plants, seed plants, and flowering plants. Pl. Syst. Evol. 213: 259–287.

Kiester, A. R. 1997. Aesthetics of biological diversity. Human Ecol. Rev. 3: 151–157.

Knoll, A. H. & S. B. Carroll. 1999. Early animal evolution: Emerging views from comparative biology and geology. Science 284: 2129–2137.

Kristensen, R. M. 1983. Loracifera, a new phylum with Aschelminthes characters from the meiobenthos. Z. Zool. Syst. Evolutionsforsch. 21: 163–180.

Laurance, W. F., K. R. McDonald & R. Speare. 1996. Epidemic disease and the catastrophic decline of Australian rain forest frogs. Conservation Biol. 10: 406–413.

Liem, D. S. 1973. A new genus of frog of the family Lep-

todactylidae from SE Queensland, Australia. Mem. Queensland Mus. 16: 459–470, pl. 30.

Londoño, A. C., E. Alvarez, E. Forero & C. M. Morton. 1995. A new genus and species of Dipterocarpaceae from the Neotropics: I. Introduction, taxonomy, ecology, and distribution. Brittonia 47: 225–236.

Longcore, J. E., A. P. Pessier & D. K. Nichols. 1999. *Batrachochytrium dendrobatidis* gen. et sp. nov., a chytrid pathogenic to amphibians. Mycologia 91: 219–227.

MacKinnon, J. 2000. New mammals in the 21st century? Ann. Missouri Bot. Gard. 87: 63–66.

Madigan, M. T. 2000. Extremophilic bacteria and microbial diversity. Ann. Missouri Bot. Gard. 87: 3–12.

Madriñán-Restrepo, S. 1996. Systematic studies in the Lauraceae. Monograph of *Rhodostemonodaphne*. Ph.D. Dissertation, Department of Organismic and Evolutionary Biology, Harvard University.

Maguire, B. & P. S. Ashton. 1977. Pakaraimoideae, Dipterocarpaceae of the Western Hemisphere. II. Systematic, geographic and phyletic considerations. Taxon 26: 341–385.

Manhart, J. R. 1995. Chloroplast 16S rDNA sequences and phylogenetic relationships of fern allies and ferns. Amer. Fern J. 85: 182–192.

Márquez-Guzmán, J., M. Engleman, A. Martínez-Mena, E. Martínez & C. Ramos. 1989. Anatomía reproductiva de *Lacandonia schismatica* (Lacandoniaceae). Ann. Missouri Bot. Gard. 76: 124–127.

Martin, J. W., L. Gershwin, J. W. Burnett, D. G. Cargo & D. A. Bloom. 1997. *Chrysaora achlyos*, a remarkable new species of Scyphozoan from the Eastern Pacific. Biol. Bull. 193: 8–13.

Martínez, E. & C. H. Ramos. 1989. Lacandoniaceae (Triuridales): Una nueva familia de México. Ann. Missouri Bot. Gard. 76: 128–135.

Meier, B., R. Albignac, A. Peyriéras, Y. Rumpler & P. Wright. 1987. A new species of *Hapalemur* (primates) from South East Madagascar. Folia Primatologica 48: 211–215.

Moore, L. R., G. Rocap & S. W. Chisholm. 1998. Physiology and molecular phylogeny of coexisting *Prochlorococcus* ecotypes. Nature 393: 464–467.

Morell, V. 1996. New mammals discovered by biology's new explorers. Science 273: 1491.

————. 1999. Are pathogens felling frogs? Science 284: 728–731.

Morrone, J. J., L. Katinas & J. V. Crisci. 1996. On temperate areas, basal clades and biodiversity conservation. Oryx 30: 187–194.

Nelson, B. W., C. A. C. Ferreira, M. F. da Silva & M. L. Kawasaki. 1990. Endemism centres, refugia and botanical collection density in Brazilian Amazonia. Nature 345: 714–716.

Nickrent, D. L. & R. J. Duff. 1996. Molecular studies of parasitic plants using ribosomal RNA. Pp. 28–52 *in* M. Moerno et al. (editors), Advances in Parasitic Plant Research. Junta de Andalucia, Dirección General de Investigación Agraria, Cordoba, Spain.

————, ————, A. E. Colwell, A. D. Wolfe, N. D. Young, K. E. Steiner & C. W. dePamphilis. 1998. Molecular phylogenetic and evolutionary studies of parasitic plants. Pp. 211–241 *in* P. S. Soltis, D. E. Soltis & J. J. Doyle (editors), Molecular Systematics of Plants II. DNA Sequencing. Kluwer Academic, Boston.

———— & E. M. Starr. 1994. High rates of nucleotide substitution in nuclear small-subunit (18S) rDNA from holoparasitic flowering plants. J. Molec. Evol. 39: 62–70.

Nussbaum, R. A. & M. Wilkinson. 1996. A new genus of lungless tetrapod: A radically divergent caecilian (Amphibia: Gymnophiona). Proc. Roy. Soc. London, B, Biol. Sci. 261: 331–335.

Pace, N. R. 1997. A molecular view of microbial diversity and the biosphere. Science 276: 734–740.

Patterson, B. D. 1994. Accumulating knowledge on the dimensions of biodiversity: Systematic perspectives on Neotropical mammals. Biodiversity Lett. 2: 79–86.

Pessier, A. P., D. K. Nichols, J. E. Longcore & M. S. Fuller. 1999. Cutaneous chytridiomycosis in poison dart frogs (Dendrobates spp.) and White's tree frogs (Litoria caerulea). J. Veterinary Diagnostic Investigation 11: 194–199.

Pimm, S. L., G. J. Russell, J. L. Gittleman & T. M. Brooks. 1995. The future of biodiversity. Science 269: 347–350.

Prance, G. T., H. Beentje, J. Dransfield & R. Johns. 2000. The tropical flora remains undercollected. Ann. Missouri Bot. Gard. 87: 67–71.

Pryer, K. M., A. R. Smith & J. E. Skog. 1995. Phylogenetic relationships of extant ferns based on evidence from morphology and rbcL sequences. Amer. Fern J. 85: 205–282.

Quammen, D. 1996. The Song of the Dodo. Island Biogeography in an Age of Extinction. Touchstone, Simon and Schuster, New York.

Queiroz, K. de & J. Gauthier. 1992. Phylogenetic taxonomy. Annual Rev. Ecol. Syst. 23: 449–480.

——— & ———. 1994. Toward a phylogenetic system of biological nomenclature. Trends Ecol. Evol. 9: 27–31.

Raven, P., F. J. Ayala, G. C. Bowker et al. 1998. Teaming with life: Investing in science to understand and use America's living capital. The President's Committee of Advisors on Science and Technology (PCAST). Office of the President, Washington, D.C.

Redhead, S. A., J. F. Ammirati, G. R. Walker, L. L. Norvell & M. B. Puccio. 1994. Squamanita contortipes, the Rosetta Stone of a mycoparasitic agaric genus. Canad. J. Bot. 72: 1812–1824.

Reid, W. V. 1998. Biodiversity hotspots. Trends Ecol. Evol. 13: 275–280.

Rice, K. A., M. J. Donoghue & R. G. Olmstead. 1997. Analyzing large data sets: rbcL 500 revisited. Syst. Biol. 46: 554–563.

Richardson, L. L., W. M. Goldberg, K. G. Kuta, R. B. Aronson, G. W. Smith, K. B. Ritchie, J. C. Halas, J. S. Feingold & S. L. Miller. 1998. Florida's mystery coral-killer identified. Nature 392: 557–558.

Rodman, J. E., K. G. Karol, R. A. Price & K. J. Sytsma. 1996. Molecules, morphology, and Dahlgren's expanded order Capparales. Syst. Bot. 21: 289–307.

Rothwell, G. R. & R. A. Stockey. 1994. The role of Hydropteris pinnata gen. et sp. nov. in reconstructing the cladistics of heterosporous ferns. Amer. J. Bot. 81: 479–492.

Sanderson, M. J., B. G. Baldwin, G. Bharathan, C. S. Campbell, D. Ferguson, J. M. Porter, C. Von Dohlen, M. F. Wojciechowski & M. J. Donoghue. 1993. The growth of phylogenetic information and the need for a phylogenetic database. Syst. Biol. 42: 562–568.

Schaller, G. B. & E. S. Vrba. 1996. Description of the giant muntjac (Megamuntiacus vuquangensis) in Laos. J. Mammalogy 77: 675–683.

Schatz, G. E., P. P. Lowry II & A. Ramisamihantanurina. 1998. Takhtajania perrieri rediscovered. Nature 391: 133–134.

Scott, J. M. & M. D. Jennings. 1998. Large-area mapping of biodiversity. Ann. Missouri Bot. Gard. 85: 34–47.

Setoguchi, H., T. A. Osawa, J-C. Pintaud, T. Jaffre & J-M. Veillon. 1998. Phylogenetic relationships within Araucariaceae based on rbcL gene sequences. Amer. J. Bot. 85: 1507–1516.

Shevock, J. R., B. Ertter & D. W. Taylor. 1992. Neviusia cliftonii (Rosaceae: Kerrieae), an intriguing new relict species from California. Novon 2: 285–289.

Soltis, D. E. & P. S. Soltis. 1997. Phylogenetic relationships in Saxifragaceae sensu lato: A comparison of topologies based on 18S rDNA and rbcL sequences. Amer. J. Bot. 84: 504–522.

Soltis, D. E., P. S. Soltis, D. L. Nickrent, L. A. Johnson, W. J. Hahn, S. B. Hoot, J. A. Sweere, R. K. Kuzoff, K. A. Kron, M. W. Chase, S. M. Swensen, E. A. Zimmer, S-M. Chaw, L. J. Gillespie, W. J. Kress & K. J. Sytsma. 1997. Angiosperm phylogeny inferred from 18S ribosomal DNA sequences. Ann. Missouri Bot. Gard. 84: 1–49.

Soltis, D. E., P. S. Soltis, M. E. Mort, M. W. Chase, V. Savolainen, S. B. Hoot & C. M. Morton. 1998. Inferring complex phylogenies using parsimony: An empirical approach using three large DNA data sets for angiosperms. Syst. Biol. 47: 32–42.

Springer, M. S., G. C. Cleven, O. Madsen, W. W. de Jong, V. G. Waddell, H. M. Amrine & M. J. Stanhope. 1997. Endemic African mammals shake the phylogenetic tree. Nature 388: 61–64.

Stanhope, M. J., O. Madsen, V. G. Waddell, G. C. Cleven, W. W. de Jong & M. S. Springer. 1998. Highly congruent molecular support for a diverse superordinal clade of endemic African mammals. Molec. Phylogenetics Evol. 9: 501–508.

Sulloway, F. J. 1982. Darwin and his finches: The evolution of a legend. J. Hist. Biol. 15(1): 1–53.

Tan, B. C. & J. Yu. 1997. Mosses of Qinghai-Tibetan Plateau, China. J. Hattori Bot. Lab. 82: 305–320.

Thomson, K. S. 1989. The second Coelacanth. Amer. Sci. 77: 536–538.

Tyler, M. J., D. C. Shearman, R. Franco, P. O'Brien, R. F. Seamark & R. Kelly. 1983. Inhibition of gastric acid secretion in the gastric brooding frog, Rheobatrachus silus. Science 220: 609–610.

Vane-Wright, R. I., C. J. Humphries & P. H. Williams. 1991. What to protect?—Systematics and the agony of choice. Biol. Conservation 55: 235–254.

Vergara, F., C. Ferrándiz, E. Meyerowitz & E. R. Alvarez-Buylla. 1999. Molecular basis and evolution of the inside-out flower of Lacandonia schismatica. Abstract 15.13.2, p. 188 of Abstracts of the XVI International Botanical Congress, St. Louis, Missouri.

Wainright, P. O., G. Hinkle, M. L. Sogin & S. K. Stickel. 1993. Monophyletic origins of the Metazoa: An evolutionary link with fungi. Science 260: 340–342.

Wake, D. B. 1996. A new species of Batrachoseps (Amphibia: Plethodontidae) from the San Gabriel Mountains, southern California. Contr. Sci. Nat. Hist. Mus. Los Angeles County 463: 1–12.

Weschler, L. 1995. Mr. Wilson's Cabinet of Wonder. Vintage Books, Random House, New York.

Wilkinson, M. A. & R. A. Nussbaum. 1997. Comparative morphology and evolution of the lungless caecilian Atretochoana eiselti (Taylor) (Amphibia: Gymnophiona: Typhlonectidae). Biol. J. Linn. Soc. 62: 39–109.

———, Sebben, E. N. F. Schwartz & C. A. Schwartz. 1998. The largest lungless tetrapod: Report on a second