# REVIEWS

*Cladistics* 2(3):285–294

## South African perspectives on species: an evaluation of the recognition concept

**Species and Speciation.**—E. S. Vrba (ed.). 1985. Transvaal Museum Monograph No. 4, Transvaal Museum, Pretoria, South Africa. xviii+176 pp. $30.00 (hardbound).

This volume is the outcome of a symposium held at the Transvaal Museum in Pretoria, South Africa, in September 1982. It contains introductory comments by E. S. Vrba (organizer and editor of the proceedings), a special address on biological and social evolution, and 21 other contributions arranged in sections on "Species Concepts," "Climate, Population Structure and Speciation," "Development and Speciation," "Faunal Case Histories," "Speciation in Hominidae," and "Species in Relation to Ecosystems." Fifteen of the 24 authors currently reside in South Africa, and 8 of the 9 remaining contributors worked there formerly. Thus, although the book does not represent the full spectrum of ideas on the subject, it does present the views of many of the leading evolutionary biologists of South Africa. Seen in this light, it is as interesting for the views that are missing as for those represented—for agreements as well as disagreements. In keeping with most books of its kind, only two of the authors are botanists; entomology, with six contributors, is especially well represented. Not surprisingly, about one-third of the papers focus directly on African organisms, and most of the rest make use of African examples.

My review focuses on contributions of special relevance to cladists and presents only a brief summary of the remainder. Many of my comments concern the so-called recognition concept of species developed by H. E. H. Paterson in this volume and elsewhere (e.g., Paterson, 1978, 1981). Indeed, I have taken advantage of this opportunity to evaluate this important approach to the species problem, which, judging by the present volume, has already captured the imaginations of many South African workers.

Before proceeding with a review of the scientific papers, I must comment briefly on the special address delivered by M. C. O'Dowd on "The relationship between theories of biological and social change." Mr. O'Dowd is described as "an alternate director of the Anglo American Corporation of South Africa Limited and chairman of the A.A.C. and De Beers Group Chairman's Fund," located in Johannesburg (p. 3). The "Chairman's Fund" provided money for the meeting, and this is presumably the reason that O'Dowd's contribution is included here, as the same paper was published in 1982 in the *South African Journal of Science.*

O'Dowd's basic proposition is that social and biological evolution have little in common and that ideas have been illegitimately transferred from the study of one to the other. Many of his assertions are uncontroversial, even trivial: "biological evolution relates to genetically transmitted characteristics . . . social evolution is concerned with learnt behaviour" (p. 4). But a disturbing number of O'Dowd's claims are highly suspect, such as that "most living creatures are in equilibrium with their environment and optimally adapted to it" (p. 8). This last view, and other sentiments discussed below, are among the best examples I have seen of what Lewontin (1982) described as "barroom wisdom."

O'Dowd's distinction between progress and retrogression in social evolution is built upon the typological belief that humans have "a core of fixed nature" (p. 10). In par-

ticular, he assumes "the existence of three innate urges": the "vast majority of individuals" (1) "wish to live rather than to die," (2) "wish their own offspring to survive them," and (3) "have a sexual urge which is entirely independent of any objective need ... to reproduce" (p. 10). He proposes that "progress is that which makes it more possible for people to satisfy their innate and ineradicable needs and retrogression is that which makes it less possible" (p. 10). Armed (one presumes) with this criterion, O'Dowd reaches several rather astonishing conclusions but without a hint as to how these were derived. For instance, although he rejects the idea that evolution justifies imperialism in general, some acts of imperialism are seen as progressive: "the conquest by the European powers in Africa and Asia in the 19th century certainly also had large constructive elements" (p. 5). Further, according to O'Dowd, socialism, "which essentially claims that every man has a human right to anything which anybody else has, if it is more than what he has himself" (p. 7), is a retrogressive form of plunder and, in this respect, is in the same league as fuedalism. In contrast, "the more decentralized decision-making is, the freer people are to make their own decisions, to back them with their own resources and to take the consequences both good and bad, the faster progress will be" (p. 6). Remembering O'Dowd's status in South Africa, one cannot help wondering if it is simply coincidence that he considers socialism retrogressive and capitalism progressive. This suspicion arises repeatedly. Why, for example, does O'Dowd believe that "even oppressive government is normally found to be preferable to anarchy"? And why does he consider it "by no means a wild speculation" that a hypothetical human variant with a higher urge to reproduce "might be significantly less intelligent on average than *Homo sapiens*" (p. 13)?

I find it difficult to avoid the conclusion that O'Dowd's views represent a form of biological determinism (Lewontin, 1982), in which it supposedly follows from basic and essential human urges that some endeavors are inherently progressive (such as capitalism) and others inherently retrogressive (such as socialism). It is unfortunate that these opinions should be included in this otherwise respectable forum, and it could even have harmful consequences. It is not difficult to imagine that O'Dowd's views could be cited as justification for the deplorable social conditions in South Africa.

Having dispensed with the special symposium address, I now return to a consideration of the scientific contributions. Vrba's introductory article is a superb overview of the volume and of her own ideas on species and speciation. She agrees with Ghiselin (1974), and many other authors, that species are individuals wherein the "crucial organization" is conferred by sexual reproduction (p. x). Thus, contrary to evolutionary species concepts (e.g., Wiley, 1978), when sex is absent so are species. According to Vrba the recognition concept of species advanced by Paterson (see below) is "fundamentally compatible" with the idea that species are individuals: "both draw on the reproductive activities among organisms, on selection and on the causes of evolution" (p. x), and both allow that a species can persist after giving birth to a daughter species. Although this certainly sounds appealing, I will suggest below that on closer inspection the recognition concept does not rest easily with individuality (see discussion of Paterson). Vrba also concurs with Paterson's view that postmating isolation is unlikely to initiate speciation because selection for divergence on secondary contact (character displacement or "reinforcement") is highly improbable. Instead, most speciation is seen as an incidental outcome of divergence in allopatry. Although I generally agree, it does not seem necessary that divergence in allopatry be due to selection directly on fertilization characters, as implied by Paterson's recognition concept. In some (perhaps many) instances, divergence of fertilization systems may be initiated as an incidental byproduct of selection acting on other characters (see discussion of Toms's contribution below).

In many respects Vrba presents a well-rounded synopsis of the relevant literature, but there are several revealing ommisions. For example, Endler (e.g., 1977) is not cited

in her discussion of parapatric speciation, and there is no mention made of Cracraft (e.g., 1982) in connection with the possible causal connection between speciation and major changes in the physical environment. The contributions of botanists such as Stebbins, Grant, and Levin are also neglected; Levin (e.g., 1979), in particular, has expressed views that are very much in line with the recognition concept. Vrba's section on phylogenetic patterns in the study of speciation is devoted to paleontological evidence and an argument that the recognition concept predicts a punctuated equilibrium pattern (as though this cannot be predicted under many other views); no reference is made to cladograms or vicariance biogeography (e.g., Wiley, 1981). In concluding her remarks, Vrba calls for interdisciplinary research among molecular and population geneticists, developmental biologists, and paleontologists; once again, no mention is made of the role that phylogenetic systematists might play in the study of species and speciation.

N. Eldredge, the only contributor without a direct connection to South Africa, was invited to participate in the symposium to provide a philosophical and paleontological perspective. He agrees that species, like individuals of all sorts, have births, histories, and deaths. The difference, according to Eldredge, between species and clades is that reproductive activity provides "the cohesion that holds species together through time," whereas "speciation is the 'glue' that provides cohesion to monophyletic clades" (p. 18). I suspect that this very broad use of the word cohesion (or "glue") for both interbreeding and speciation may serve to confuse more than clarify the different processes responsible for the existence of species versus clades. Eldredge contends here, as he has elsewhere, that the recognition that species are individuals "requires abandonment of the relatively simple structure of the modern synthesis in favour of a more expressly hierarchically structured evolutionary theory" (p. 17). He considers that species generally lack emergent properties—that they are replicators but not interactors (Hull, 1980)—and hence that species selection does not occur. However, he sees species as especially significant entities because they are storehouses of genetic information and provide "the organisms taking part in particularized economic ('ecologic') situations" (p. 19). It is not entirely obvious though that species are unique in this regard—the same might also be said of populations within a species, or even of higher taxa.

Paterson's paper on the recognition concept of species is of central importance to this volume in that his views are referred to in almost every other contribution, most authors tacitly accepting his caricature of the biological species concept (which he calls the isolation concept) and his distinction between the two views. According to Paterson, the isolation concept is "relational" because species can only be delimited by comparison with others—by identifying mechanisms by which they are reproductively isolated. He contends that the word "mechanism" in this context implies that isolation is necessarily a function that was selected and that therefore the isolation concept implies direct selection for premating isolating mechanisms, a process that necessarily occurs in sympatry or parapatry. He objects strenuously to this view on the basis of his belief that character displacement leading to reproductive isolation is exceedingly unlikely in theory and may never have occurred in nature. Instead, according to Paterson, postzygotically isolated populations of small size tend to go extinct before divergence, and therefore, as Vrba (p. xiii) puts it, "are at best still-born buds because they do not participate in life's branching pattern."

Paterson attributes the isolation concept described above to Dobzhansky and Mayr, but even his carefully selected quotations from these authors (e.g., Dobzhansky, 1970:376) do not seem to support this contention. Indeed, these show quite clearly that both Dobzhansky and Mayr accepted several different causes of the evolution of isolating mechanisms. Thus, isolation may be a byproduct of divergence in allopatry *or* it may evolve through displacement following secondary contact. Indeed, it is widely known

that Mayr, in particular, has been an outspoken proponent of the view that speciation requires some divergence in allopatry.

Although I think that some of Paterson's assertions regarding the views of Dobzhansky and Mayr are misguided, I do think he is correct in pointing out that some of their discussions of the problem have a distinct teleological flavor. In particular, I agree that occasional statements to the effect that species represent adaptations are inconsistent with the view that isolating mechanisms arise as incidental byproducts of divergence. Paterson attributes such sentiments, and the allure of the isolation concept in general, to "deep-seated biases inherent in our Western cultural background," such as "the creation stories in the Book of Genesis." I find this a rather unconvincing explanation, and somewhat underhanded at that. I am more inclined to attribute such sentiments to simple confusion and a natural tendency in the early days of the modern synthesis to exaggerate the "role" of biological species.

Obviously, Paterson wishes to shackle Dobzhansky and Mayr with the narrow view that species must arise by reinforcement in order to emphasize that this differs from his own recognition concept. Under the latter view, species are delimited by the possession of a common fertilization system or, more specifically, by the subset of presumed adaptations constituting the species-specific mate recognition system (SMRS). It is supposed that stabilizing selection maintains the SMRS in the "normal habitat" and that change is most likely to occur in populations that have entered a new habitat wherein there might be selection for a different fertilization system. Speciation is complete when "the new fertilization system has become sufficiently different from that of the members of the parent population, for then the new fertilization system will delimit a new field for gene recombination" (p. 26). Although Paterson asserts repeatedly that species are defined "independently" (not in relation to others) under the recognition concept, it appears from this last statement that the fertilization system of a daughter species must at least be compared with that of its parent.

The last quotation also implies that effective gene recombination is central to the recognition concept, and this leads, in turn, to the assertion that the recognition concept is consistent with the idea that species are individuals that exist as products of interbreeding. However, I suggest that under the recognition concept, species are phenetic classes *defined by* similarities and differences in a set of fertilization characters. That such characters are not simply viewed as symptoms of individuality by Paterson is revealed in his example of unsuccessful hybridization between organisms with different ploidy. In this case there is absolutely no effective gene recombination between the parents—which are therefore on separate evoluationary tracks—yet Paterson considers these to belong to the same species since their SMRSs are sufficiently similar for fertilization to occur. But, if we agree that effective interbreeding—the production of viable and fertile offspring—is responsible for the existence of species as individuals, why should the act of fertilization be raised to a position of supreme importance, and postmating isolating mechanisms entirely ignored? It seems that according to the recognition concept, species need not be cohesive via actual gene exchange, and even the potential to successfully interbreed is irrelevant. The only thing that counts is the potential to achieve fertilization. It should also be noted that this potential may be a function of retained ancestral traits and that recognition species might therefore be positively paraphyletic. Adoption of such species for purposes of cladistic analysis might severely limit the resolution of phylogenetic relationships (Donoghue, 1985).

In the end, I do think Paterson is performing a valuable service in trying to tease apart the alternative causes of speciation discussed by Dobzhansky, Mayr, and others. However, although it is useful to identify extreme cases, I see little virtue in making a straw man of the biological species concept. Furthermore, I am not convinced of the superiority of Paterson's recognition concept. This view rests on a strong assumption that there is never direct selection for isolating mechanisms, with the consequence that

primacy is given to the act of fertilization over effective interbreeding and common ancestry. This provides, I think, a very clear example of the subtle influence that a theory of evolutionary process can exert upon the formulation of a basic concept, which can in turn affect the analysis of phylogenetic pattern.

M. J. Scoble's paper concerns the ontological status of the multidimensional species recognized by most taxonomists. In particular, he asks whether the biological species concept or the recognition concept "gives an adequate theoretical explanation of the species described by taxonomists" (p. 32). He concludes that the recognition concept is superior, in spite of his realization that recognition species will be classes rather than individuals. I find Scoble's general question rather puzzling, since it seems doubtful that many of the species recognized by taxonomists can or should be "explained". I suspect that many such species are neither cohesive nor monophyletic, because I agree fully with Scoble that the potential to interbreed cannot be accurately inferred from morphology and that there may be little or no gene flow between separate populations placed in the same taxonomic species (Mishler and Donoghue, 1982).

Cladists will be especially amused (or perhaps annoyed) by D. J. Brothers's paper, which presents yet another argument that paraphyletic higher taxa may be natural and therefore acceptable in classifications. He begins his argument by adopting the evolutionary species concept (Simpson, 1961; Wiley, 1978) on the grounds that it "may be applicable to all organisms" (p. 36). He then contends that acceptance of such a concept has important implications for the recognition of higher taxa. Specifically, he claims that if one accepts that asexual organisms form natural species (bound by "phenetic cohesion" as opposed to interbreeding) and that such species may function as ancestors, one must also accept that phenetically defined paraphyletic higher taxa are natural. Further he asserts that because "epiphenotypically distinct" paraphyletic groups "show qualities of 'relative stability' and 'cohesion' in addition to their unitary origins, and also produce descendants of similar type, they seem to be more natural (by virtue of their possession of more of the properties of individuals) than are epiphenotypically diverse holophyletic groups, which have unitary origins but lack cohesion and cannot produce descendants" (p. 41). Such paraphyletic taxa might even be considered individuals if we would agree to Brothers's "slightly broadened concept of an 'individual' ... as referring to any entity which exhibits such 'relative stability' whether or not it perforce evolves as a single unit or lineage" (p. 40). Objections to paraphyly by Platnick (1980) and Patterson (1980) are dismissed as irrelevant on the grounds that these are "consequences of the transformed cladistic approach, which does not aim to make evolutionary sense" (p. 39).

This line of reasoning would indeed be a major blow to cladistics if it were not riddled with logical blunders. Note that Brothers's basic argument is that *if* we accept an evolutionary species concept, and *if* we therefore permit the recognition of paraphyletic clones, *then* it is logically inconsistent to reject paraphyletic higher taxa. This may be, but why must we accept that paraphyletic clones are natural taxa in the first place? These are certainly not natural as complete systems of common ancestry, nor by virtue of the process of interbreeding. In fact, it seems to me that such groups do not exist as units in nature, and for precisely this reason they should not be admitted in the phylogenetic system. Once paraphyletic clones are rejected, Brother's argument crumbles—it becomes perfectly consistent to reject paraphyletic higher taxa, which likewise are neither monophyletic nor cohesive. Thus, what Brothers considers to be an airtight argument in favor of evolutionary classification turns out to be a devastating argument against adopting an evolutionary species concept, wherein asexual classes are recognized alongside individual species united through the process of interbreeding.

The section on climate and population structure contains four contributions. In the first, C. K. Brain makes a convincing case that cycles of temperature change in South

Africa have been sufficient to bring about isolation and divergence of populations. H. P. Linder estimates the extent of gene flow in the Cape flora, using information on pollen and seed movement in similar plants from other regions. He concludes that gene flow is probably rare between geographically separated populations of a species and that divergence is therefore possible without specific reproductive isolating mechanisms. Although I think Linder is probably right, it is noteworthy that some recent studies using paternity analysis indicate that *effective* gene flow may be considerably greater than previously estimated (Ellstrand and Marshall, 1985). Because much of the diversity in the Cape flora is associated with ecological replacement within geographic subregions, and close relatives are frequently sympatric, Linder also proposes that "allopatry is unlikely to have played a role" (p. 56) in at least some cases of speciation. Limited gene flow combined with steep ecological gradients would certainly facilitate divergent adaptation to adjacent habitats, but the patterns described are not inconsistent with allopatric speciation, especially considering the climatic fluctuations and range changes described by Brain. A. C. Kemp examines data on raptors and reaches the unremarkable conclusion that "studies of individual life histories seem relevant to the study of evolution" (p. 68). He touches on the idea of a population size below which extinction will occur and explores possible differences in the timing of adaptive change under isolation by range extinction versus isolation by dispersal eto a new environment. In the final paper in this section, T. J. Robinson and C. Z. Roux challenge Paterson's basic contention that reinforcement of differences is highly unlikely to occur due to the inevitable and rapid extinction of the smaller of two genetically differentiated populations (Paterson, 1978). They contend that this conclusion rests on an oversimplified model (i.e., a single locus, negative heterosis, and unrestricted random mating) and that "low migration rates in multiniche situations can provide sufficient time and opportunity for speciation by reinforcement" (p. 73). Although their argument does not address the frequency of such displacement events, it does demonstrate that displacement is feasible under some realistic conditions.

The two papers devoted to development and speciation focus on the observation that development may constrain the variation expressed in populations. B. Fabian summarizes developmental studies showing that phenotypic characters can be altered by perturbing development but that, owing to buffering mechanisms, not all perturbations of development will result in phenotypic change. He argues that such buffering mechanisms may cause calculable periods of stasis and that the accumulation of developmental errors will eventually bring about speciation, irrespective of changes in the external environment. This view is reminiscent of recent ideas on entropy and speciation (Brooks and Wiley, 1986). Fabian does not make a concrete connection between the appearance of a novel trait in a population and speciation, and, at least in my view, the link is not obvious. E. Holm contends that both peramorphosis and paedomorphosis lead to specialization to a narrow niche and are likely to limit long-term survival, assertions that seem to contradict Gould's (1977) idea that heterochrony sometimes allows escape from overspecialization. His conclusions that generalists "represent the 'middle of the road' in heterochrony," that peramorphosis is linked to "over-adaptation to the environment," and that paedomorphosis is associated with the "inability to cope" with harsh environments (p. 91) follow from a graphical model relating the concept of "burden" (Riedl, 1978), "adaptation" (equated with selection for increased complexity), and "economy" (equated with selection for reduction). Unfortunately, adaptation and economy are contrasted here as though increased economy cannot be an adaptation. Once this false dichotomy is abandoned, so too can the idea that paedomorphosis is a response to "lack of niche pressure" (p. 91). Instead, it can be an adaptation brought about by selection on timing and/or size directly.

Two "faunal case histories" address basic issues in community ecology. G. M. Branch

focuses on the role of competition in intertidal communities, pointing out that the effect of competition will depend on whether organisms are mobile or sessile, whether food or space is limiting, and whether competition involves interference or exploitation. He suggests that the most important evolutionary role of competition will be during the establishment of a new species, and that whether a new species is a "generalist" or a "specialist" is a function of what similar organisms are present at its inception. Of more direct interest in the present context, he argues that although character displacement can and sometimes does occur, its effects are likely to be local rather than dispersed through the range of a species. C. B. Cottrell contemplates the explanation for his observation that there are few associations between larvae of butterflies of the southwestern Cape region and the distinctive plants of the area. He favors the idea that the plants evolved sclerophyllous leaves and low nutritive content in response to growth on poor soils and drought, and that these characteristics incidentally discouraged caterpillars.

Two other case histories concern the evolution of acoustical mate recognition systems. R. B. Toms's paper on speciation in tree crickets presents one of the most clearheaded arguments in the book. He considers how changes might have occurred in species-specific "calling songs" of male tree crickets, rejecting both character displacement (which he equates with the isolation concept) and the idea that the mating system characters are themselves adaptations that have been fine-tuned to different habitats (which he equates with the recognition concept). Based on observations of wing sizes and on manipulative experiments, he argues that changes in mate recognition systems have often been initiated as automatic consequences of changes in wing size/weight. N. I. Passmore describes the acoustic signals of males of two sibling species of ghost frogs, concluding that the differences between them were selected in relation to acoustical characteristics of their differing habitats (also see Ryan, 1985). One wonders which condition is ancestral and which derived, and whether the evolution of these mating calls might also have been affected by the signals of sympatric frogs or other animals.

The last of the case histories, by T. M. Gosliner, is out of place in this volume (as the word species never appears); however, his thoughts on parsimony and parallelism may be of some interest to cladists. He asserts that the use of parsimony is inappropriate in choosing among alternative phylogenetic hypotheses unless it is determined beforehand that the universe and evolution are parsimonious (what exactly this means is never specified). This claim will amuse those who have followed recent discourse on this topic by Farris (1983), Kluge (1984), Sober (1985), Felsenstein and Sober (1986), and others. His belief that homoplasy has exceeded divergence in opisthobranch gastropods leads to the remarkably general conclusion that "there is nothing in our experience which would suggest that divergence exceeds homoplasy or that it should be the case" (p. 107). One wonders why hierarchical systems of classification have been so successful. Gosliner suggests weighting against characters that vary among outgroups and in favor of characters whose adaptive value seems obvious, and on this basis he prefers a 17-step cladogram of three gastropod genera to one with 13 steps. This is hardly an alternative to parsimony but instead an example of the use of parsimony on characters that have been heavily weighted on highly questionable grounds.

The section devoted to speciation in Hominidae provides some insight into the continuing disagreements over the evolution of the group, despite its minute size and the enormous efforts devoted to the problem. P. V. Tobias proposes that there was relative stasis in hominids between 3.7 and 2.3 million years ago (Myr), cladogenesis cerca 2.3 Myr, and gradual change involving reticulation between semi-isolated populations from 2.3 Myr onward. Although I would not be at all surprised if hominid evolution is neither fully consistent with the punctuated equilibrium model nor with phyletic gradualism, I would find Tobias's scenario much more convincing if it were anchored to an explicit cladistic hypothesis. I was astonished at his faith in stratigraphic information in assessing

the direction of character evolution, especially given the small sample available in most instances. Why not consider information on outgroups? Tobias apparently accepts chronospeciation as well as speciation by splitting, and he acknowledges "incomplete cladogenesis" (p. 139) and bursts of change within species. Unfortunately, he fails to specify how these are to be distinguished. F. E. Grine's critique of previous ideas on the role of competition in early hominid evolution is a much tighter argument, although here again a phylogenetic framework would have helped. He argues convincingly against competitive exclusion arguments for the existence of only one species of hominid at a time, as well as the idea that character displacement led to differences in tooth size. He outlines the simpler alternative that differences in dentition evolved as adaptations to different food types—in particular, robust australopithecines adapted to tougher foods under increasingly xeric conditions, independent of the presence of *Homo*. In the final paper on hominids, A. Turner maintains that "a number of contentious issues in paleoanthropology can benefit from considerations based on the Recognition Concept" (p. 157), but his claims are unconvincing. For example, he disputes claims of phyletic gradualism in homonid evolution (Cronin et al., 1981) on the grounds that the recognition concept favors the punctuation model. In his argument, he equates stasis with "the continuity of a taxon" (p. 154), thereby uncoupling it from evidence pertaining to the tempo of morphological change.

The final section, on species in ecosystems, contains three papers that are only indirectly connected to the basic theme of the book. M. Seely discusses the extraordinary diversity of tenebrionid beetles in the Namib desert, suggesting that relaxed predation has allowed the evolution of conspicuous coloration and diurnal activity. She argues that these traits are physiological adaptations that increase the amount of food consumed and the rate of food processing. Based on a series of simulations, N. Owen-Smith argues that African ungulates of different sizes will seek out vegetation types (differing in leaf size and leaf/stem ratio) that will maximize their fitnesses. He suggests that if vegetation were to change dramatically, there might be behavioral shifts in habitat utilization followed by directional selection for improved performance, which "may well lead to an alteration in mate recognition signals and hence to speciation" (p. 170). According to his model, such vegetation changes as occurred during the Pleistocene would favor grazing bovids relative to browsers or to grazing equids. B. Walker considers that "the existence of at least some species today is due to the fact that selection for system-level properties allowed the system of which they are a part to persist, and not to be replaced by some other system" (p. 176). He supposes that stability/resilience and the efficiency of energy and nutrient movement may be emergent properties of ecosystems that are subject to selection, but concedes that evidence to this effect "does not yet seem to exist" (p. 174). In effect, ecosystems are treated here as types or classes—given sufficient change in species composition, one ecosystem becomes another. Discussions of this sort might benefit from viewing ecosystems as individuals that can undergo change in species composition through time without becoming a new ecosystem.

Overall, this volume is an important contribution to the literature on species and speciation and will amply repay careful reading. As a group, the papers provide an especially good introduction to the recognition concepts of species and, to a lesser extent, an evaluation of it. I fully agree with Vrba (p. xii) that "the distinction between the isolation and recognition concepts is worthy of wider attention than it has received to date," and this book is certain to raise consciousness about this distinction outside of South Africa. However, overly narrow characterizations of the biological species concept (e.g., that it hinges on character displacement) and shallow claims on behalf of the recognition concept (e.g., its consistency with the punctuated equilibrium model) may do more harm than good. There certainly is value in contrasting extreme positions,

but this is not to say that we need to choose among them, for there may be even better alternatives.

Although I can appreciate the focus in this volume on the causes of divergence, this emphasis tends to distract attention from another approach to the species problem. Rather than choose among species concepts on the basis of the presumed frequency of different processes of divergence, perhaps a concept can be developed that is more generally consistent with the processes of interbreeding and descent from a common ancestor (e.g., Cracraft, 1983; Donoghue, 1985). If so, this might be a powerful tool in studying the nature of speciation. That the possibility of a species concept emphasizing phylogenetic pattern has only recently been explored may reflect an underlying attitude, glaringly apparent in the present volume, that the study of species and speciation is properly the domain of population geneticists and paleontologists and that systematists have little to offer. Under this view, speculation on the mechanism of change is valued well above analysis of phylogenetic patterns. Indeed, discussion of the role that cladograms of populations or of geographic areas of endemism might play in the study of speciation is almost completely absent from this volume, in spite of a considerable literature on these topics prior to the symposium (e.g., Wiley, 1981). One hopes that this will change and that, in the future, process theories will be tested in a phylogenetic context. It is obvious from these proceedings that cladists will have to be even more active and effective in communicating the relevance of phylogeny to ecologists and evolutionary biologists. **—Michael J. Donoghue, Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721.**

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