

address theoretical cladistics, it is a surprise that one paper alone is in a section on theory. D. R. Brooks evaluates classifications from an information-theoretical view. Whether one will agree with his conclusions may ultimately rest on agreement with his basic premise, that classifications are meant to convey specific information about characteristics of organisms.

The section on botanical cladistics is significant in the first place by its very presence in the volume. Cladistics has been almost entirely the domain of zoologists, and the increasing interest in it on the part of botanists has been beneficial to all concerned. These papers fall into two categories: how certain special concerns of botanists (for example, hybridization) may affect cladistic theory, and cladistic analyses of actual plant groups. V. Funk concentrates on hybridization, parallelism, and the general lack of even rudimentary phylogenies for use in character analysis. K. Bremer and H.-E. Wanntorp consider the implications of cladistic analysis on classification, from the "phylum" to the "subfamily" level. Not surprisingly, the implications are profound, since many higher plant taxa are not monophyletic groups. The contributions of Sanders (on mints), Bolick (on a genus of composite shrubs), and Churchill (on a family of mosses) all illustrate actual analyses. Although they occasionally exhibit some confusion regarding some cladistic principles, the authors clearly show that, indeed, plants are tractable to cladistic analysis.

One of the most intriguing aspects of cladistics to emerge in recent years is its impact on biogeography. Working on the assumption that much or most of the distributional history of organisms is intimately tied to the history of their environments, cladistic biogeographers look for congruent patterns of plant and animal distributions and attempt to find general environmental causes for these patterns. One finds some surprises in this section of the book. For example, one of the prime subjects for students of southern continental distribution patterns since the time of Joseph Hooker is *Nothofagus*, the southern beeches. Yet, using vicariance methodology, C. J. Humphries concludes that *Nothofagus* had already undergone most of its diversification before the Gondwanian breakup and is not informative about the relationships of the southern continents (his conclusions are partly dependent on an unfortunately meager character data base). Further, Humphries examines the history of how biogeographers, unhindered by precise hypotheses of relation-

ships within the group, used *Nothofagus* to show that prevailing geological theories were correct.

D. R. Brooks, T. B. Thorson, and M. A. Mayes use biogeography to suggest hypotheses of coevolution between South American freshwater stingrays and their helminth parasites. From the testing of a series of precisely constructed hypotheses, the authors conclude that the stingrays and their parasites represent radiations of originally Pacific species that were trapped by the Andean orogeny. Further, on the basis of parasitological relationships, Brooks *et al.* propose a hypothesis of relationships of the rays themselves. Mickevich briefly outlines a method by which biogeographic hypotheses can be evaluated, given certain kinds of data, based on her transformation series analysis. I had some difficulties in following some of the arguments presented in this paper because of some typographical errors and figures that were not as useful as they could have been. N. Platnick discusses conditions in which widespread taxa can be of use in biogeographical studies.

Advances in Cladistics should have been more carefully edited. In many places one gets the impression that the illustrations are based on slides from oral presentations inadvertently left in the papers through subsequent revisions. Some figures make little or no contribution to the explications, and it is a perva-

sive weakness that captions are virtually uninformative. Some papers are marred by critical typographical errors that raise sometimes insurmountable barriers to the reader.

A noteworthy aspect of this book is the participation of so diverse a group of biologists. Specialists in groups as different as mints and helminths were attracted to an organizing principle that allows communication and critical appraisal of hypotheses in comparative biology. Phylogenetic analysis, the foundation of this principle, promises to bring new vitality to comparative and evolutionary biology in coming years. This is not a book for the novice—it is, after all, a symposium volume written by specialists for each other. Nevertheless, given even a passing knowledge of systematic theory, the persistent reader can benefit.

A volume of contributions from the second annual meeting of the Hennig Society is now in preparation. Many issues discussed in the first volume will be addressed in the second, and comparisons will show the progress in the field in the intervening year. The quality, scope, and imagination expressed in this series may be the barometer of how this vigorous and growing brand of comparative biology is faring.

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Adaptive Syndromes

The Mammalian Radiations. An Analysis of Trends in Evolution, Adaptation, and Behavior. JOHN F. EISENBERG. University of Chicago Press, Chicago, 1982. xx, 610 pp., illus. \$45.

The main theme of this book is the several adaptive radiations that have occurred among mammals at various times and places on this planet. The theme is not a new one, and every elementary textbook of vertebrate biology or evolution has examples drawn from the evolutionary convergences demonstrated by the mammalian radiations. However, Eisenberg's contribution is noteworthy because he treats these radiations as natural experiments—tests of evolutionary hypotheses. That such a detailed comparative analysis is now possible is due to recent rapid advances in our under-

standing of the phylogenetic relationships of mammals. This in turn is due to modern techniques that utilize not only the classical functional-morphological comparisons but also biochemical, immunological, and chromosomal data to establish and test hypotheses of relationship. Moreover, these new data are capable of analysis within the new taxonomic paradigm afforded by cladistic analysis. Add to these developments a radically new understanding of the evolution of the earth's surface during the "Age of Mammals" and one has the necessary material for the sort of evolutionary, ecological, and behavioral synthesis that Eisenberg has attempted.

This volume, although formally divided into four parts, really contains three rather distinct books. The first of these is a history of the evolution of mammals,

concentrating in part 1 on what the author terms the early radiations—that is, those that occurred in the Mesozoic and early Cenozoic. These early mammalian radiations occurred on island continents or subcontinents and involved the primitive egg-laying mammals, or monotremes, and the much more diverse marsupials, the former being restricted to the Australian region whereas the latter have survived in both Australia and South America (and marginally in North America). The South American edentates and Afro-Asian pangolins, or scaly anteaters, also receive attention, as does the unique insular fauna of Madagascar. The Malagasy insectivores, or tenrecs, are regarded as a key to understanding the later evolution of placental mammals and are given considerable attention. The natural histories of these diverse mammals are compared, including such matters as their reproductive strategies, their adaptive syndromes (for this read, what they eat, who eats them, how they seek food or avoid predators). Finally, the nature of their behavioral systems is taken up. All of these are considered by means of exemplar species for which adequate or good data are available. From this comparison of the early radiations Eisenberg attempts to develop a “mammalian baseline”—a basic set of primitive behavioral patterns with which to compare the patterns seen in more specialized and more recently evolved mammals. In the second half of this first “book” (part 2), an overview of mammalian radiations on the contiguous continental landmasses, the remaining taxa of mammals are examined in a systematic way. Part 2 ends with a summary chapter on the basic trends that Eisenberg believes he can discern in the patterns of feeding niches, coevolution, and competition among the Mammalia and in existing species diversity and its converse, the problem of species extinction.

In the second “book” (part 3, Macrophysiology and Adaptation) Eisenberg backs off and takes a new, orthogonal view of the same data. He considers, by means of cross-taxon comparisons, those elements that were considered in a systematic fashion in the first two parts. The problem of mammalian body size and its evolution is a unifying theme, and the treatment is an excellent synthesis of the enormous literature that has developed in recent years on the relationships among body size, metabolic rate, reproductive strategies, home range size, foraging strategies, social behavior, and the like. The amount of material Eisenberg attempts to draw together and the com-

plexity of these multiple relationships often produce an intellectual mixture that is difficult to digest, but by the same token it is a stimulating exercise.

The final quarter of the text (part 4, Behavior as a Subject for Study) brings us to Eisenberg’s grail. Its title is a tip-off to its eclectic nature. Again, the comparative, “adaptationist,” approach is employed; behavior is regarded as adaptive and ultimately the product of natural selection. Let the author speak: “The ultimate question, then, is, whether such comparisons of independently developed [mammalian] radiations can confirm our hypotheses concerning the adaptive nature of the social organization itself” (p. 345). By classifying the behavioral elements common to generalized terrestrial mammals, and the interaction systems of these species, Eisenberg attempts to reconstruct primitive mammalian behavioral patterns as a basis for consideration of his final topic, the structure and evolution of social organizations. The book ends with a short synthesis and coda. These include a penultimate figure sketching hypothetical pathways toward the evolution of complex societies, and the ultimate figure (No. 157!) appropriately entitled “The ultimate problem.” One must admire the author’s confidence. This is not the end, however. Appendix 1 is a classification of living mammals to the family level, usually with the genera cited in the text listed under their families. The next several appendixes include body measurements and weights, longevity records, data on reproduction and development, metabolic rates, and encephalization quotients for selected mammalian species.

I have devoted considerable space to the contents of the book because there is so much included. I must emphasize, however, that this is not a mere compendium of interesting facts about mammals. Eisenberg has attempted to draw the entire untidy mass into a coherent picture. I would like to be able to say that he has written a lucid, tightly reasoned chain of logical arguments producing fundamental new insights that lead the reader to a new level of comprehension of the pattern and process of mammalian evolution. That this is not so is completely understandable considering the volume and complexity of the material with which he deals. The fragmentary nature of many of the data available has constrained his comparative approach to a series of bivariate graphs, which constitute the analytical portion of the work, but given the large number of variables this is simply not adequate to convey a

coherent picture. Nevertheless, incomplete as they are, his analyses mark a new level of abstraction in our understanding of mammalian evolution.

The book is not without numerous irritating minor flaws. Mammalian systematists may cavil at misspellings and inconsistencies. There are more typographical errors than I would have expected in a book from a major university press. Some of the graphs are either inadequately labeled or outright mislabeled, thus being obscure when they should illuminate. It would have been convenient had the cladograms in parts 1 and 2 been labeled so that one could easily move from higher to lower taxonomic levels rather than having to search blindly through later pages of the book. There are a few outright errors, such as figure 20, in which a skull that is apparently that of a chipmunk is identified as that of the deer mouse (*Peromyscus*). For the nonspecialist, the index and glossary may be inadequate; for example, if one wished to know the difference between a haplorhine and a strepsirhine primate (p. 302) one would search those sources in vain. Very little literature in Russian and other Slavic languages is cited.

These problems detract from, but do not negate, the great value of this book. As I mentioned at the outset, the examples of adaptive radiation in mammals have been before us for a long time. We have been amazed by the spectacle of “wolves” in Australia, South America, and the rest of the world, each “wolf” the product of an independent adaptive radiation. Amazement has turned to puzzlement as we have contemplated not just single examples of convergent evolution but multiple ones, involving gliding foliovores (“flying squirrels”), fossorial rhizivorous rodents (“gophers”), and many others in faunas long isolated from one another. Eisenberg has provided us with partial answers to these puzzles. The mammals are shaped in an evolutionary sense in response to the interaction between “phylogenetic inertia” and available ecological niches. The niches themselves are, although differing in detail on different continents, shaped by the physical structure of habitats (grassland, forest, and so on) and the availability of discrete types of foods (grass, leaves, and so on). Exploitation of these food resources, and the ongoing coevolution of food plants and their herbivores, herbivores and their predators, serve to shape the final equilibrium product that we see as the mammalian community. You are what you eat—myrme-

cophagy ("ant-eating") results in convergence toward what appears to be an optimal means of exploiting this trophic resource, regardless of the initial stock from which the anteater has sprung. Moreover, optimal exploitation seems to depend on a particular body plan, or morphotype.

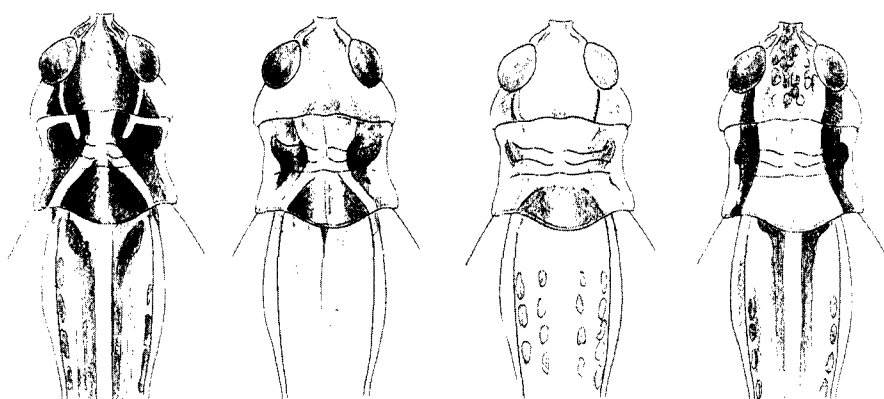
It is refreshing to me, at least, to see an argument as well reasoned as this one that is frankly "adaptationist" in its outlook. The "adaptationist program" has come under attack in recent years by a number of biologists who question the interpretation of organismic structure and function (and behavior) solely in terms of adaptations produced as a result of natural selection. One of the most eloquent spokesmen for this group of iconoclasts is Stephen Jay Gould. I once heard a witty and fascinating talk of his entitled "The Spandrels of Saint Marks," in which he argued that many seemingly adaptive features of animal structure are simply the product of other evolutionary pressures, just as the decorations in the spaces between adjacent church arches are the opportunistic result of a quite different solution to a structural problem. One may agree with Gould that not every squinch and pendentive of mammalian architecture is adaptive. Nevertheless, Eisenberg's book provides abundant evidence that adaptation has been by far the most important evolutionary factor leading to the great richness and diversity of the mammals with which we share the world today.

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Insects: A Manual

The North American Grasshoppers. Vol. 1, Acrididae: Gomphocerinae and Acridinae. DANIEL OTTE. Harvard University Press, Cambridge, Mass., 1981. xii, 276 pp., illus., + plates. \$45.

Insects play major roles in all terrestrial ecosystems, but their use in ecological research is impeded by inadequate knowledge of their taxonomy and a lack of authoritative identification manuals. These impediments are unfortunate because the abundance, diversity, and short generation time of insects often make them, rather than vertebrates, animals of choice in testing ecological the-



"Pattern variation in *Aulocara elliotti* females." The species, "very abundant in the western half of the United States, southern portions of the prairie provinces of Canada, and north-central Mexico," is "often associated with bare patches of ground." [From *The North American Grasshoppers*, vol. 1]

ory. The plenitude of insect species contributes to the poor state of their taxonomy. North America, for example, has 2,000 species of tetrapod vertebrates but more than 90,000 species of insects. Even in insect groups that are taxonomically well worked, identification of North American species is generally impossible without help from a specialist. Specialists are scarce, and to identify insects for field biologists they usually must take time from their own research—yet another reason why many insect species are still to be discovered, recognized, and described.

Daniel Otte has made a praiseworthy start toward easing the problems of species identification of North American grasshoppers, an insect group that has been taxonomically well studied and that is important both ecologically and economically. In this, the first of a projected three volumes that will include all species north of Panama, Otte treats the 127 species of two subfamilies in a manner that makes the user as confident of grasshopper identifications as he or she would be of bird identifications in using Peterson's *Field Guide to the Birds*. Otte accomplishes his purpose with clear, concise text and an abundance of pertinent, well-executed illustrations. Like Peterson, he does his own artwork, and each drawing shows features that facilitate correct choices among candidate species.

Like birds, grasshoppers often vary intraspecifically in hue and pattern. Otte illustrates much of this variation in full color—16 plates, including 159 portraits of whole insects and 44 "bust" drawings (head and prothorax). Further, he inserts unnumbered hundreds of line drawings of portions of grasshoppers, showing key interspecific differences and noteworthy

intraspecific variants. He depicts the known distribution of each species by bold points on a base map.

The North American Grasshoppers is directed primarily toward professional biologists rather than amateur naturalists. It spares no space for common names or suggestions of how to maintain a hobby interest in grasshoppers. On the other hand, it is not written chiefly for other taxonomists. A three-page glossary helps the nonspecialist build needed vocabulary, and one page is devoted to how taxonomists pronounce the 42 valid generic names. (An ecologist thus need not risk embarrassment in talking to a grasshopper expert about *Boopedon* or *Xeracris*—"Bohohpedon" or "Zeer-acris.") Taxonomic esoterica, such as nomenclatural histories and locations of type specimens, are made brief and consigned to appendixes. The main text keeps to the business of state-of-the-art species identifications using well-illustrated dichotomous keys, tables of identifying features, and succinct species accounts that deal with geographical distribution, recognition, habitat, seasonal life cycle, and references.

I know of no finer or more authoritative identification manual for any group of animals. For North American insect species, this book has no equal. Adolescent field biologists may become partial to taxonomic groups in which they can identify the species they encounter. If this be so and if Otte completes the remaining volumes of his projected trilogy, we should observe within the decade a surging of research on grasshoppers.

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