SCHEINER, S. M. 1992. Grand syntheses in the making. Science 258:1820–1822.

SCHLUTER, D., AND L. GUSTAFSSON. 1993. Maternal inheritance of condition and clutch size in the collared flycatcher. Evolution 47:658–667.

SCHMID-HEMPEL, P. 1990. In search of optima: Equilibrium models of phenotypic evolution. Pages 321–347 *in* Population biology: Ecological and evolutionary viewpoints (K. Wöhrmann and S. K. Jain, eds.). Springer-Verlag, Berlin.

SCHMIDT, K. P., AND D. A. LEVIN. 1985. The comparative demography of reciprocally sown populations of *Phlox drummondii* Hook. I. Survivorships, fecundities, and finite rates of increase. Evolution 39:396–404

SEMLITSCH, R. D., R. N. HARRIS, AND H. M. WILBUR. 1990. Paedomorphosis in *Ambystoma talpoideum*: Maintenance of population variation and alternative life history pathways. Evolution 44:1604–1613.

SEMLITSCH, R. D., AND H. M. WILBUR. 1989. Artificial selection for paedomorphosis in the salamander *Ambystoma talpoideum*. Evolution 43:105–112.

STEARNS, S. C. 1976. Life-history tactics: A review of the ideas. Q. Rev. Biol. 51:3–47.

STEARNS, S. C., AND R. E. CRANDALL. 1981. Quantitative predictions of delayed maturity. Evolution 35:455–463.

STEARNS, S. C., AND R. E. CRANDALL. 1984. Plasticity for age and size at sexual maturity: A life-history response to unavoidable stress. Pages 13–33 *in* Fish reproduction: Strategies and tactics (W. Potts and R. J. Wooten, eds.). Academic Press, New York.

STEWART, J. R. 1992. Placental structure and nutritional provision to embryos in predominantly lecithotrophic viviparous reptiles. Am. Zool. 32:303–312.

STRATHMANN, R. R. 1985. Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. Annu. Rev. Ecol. Syst. 16:339–361.

TILLEY, S. G. 1980. Life histories and comparative demography of two salamander populations. Copeia 1980:806–821.

TILLEY, S., AND J. BERNARDO. 1993. Life history evolution in plethodontid salamanders. Herpetologica 49:154–163.

TREXLER, J. C., AND J. TRAVIS. 1990. Phenotypic plasticity in the sailfin molly, *Poecilia latipinna* (Pisces: Poeciliidae). I. Field experiments. Evolution 44:143–156.

WERNER, E. E. 1986. Amphibian metamorphosis: Growth rate, predation risk, and the optimal size at transformation. Am. Nat. 128:319–341.

WERNER, E. E. 1988. Size, scaling and the evolution of complex life cycles. Pages 60–79 *in* Size-structured populations: Ecology and evolution (B. Ebenman and L. Persson, eds.). Springer-Verlag, New York.

WILBUR, H. M. 1980. Complex life cycles. Annu. Rev. Ecol. Syst. 11:67–93.

WILBUR, H. M., AND P. J. MORIN. 1988. Life history evolution in turtles. Pages 387–439 *in* Biology of the Reptilia, Volume 16. Defense and life history (C. Gans and R. B. Huey, eds.). Alan R. Liss, New York.

WILLIAMS, G. C. 1966. Adaptation and natural selection. Princeton Univ. Press, Princeton, New Jersey.

WILLIS, J. H., J. A. COYNE, AND M. KIRKPATRICK. 1991. Can one predict the evolution of quantitative characters without genetics? Evolution 45:441–443.

WILLSON, M. F. 1981. On the evolution of complex life cycles in plants: A review and an ecological perspective. Ann. Mo. Bot. Gard. 68:275–300.

WOLFF, K. 1990. Genetic analysis of ecologically relevant morphological variability in *Plantago lanceolata* L. 5. Diallel analysis of two natural populations. Theor. Appl. Genet. 79:481–488.

YODZIS, P. 1989. Introduction to theoretical ecology. Harper and Row, New York.

Joseph Bernardo, Department of Zoology, Box 90325, Duke University, Durham, North Carolina 27708-0325, USA.

Syst. Biol. 43(1):148–151, 1994

Biology of Whiptail Lizards (Genus *Cnemidophorus*).—John W. Wright and Laurie J. Vitt (eds.). 1993. Oklahoma Museum of Natural History, Norman. 417 pp. $29.00 (cloth).

This book is based on a 1984 symposium organized during a joint meeting of the American Society of Ichthyologists and Herpetologists, the Herpetologists' League, and the Society for the Study of Amphibians and Reptiles on the campus of the University of Oklahoma at Norman. Pages vii–x present a list of authors and titles of papers presented at the original symposium (36 authors for 30 contributed papers), and pages xi–xii list 12 papers related to symposium topics that were published in peer-reviewed journals in the years 1983–1991. This volume reports original findings through September 1992 and is organized into 15 chapters written by 22 authors; several related papers also recently appeared in a publication by Dawley and Bogart (1989). The book is dedicated to Charles H. Lowe and Richard G. Zweifel, whose work in the 1940s and 1950s laid the foundation for the next several decades of research on whiptail lizards, and the topics covered include an overview of the taxonomic history of the genus *Cnemidophorus*, its current content and some phylogenetic hypotheses, several aspects of both population and community ecology, social behavior, the psychobiology of parthenogenetic reproduction, and physiology of hibernation. Other than anecdotal observations presented in several chapters, the systematic content of the book is largely confined to chapters 1 and 2, which will be the focus of this review.

The first chapter, by C. H. Lowe, provides an overview of the taxonomic history of the genus, which Lowe divides into discrete periods on the basis of the nature of the contributions. For example, the first phase of study spans seven decades (1830–1900), beginning with the origin of the generic name (by Wagler in 1830) and continuing through the shift of interest from Europe to the United States, with the field work of Baird and Girard (1852–1859) and E. Hallowell (1853–1860). The first modern synopsis was attempted by E. D. Cope in 1892, although he found species boundaries extremely difficult to diagnose. The period from 1900 to about 1950 was characterized by more in-depth taxonomic treatments (including Burt's 286-page monograph published in 1931) in which recognized species were arranged into species groups. Burt (1931) recognized a total of 14 species organized into five species groups.

Today at least 45 species are recognized within *Cnemidophorus*, and according to Lowe (p. 4), the inability to discriminate this plethora of taxa prior to the 1950s "resulted from what is called the discriminate power of their scales (or levels) of measurement." Lowe continues (p. 4) with what is a confusing and poorly written section describing methods of the pre-1950s workers as being

> primarily nominal and ordinal rather than interval. While nominal and ordinal data are not isomorphic with the numbering system we call arithmetic (which is necessary for parametric statistical testing on null hypotheses), there were before 1950 nonparametric tests for data on the classical nominal and ordinal scales of measurement by which null hypotheses could then, as now, be tested.

All that need be said here is that prior to 1950, workers could have, but did not, test their ideas about species identities with nonparametric methods appropriate for the qualitative types of characters collected at that time. The jargon Lowe uses in this section is unnecessary and detracts from his bottom-line message.

Lowe continues by describing later examples of statistical tests employed with meristic data (scales around midbody, number of scales between paravertebral stripes, etc.) to reject null hypotheses. This approach, specifically the use of Dice–Leraas diagrams with two standard errors as the basis for rejecting the null hypothesis at a level of $\alpha = 0.05$, permitted the first rigorous quantitative assessments of taxonomic boundaries. Following these were the first reports of all-female populations of *Cnemidophorus* independently by Duellman and Zweifel, and Maslin in 1962 and then the Lowe and Wright proposition (in 1966) that these parthenogenetic populations originated by interspecific hybridization between sexual taxa.

Lowe describes the 1960s and 1970s as a period of substantial progress in various aspects of phylogeny, taxonomy, reproduction, genetics, speciation, behavior, and ecology (p. 6). Lowe views this symposium (in 1984) as foretelling that the major efforts in future studies of *Cnemidophorus* would not be primarily in systematics, because much of this had, in his view, already been achieved. Lowe does not exactly specify what he means by this important phase of systematic work being essentially complete, and in the next paragraph (p. 6) he goes on to state that knowledge of relationships within this group has been brought to its present high level of resolution by chromosomal studies, which have permitted the recognition of four species groups. These groups have been verified by additional allozyme, mtDNA, and histocompatability studies.

I disagree with Lowe's assessment of the state of phylogenetic studies of *Cnemidophorus* for the following reasons. First, the majority of studies summarized by Lowe either predate the widespread use of character-based parsimony methods (the citations given ranged from 1962 through 1986, and 19 of the 33 papers given were published prior to 1975) or were not strictly phylogenetic in their focus. More recent mtDNA restriction-site studies have corrected some of these shortcomings, but the majority of these deal only with species relationships within some of the historically recognized species groups. No rigorous phylogenetic investigation has yet been carried out to confirm monophyly of some of the species groups or to evaluate group relationships and the deep history of the genus. It is more accurate to state that the systematic work to date provides some hypotheses that require additional testing of species boundaries and phylogenetic relationships.

Second, as evident in chapter 2 by Wright, many historical entities have been identified but not yet named, so there is a considerable amount of work to be done even at the level of alpha taxonomy. There is an especially acute need to complete basic collecting, alpha taxonomy, and then testing of hypotheses of species boundaries and relationships of the South American groups. The recent paper by Cole and Dessauer (1993) represents a good first effort in this direction.

The final exclusively systematic topic dealt with by Lowe is his brief mention (pp. 6–7) of the controversy surrounding the application of Linnaean binomials to unisexual taxa. Lowe simply introduces the topic, but it is treated in more detail in the next chapter.

The second chapter, by Wright, provides a thorough overview and summary of the current content of the genus *Cnemidophorus* and is especially valuable because it provides color plates of all recognized species and range maps of the six species groups. Wright draws attention to earlier conservative approaches used to define species boundaries but not to reconstruct phylogenetic relationships and emphasizes the point that of the 45+ species currently recognized, one third of which are unisexual, virtually all with formal names (species and subspecies) have been diagnosed primarily on external morphological characters, chromosomes (which are seldom diagnostic at these levels of divergence), and to a lesser extent multilocus isozyme data. The Appendix to this chapter summarizes the accepted names for all species, arranged by group. Two of the six species groups contain only unisexual taxa (the *cozumelae* and *tesselatus* groups), and two of the remaining four include both bisexual and unisexual taxa (*lemniscatus* and *sexlineatus* groups). On page 32, Wright highlights the fact that the *lemniscatus* group is one of the least understood (see also Cole and Dessauer, 1993), primarily because of major sampling gaps across the large range of this group in South America.

Pages 34–66 provide a valuable summary of current interpretations of the origin and evolution of parthenogenetic species of *Cnemidophorus.* This section includes a review of the first published reports (4 papers dating from 1958 to 1962) and the early "weed hypothesis" of Wright and Lowe (1968), early studies of geographic variation and systematic/taxonomic issues (8 papers, 1964–1968), aspects of unisexual reproduction (6 papers, 1968–1977), the origin and evolution of various unisexual populations (15 papers, 1965–1984), hybridization between parthenogenetic and bisexual species (8 papers, 1966–1971), histocompatibility studies (3 papers, 1967–1977), and the recent series of studies based on the mtDNA genome (11 papers, 1979–1992). Wright briefly contrasts the hypotheses of hybrid versus spontaneous origin for the parthenogenetic populations (11 papers, 1966–1989) and discusses the nomenclatural issues posed by these lineages. Four general patterns emerge from these studies: (1) all parthenogenetic *Cnemidophorus,* including 2n and 3n populations, appear to have originated via interspecific hybridization; (2) the unisexual lineages appear to be relatively young; (3) some of the unisexual lineages have the highest levels of genetic variability (42–68% allozyme heterozygosity) known for any organism; and (4) several unisexual species show little or no between-population variation in genotype/haplotype profiles over large geographic areas (this observation suggests that the establishment of these lineages may have been restricted to single hybridization events, in sharp contrast to some unisexual species of gekkonid lizards; Moritz et al., 1989).

From a phylogenetic perspective, several weaknesses are evident in this review. Wright points out some of the species problems in *Cnemidophorus,* and much of the confusion seems to stem from failure of many workers to adopt an operational species concept before beginning any phylogenetic investigation. The conservative approach recently advocated by Davis and Nixon (1992) might be especially useful, but regardless of the concept adopted, investigators should extend the logic of the hypothesis-testing approach discussed by Lowe and clearly define what criteria will be used to diagnose species and then design sampling protocols to test hypotheses of species boundaries.

A second major gap in the data base is the absence of corroboration for the hypothesized relationships of the species groups (i.e., the deep history of *Cnemidophorus*). Wright presents a very brief discussion of these relationships on pages 33–34 and summarizes them in figure 1 (p. 29). This is the hypothesis presented by Lowe et al. in 1970, and it is based on nondifferentially stained karyotypes with a $2n = 52$ "prototype" designated as the ancestral configuration. No justification or rationale is given for this choice as the ancestral karyotype, so we cannot be certain if the polarities of the rearrangements postulated in figure 1 are accurate. Two groups have identical karyotypes (*deppei* and *hyperythrus*) and therefore cannot be fully resolved with this data set alone. Wright emphasizes the point that the two exclusively unisexual groups (*cozumelae* and *tesselatus*) are artificial constructs rather than historical monophyletic units. What is presented is a very preliminary working hypothesis for aspects of the deep history of this genus, and this chapter could have been improved by Wright's emphasis of this point. Considerable advances have been made both in outgroup approaches to character polarization (Maddison et al., 1984) and phylogenetic analyses of clades containing taxa of hybrid origin (McDade, 1990, 1992), and much exciting phylogenetic work remains to be completed for this radiation.

On page 31, Wright describes several cases of parapatric contact zones characterized by limited hybridization (based on morphological assessments) between different combinations of formally named taxa, specifically a number of subspecies of the *tigris* group distributed across mainland Mexico. He then strongly emphasizes the point that many species have undergone recent and rapid evolution and are just now developing secondary isolating mechanisms, yet the single zone that has been examined with independent molecular markers (a *marmoratus* × *tigris* contact in New Mexico; see Dessauer and Cole, 1991) showed that the populations involved were characterized by fixed or nearly fixed differences at six isozyme loci, as well as color and pattern differences. This level of divergence does not support the idea of very recent origins of these taxa, and the fact that other combinations of contacts are known suggests that the *tigris* group might be a valuable resource for detailed comparative studies of hybrid zone questions (recently reviewed by Harrison, 1993).

On pages 30 and 33, Wright annoyingly cites a recent paper by himself (Wright, 1993) and then gives a complete title and citation as "In press' but fails to name the journal. This is inexcusable if the paper really is in press.

These criticisms aside, the editors have done a valuable service in pulling together a great deal of information on a large and fascinating tetrapod genus. From an evolutionary perspective, the book could have been improved by inclusion of updated reviews of issues concerning the ecological and evolutionary consequences of parthenogenesis, the significance of clonal diversity or its absence, and the meiotic mechanisms associated with the establishment and maintenance of parthenogenetic reproduction in vertebrates. However, because many of these topics were treated by Dawley and Bogart (1989) their absence here does not seriously detract from this volume. Evolutionary biologists interested in a broad array of comparative questions will find this book a grab bag of ideas for the formulation of new hypotheses.

References

BURT, C. E. 1931. A study of the teiid lizards of the genus *Cnemidophorus* with special reference to their phylogenetic relationships. Bull. U.S. Natl. Mus. 154:1–286.

COLE, C. J., AND H. C. DESSAUER. 1993. Unisexual and bisexual lizards of the *Cnemidophorus lemniscatus* complex (Squamata: Teiidae) of the Guiana Region, South America. Am. Mus. Novit. 3081:1–30.

COPE, E. D. 1892. A synopsis of the species of the teiid genus *Cnemidophorus*. Trans. Am. Philos. Soc. 17:27–52.

DAVIS, J. I, AND K. C. NIXON. 1992. Populations, genetic variation, and the delimitation of phylogenetic species. Syst. Biol. 41:421–435.

DAWLEY, R. M., AND J. P. BOGART (eds.). 1989. Evolution and ecology of unisexual vertebrates. N.Y. State Mus. Bull. No. 466, Albany, New York.

DESSAUER, H. C., AND C. J. COLE. 1991. Genetics of whiptail lizards (Reptilia: Teiidae: *Cnemidophorus*) in a hybrid zone in southwestern New Mexico. Copeia 1991:622–637.

HARRISON, R. G. (ed.). 1993. Hybrid zones and the evolutionary process. Oxford Univ. Press, New York.

LOWE, C. H., J. W. WRIGHT, C. J. COLE, AND R. L. BEZY. 1970. Chromosomes and evolution of the species groups of *Cnemidophorus* (Reptilia: Teiidae). Syst. Zool. 19:128–141.

MADDISON, W. P., M. J. DONOGHUE, AND D. R. MADDISON. 1984. Outgroup analysis and parsimony. Syst. Zool. 33:83–103.

MCDADE, L. A. 1990. Hybrids and phylogenetic systematics. I. Patterns of character expression in hybrids and their implications for cladistic analysis. Evolution 44:1685–1700.

MCDADE, L. A. 1992. Hybrids and phylogenetic systematics. II. The impact of hybrids on cladistic analysis. Evolution 46:1329–1346.

MORITZ, C., W. M. BROWN, L. D. DENSMORE, J. W. WRIGHT, D. VYAS, S. DONNELLAN, M. ADAMS, AND P. BAVERSTOCK. 1989. Genetic diversity and the dynamics of hybrid parthenogenesis in *Cnemidophorus* and *Heteronotia* (Gekkonidae). Pages 87–112 *in* Evolution and ecology of unisexual vertebrates (R. M. Dawley and J. P. Bogart, eds.). N.Y. State Mus. Bull. No. 466, Albany, New York.

WRIGHT, J. W., AND C. H. LOWE. 1968. Weeds, polyploids, parthenogenesis, and the geographical and ecological distribution of all-female species of *Cnemidophorus*. Copeia 1968:128–138.

Jack W. Sites, Jr., Department of Zoology, Brigham Young University, Provo, Utah 84602, USA.