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Phylogenetic Relationships of Whiptail Lizards of the Genus *Cnemidophorus* (Squamata: Teiidae): A Test of Monophyly, Reevaluation of Karyotypic Evolution, and Review of Hybrid Origins

TOD W. REEDER,[1] CHARLES J. COLE,[2] AND HERBERT C. DESSAUER[3]

CONTENTS

[1] Research Associate, Division of Vertebrate Zoology (Herpetology), American Museum of Natural History; Assistant Professor, Department of Biology, San Diego State University, San Diego, CA 92182–4614; e-mail: treeder@sunstroke.sdsu.edu.

[2] Curator, Division of Vertebrate Zoology (Herpetology), American Museum of Natural History; e-mail: cole@amnh.org.

[3] Research Associate, Division of Vertebrate Zoology (Herpetology), American Museum of Natural History; Professor Emeritus, Department of Biochemistry and Molecular Biology, Louisiana State University Medical Center, New Orleans, LA 70119-2799.

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ABSTRACT

Phylogenetic relationships of the whiptail lizards of the genus *Cnemidophorus* are inferred based on a combined analysis of mitochondrial DNA, morphology, and allozymes. Within the Teiini, *Teius* and *Dicrodon* are the most basal lineages, and these two taxa form a graded series leading to a cnemidophorine clade containing *Ameiva*, *Cnemidophorus*, and *Kentropyx*. *Cnemidophorus* monophyly is not supported, with members of the neotropical ''*C.*'' *lemniscatus* species group (except ''*C.*'' *longicaudus*) being more closely related to species in other neotropical cnemidophorine taxa (*Ameiva* and *Kentropyx*). *Ameiva* is also paraphyletic.

The ''*Cnemidophorus*'' *lemniscatus* species group is also paraphyletic, with a ''*C.*'' *murinus* + ''*C.*'' *lemniscatus* complex clade being more closely related to *Kentropyx* than to ''*C.*'' *lacertoides*, ''*C.*'' *longicaudus*, and/or ''*C.*'' *ocellifer*. Although the ''*C.*'' *lemniscatus* species group is paraphyletic, the three remaining bisexual ''*Cnemidophorus*'' species groups (*deppii*, *sexlineatus*, and *tigris* species groups) are each monophyletic. Together, these three groups form a clade (= North American ''*Cnemidophorus*'' clade), with the *deppii* and *tigris* species groups being sister taxa. Within the ''*Cnemidophorus*'' *deppii* species group, the Baja California ''*C.*'' *hyperythrus* is the sister species to a more exclusive mainland Mexico clade containing ''*C.*'' *deppii* and ''*C.*'' *guttatus*. Except for a ''*C.*'' *inornatus* + ''*C.*'' *sexlineatus* clade and a monophyletic ''*C.*'' *gularis* complex, the inferred inter- and intraspecific relationships within the *sexlineatus* species group are weakly supported. In none of the inferred phylogenies are the ''*C.*'' *costatus* populations (''*C.*'' *c. costatus* and ''*C.*'' *c. griseocephalus*) represented as each other's closest relatives.

Because of *Cnemidophorus* paraphyly, nomenclatural changes are recommended. *Aspidoscelis* Fitzinger, 1843, is resurrected for the North American ''*Cnemidophorus*'' clade containing the *deppii*, *sexlineatus*, and *tigris* species groups (and the unisexual taxa associated with them). Lizards of the genus *Aspidoscelis* differ from all other cnemidophorine lizards by the combined attributes of absence of basal tongue sheath, posterior portion of tongue clearly forked, smooth ventral scutes, eight rows of ventral scutes at midbody, absence of anal spurs in males, mesoptychial scales abruptly enlarged over scales of gular fold (more anterior mesoptychials becoming smaller), three parietal scales, and three or four supraocular scales on each side.

Previous studies using morphology and allozymes have determined that the unisexual *Kentropyx borckiana* originated from a historical hybridization event between the bisexual species *K. calcarata* and *K. striata*. In this study mitochondrial DNA confirms *K. striata* as the maternal ancestor of *K. borckiana*.

A review of our current knowledge of teioid unisexuals and their hybrid origins is provided. Also, a reevaluation of teiine chromosomal evolution is presented from a phylogenetic perspective. These reviews elucidate the paradox that the capability of instantly producing parthenogenetic clones through one generation of hybridization has existed for approximately 200 million years, yet the extant unisexual taxa are of very recent origins. Consequently, these lineages must be ephemeral compared to those of bisexual taxa.

INTRODUCTION

CNEMIDOPHORUS BACKGROUND AND CLASSIFICATION

Teiid whiptail lizards of the genus *Cnemidophorus* range widely in the New World, extending from the northern United States southward to Argentina, and occupy many diverse ecological communities. However, while exhibiting this extensive distribution, their greatest diversity occurs in North America, where they are a conspicuous component of the herpetofauna of the arid and semiarid regions of the southwestern U.S. and Mexico. By conservative count, there are approximately 50 species known (for recent summaries see Maslin and Secoy, 1986; Wright, 1993), with new species continuing to be found (e.g., Markezich et al., 1997; Rocha et al., 1997, 2000).

Because of their abundance and conspicuous nature, whiptails are an ecologically important squamate lizard clade, which is reflected by the great number of ecological and life history studies conducted on this group (reviewed in Wright and Vitt, 1993). *Cnemidophorus* has been (and continues to be) one of the most extensively studied genera of lizards, third only to *Sceloporus* and *Anolis* (Dunham et al., 1988). Besides their abun-

TABLE 1
***Cnemidophorus* Species Groups**[a]

Species group	No. of species[b]	Diploid no. (2n)[c]	Comments
cozumela	3	49	All parthenogenetic
deppii	5	52	All bisexual
lemniscatus	15	50	Few parthenogenetic taxa (2n & 3n)
sexlineatus	24	46	Many parthenogenetic taxa (2n & 3n)
tesselatus	4	46	All parthenogenetic (2n & 3n)
tigris	1	46	All bisexual

[a]Modified from Lowe et al. (1970).
[b]Based on Wright (1993).
[c]Number of chromosomes, which is higher in triploids and some clonal variants.

dance and geographic proximity to North American biologists, one of the reasons whiptails have been so intensively studied is the occurrence of parthenogenetic all-female species (of interspecific hybrid origin; see below) within this diverse clade. Approximately one-third of the described species are unisexual, with the majority of these all-female species occurring in the southwestern U.S. and northern Mexico (Wright, 1993). Diploid and triploid unisexual species have evolved many times in *Cnemidophorus*, in each instance the switch from sperm-dependent to sperm-independent reproduction occurring in one generation in an F_1 interspecific hybrid (for reviews, see Darevsky et al., 1985; Dessauer and Cole, 1989; Moritz et al., 1989a, 1992a; Darevsky, 1992; Cole and Dessauer, 1995), and dynamic hybridization presently occurs in nature (e.g., Walker et al., 1989; Dessauer et al., 2000; Taylor et al., 2001). Consequently, whiptail lizards are used broadly in research, particularly in reproductive biology, population genetics, physiological ecology, and evolutionary biology, often with emphasis on the instantaneous, multiple and independent origins of parthenogenetic cloning.

The species of *Cnemidophorus* are currently allocated to six species groups (table 1). Based on external morphology and karyology, these groups were erected by Lowe et al. (1970), who modified Burt's (1931) arrangement. All except the *lemniscatus* group are confined to North and Central America. The *lemniscatus* group is largely a South American radiation, with only a single species (*C. lemniscatus*) extending into Central America. Two of the northern *Cnemidophorus* species groups (*cozumela* and *tesselatus*) are composed entirely of parthenogenetic species. The origins of the unisexual species in both of these groups involve hybridization between bisexual species from different species groups (i.e., *sexlineatus* group × *deppii* group = *cozumela* group; *sexlineatus* group × *tigris* group = *tesselatus* group). The *lemniscatus* and *sexlineatus* groups each possess bisexual and unisexual species. However, unlike the aforementioned completely unisexual groups, the unisexuals in the *lemniscatus* and *sexlineatus* groups are derived exclusively from hybridizations between species within their respective groups (intragroup hybridizations).

Higher-Level Relationships and *Cnemidophorus* Monophyly

While *Cnemidophorus* has been extensively studied and much is known about its biology, ecology, and natural history, the specific phylogenetic placement of *Cnemidophorus* within the Teiidae, as well as the higher-level relationships within *Cnemidophorus*, has received little attention. Presch (1974) provided osteological evidence that the macroteiids consisted of two major groups: Teiini (including *Ameiva*, *Cnemidophorus*, *Dicrodon*, *Kentropyx*, and *Teius*) and Tupinambini (including *Callopistes*, *Crocodilurus*, *Dracaena*, and *Tupinambis*). Within the Teiini, *Ameiva*, *Cnemidophorus*, and *Kentropyx* shared the most similarities, lead-

ing Presch to hypothesize that these three taxa were more closely related to each other than any were to *Dicrodon* or *Teius*. However, there were no derived osteological characters provided to resolve the relationships among *Ameiva*, *Cnemidophorus*, and *Kentropyx*. Informally we refer to these three very similar taxa as the cnemidophorines.

Using external morphology and intuition, Burt (1931) was the first to hypothesize higher-level relationships within *Cnemidophorus* (fig. 1A). Because members of the South American *lemniscatus* group shared some characteristics with other South American teiids (e.g., *Ameiva*), Burt (1931) postulated that the *lemniscatus* group was the most primitive lineage within *Cnemidophorus*. The ancestor of the North American groups was hypothesized to have been derived from the *lemniscatus* group, with this lineage giving rise to the *deppii* (excluding *C. hyperythrus*) and *sexlineatus* groups. Burt (1931) also proposed that his *tesselatus* group (including the as-yet-to-be-described *tigris* group) and *hyperythrus* groups were derived from the *sexlineatus* group.

Based on karyology, external morphology, and knowledge of the existence of unisexual species, Lowe et al. (1970) modified the higher-level classification and hypothesized relationships within *Cnemidophorus*. The evolutionary scenario (fig. 1B) proposed by Lowe et al. (1970) was largely influenced by their assumption that the chromosomes of vertebrates evolve primarily by means of Robertsonian centric fusion, thus resulting in the reduction of diploid chromosome number. Members of the *deppii* group possess the highest diploid number (2n = 52) within *Cnemidophorus*. Given this, Lowe et al. (1970) suggested that the *deppii* group (including the *cozumela* group) represented the most ''primitive'' lineage within *Cnemidophorus*, possessing a karyotype essentially identical to that of the hypothesized ancestor of *Cnemidophorus*. Such a conclusion differed from Burt (1931), who suggested that the *lemniscatus* group was ancestral to the remaining *Cnemidophorus* species groups. Lowe et al. (1970) postulated that the *lemniscatus* group evolved from a *deppii*-like ancestor, requiring only a single centric fusion to derive the *lemniscatus* group karyotype (2n = 50) from the *deppii* group/ancestral karyotype. The *sexlineatus* and *tigris* groups were proposed to be sister taxa, with their common ancestor being derived from a *deppii*-like ancestor (via three centric fusions).

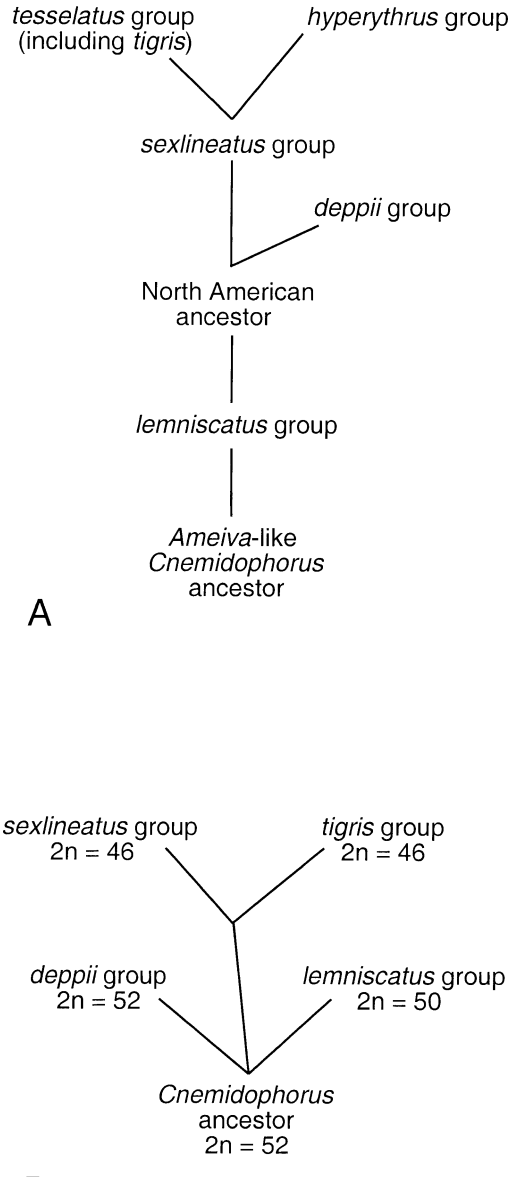

Fig. 1. Previous phylogenetic hypotheses of higher-level relationships within *Cnemidophorus*. **A.** Modified hypothesis of Burt (1931). **B.** Modified hypothesis of Lowe et al. (1970).

Based on mitochondrial DNA restriction site data, Moritz et al. (1992a) provided the first explicit phylogenetic analysis of higher-level relationships within *Cnemidophorus*. In that study, *C. lemniscatus* was used to root the resulting phylogeny. This outgroup choice was based on Burt (1931) and the fact that the greatest observed genetic distances were between *C. lemniscatus* and the remaining *Cnemidophorus* species (see also Dessauer and Cole, 1989). Moritz et al. (1992a) provided strong support for a sister group relationship between the *sexlineatus* and *tigris* groups, corroborating the hypothesis of Lowe et al. (1970). These mitochondrial data also supported the placement of the *deppii* group as the sister taxon to the *sexlineatus* group + *tigris* group clade. Monophyly of the *deppii* and *sexlineatus* groups was also supported by Moritz et al. (1992a). However, because of the limited sampling, these conclusions could only be considered preliminary. Even so, the relatively large estimated sequence divergences between *C. lemniscatus* and the remaining *Cnemidophorus* species are suggestive of a relatively basal position for the *lemniscatus* group. However, this study cannot be viewed as a rigorous test of the basal relationships within *Cnemidophorus* (e.g., hypotheses of Burt, 1931 vs. Lowe et al., 1970). Such a test would require the inclusion of other closely related teiine taxa (e.g., *Ameiva*, *Kentropyx*) as outgroups.

While there have been previous attempts to organize *Cnemidophorus* into species groups and hypothesize on the interrelationships of these groups, there has never been a rigorous attempt to demonstrate the monophyly of this group of lizards. All previous studies generally assumed that *Cnemidophorus* was monophyletic, based on the phenetic similarity between *Cnemidophorus* and other South American teiid lizards (i.e., *Ameiva*, *Dicrodon*, *Kentropyx*, and *Teius*). Historically, *Cnemidophorus* has been defined by the absence of presumably derived character states exhibited by these other South American genera (i.e., laterally compressed teeth in *Dicrodon* and *Teius*, keeled ventral scales in *Kentropyx*, basal tongue sheath in *Ameiva*). The long recognition that *Cnemidophorus* lacked apomorphies, and earlier hypotheses suggesting that various lineages of *Cnemidophorus* were independently derived from ancestral South American ''stocks'' (e.g., Burt, 1931; Lowe et al., 1970) suggest that *Cnemidophorus* monophyly is in question and should be rigorously tested. Although taxon sampling was limited (ingroup taxa = three *Cnemidophorus* species groups, *Ameiva*, and *Kentropyx*), a phylogenetic study using allozymes by Dessauer and Cole (1989) provided support for *Cnemidophorus* paraphyly, with the *lemniscatus* group hypothesized to be more closely related to *Kentropyx* than to a clade containing the *sexlineatus* and *tigris* groups.

Objectives of the Present Study

As the use of *Cnemidophorus* increases in research and the literature mushrooms, it becomes increasingly important to establish the validity of this taxon as a monophyletic group, if indeed it is. Dessauer and Cole (1989) provided preliminary evidence suggesting *Cnemidophorus* paraphyly. However, their taxon sampling was limited and/or incomplete (e.g., absence of the *deppii* group and other critical cnemidophorine lineages). Thus, it is timely to more rigorously examine the phylogenetic relationships between *Cnemidophorus* and other teiine taxa (*Ameiva*, *Dicrodon*, *Kentropyx*, and *Teius*), particularly now that the necessary samples are available. The inferred phylogenetic relationships presented below are based on diverse types of data. The bulk of these data are derived from mitochondrial ribosomal RNA (rRNA) genes, but these data are augmented with previously published allozyme data (Dessauer and Cole, 1989; Cole and Dessauer, 1993; Cole et al., 1995; Markezich et al., 1997) and morphological characters traditionally used in *Cnemidophorus* systematics.

The following questions are addressed in this paper: (1) Is *Cnemidophorus* a monophyletic group? (2) If not, what nomenclatural changes are needed and appropriate at this time? (3) What are the relationships between *Cnemidophorus* and the other teiinine genera? (4) Are the traditionally recognized bisexual species groups within *Cnemidophorus* monophyletic, and what is their relation-

ship to each other? Finally, (5) Do the newly inferred higher-level relationships require reexamination of past hypotheses of chromosomal evolution within *Cnemidophorus*? In addition we comment briefly on the reticulate phylogeny of unisexual clones of hybrid origin and determination of the maternal ancestor of *Kentropyx borckiana*, a unisexual species of hybrid origin.

MATERIALS AND METHODS

Choice of Taxa

Twenty-seven recognized *Cnemidophorus* taxa were included in the present study, representing all currently recognized bisexual species groups (*deppii*, *lemniscatus*, *sexlineatus*, and *tigris* species groups; Wright, 1993). This sample allows a preliminary test of the monophyly of these groups. Also, several additional non-*Cnemidophorus* teiine species were included in order to test *Cnemidophorus* monophyly. In all, 41 ingroup taxa (= *Ameiva*, *Cnemidophorus*, *Dicrodon*, *Kentropyx*, and *Teius*) were included (appendix 1).

The following five outgroup taxa (successively more distant) were included also: *Tupinambis* (Teiidae), *Pholidobolus* (Gymnophthalmidae), *Acanthodactylus* and *Lacerta* (Lacertidae), and *Eumeces* (Scincidae). The relationships of these outgroups to the ingroup are fairly well understood (Estes et al., 1988; Lee, 1998). However, to minimize outgroup assumptions, a global parsimony rooting approach was taken (Maddison et al., 1984), with *Eumeces* (assumed to be the most distantly related outgroup) being used to root the overall resulting tree(s).

Molecular Data

DNA Data: Total genomic DNA was isolated from small amounts of liver or erythrocytes (~100 mg) following the phenol-chloroform extraction protocol of Hillis et al. (1996). Two portions of the mitochondrial genome were amplified using the polymerase chain reaction (PCR) in Perkin-Elmer 2400 or Ericomp TwinBlock thermocyclers. One PCR product was a ~380 bp fragment from the 12S ribosomal RNA (rRNA) gene. The other PCR product was a ~500 bp fragment from the 16S rRNA gene. The primers and PCR parameters used to amplify these fragments are described in Reeder (1995). Purification of amplified DNA and automated DNA sequencing were performed following methods described in Wiens and Reeder (1997). The DNA sequences for *Acanthodactylus cantoris* and *Lacerta agilis* were obtained from GenBank (accession numbers AF080298, AF080300, AF080344, and AF080346).

The mitochondrial rDNA sequences (appendix 2) were aligned under varying gap costs (opening gap cost of 6, 9, and 12) using the multiple sequence alignment program Clustal W (Thompson et al., 1994). Sequence alignment procedures and parameters are described in Wiens and Reeder (1997). It has been demonstrated that rRNA secondary structure models can be useful in the alignment of these gene sequences (Kjer, 1995; Titus and Frost, 1996). Following the procedure outlined in Wiens and Reeder (1997), rRNA secondary structure information was used to assist in DNA sequence alignment. Regions of sequence were considered alignment-ambiguous if nucleotide positional homologies differed among the different gap cost alignments (Gatesy et al., 1993). Ambiguously aligned regions were excluded from phylogenetic analysis. In all, 1072 nucleotide positions were aligned (491 12S and 581 16S; appendix 2), with 61 positions (25 12S and 36 16S) excluded from phylogenetic analysis. Gaps (= insertion/deletion events) were coded as a fifth character state, as described in Wiens and Reeder (1997). All DNA sequences are deposited in GenBank (accession numbers AY046420–AY046503, AF080344, AF080346, AF080298, and AF080300). Upon request, the PAUP* matrix is available from one of us (T.W.R.).

We followed Dessauer et al. (1996) in using allele-specific oligonucleotide probes to screen multiple individuals of *Kentropyx borckiana* to determine the maternal ancestor of this unisexual species.

Allozyme Data: Data on 31 phylogenetically informative protein loci (= characters) were scored for 19 taxa of teiid lizards. The entire allozyme database was produced in one laboratory (H.C.D.'s), so there is complete internal consistency across the data set.

Data are the alleles detected at individual gene loci. For phylogenetic analysis, each locus was interpreted as the character and the alleles present in a taxon as character states (Buth, 1984). All allozyme characters were analyzed unordered.

The gene loci and codes for phylogenetic analysis of the allozymes are presented in appendix 3. The data were published previously in the following reports: Dessauer and Cole, 1989 (*Ameiva*, *Cnemidophorus*, *Kentropyx*, and *Tupinambis*); Cole and Dessauer, 1993 (South American *Cnemidophorus*); Cole et al., 1995 (*Kentropyx*); and Markezich et al., 1997 (South American *Cnemidophorus*). However, this is the first report in which all of these data have been cross-correlated, so the individual alleles as specified in this report (appendix 3) will not necessarily bear the same letter designation as in those original papers, some of which were alphabetized only on the basis of the alleles being compared within the individual report.

Methods of collecting, preparing, and storing tissue samples, and methods of conducting protein electrophoresis, identifying loci, and determining allele products present in the various species are detailed in the papers cited above and relevant references therein (also see Dessauer et al., 2000). The data are of discrete characters that could be scored unambiguously. Although most loci for each taxon show no intraspecific variation or polymorphism, some do. In cases where two or more alleles were recorded for a taxon, each allele was recorded as present at that locus for that taxon. We did not attempt to use frequency data (we used only presence or absence of allele character states) because degree of variability varies widely among loci, it can vary geographically, and because sample sizes vary widely among the taxa. For example, we examined only one specimen of *Tupinambis teguixin* and more than 35 of *Cnemidophorus inornatus*. The problems associated with geographic variation and sample size are illustrated by Dessauer et al. (2000), who examined more than 650 individuals of *Cnemidophorus tigris*. We did not try to integrate all of their data on rare alleles into this report.

Morphological Data

Data on the 10 morphological characters were recorded for 42 taxa of teioid lizards (including *Pholidobolus* and two populations of *Kentropyx altamazonica*). These taxa include all of the teiids for which DNA sequence data were analyzed. Because of problems with homology assessment, morphological data were not coded for any of the nonteioid taxa. Data were recorded from museum specimens, which are specified in appendix 1 (Specimens Examined).

These characters have historically been useful in recognizing generic and subgeneric species groups within the Teiidae, as suggested by previous authors (Burt, 1931; Lowe et al., 1970; Peters and Donoso-Barros, 1970; Hoogmoed, 1973). While not a large set of characters, we felt it was better to include these traditional characters than to exclude them. It has been demonstrated that even a small number of morphological characters (within the context of a large combined data set largely consisting of molecular characters) can have an effect on a phylogenetic analysis (e.g., Titus and Larson, 1996). The character descriptions, coding, and matrix are presented in appendix 4. All were discrete characters that could be scored unambiguously and for which there was little intraspecific variation.

Phylogenetic Analysis

The mtDNA, allozymic, and morphological data were combined into a single data matrix for phylogenetic analysis. Taxa missing a particular subset of the total data (e.g., allozymes) were coded as missing (?) those data. Phylogenetic analyses were performed with PAUP* 4.0b2 (Swofford, 1999). The heuristic tree search routine was used (with TBR branch swapping and 100 random taxon additions). When multiple shortest trees were discovered, the trees were summarized with a strict consensus tree (Sokal and Rohlf, 1981), thus depicting only those relationships shared among all shortest trees. A character state change was considered to unambiguously support a clade if it was placed along a branch by both ACCTRAN (Farris, 1970) and DELTRAN (Swofford and Maddison, 1987) optimizations.

Initial phylogenetic analyses were performed with uniformly weighted characters (i.e., all character state transformations had a weight of 1, irrespective of data type). However, it is fairly well understood that vertebrate mtDNA exhibits substitution biases (e.g., transitions occurring more rapidly than transversions), and different sites or regions (e.g., third codon positions, stem vs. loop regions) evolve at different rates. Thus, differential weighting of nucleotide substitutions and/or sites may be warranted. Seemingly realistic and justifiable weighting schemes can be devised for the DNA data at hand (e.g., Arevalo et al., 1994; Cunningham, 1997; Wiens et al., 1999). However, philosophical and methodological difficulties arise within the context of a combined phylogenetic analysis (e.g., what weight is applied to morphological characters vs. the differentially weighted nucleotide substitutions?). Also, different genes within a combined analysis may have different substitution properties (e.g., are the best character state transformations of gene A equivalent to those of gene B?). An objective way to differentially weight characters within the context of a combined analysis is to use the *a posteriori* method of successive approximations (Farris, 1969; Carpenter, 1988). Such a weighting strategy differentially weights all the characters based on their relative degrees of homoplasy. Those characters most consistent with the initial starting tree are given the greatest weights, regardless of data partition (i.e., DNA, allozymes, morphology). In our study, the initial tree(s) for successive weighting was that inferred from a uniformly weighted combined data analysis. Reweighting characters was performed in PAUP*, using the maximum rescaled consistency index (rci; Farris, 1989) (base weight = 100; weights truncated instead of being rounded [as in Hennig86]).

While originally envisioning means of objectively determining character weights, Kluge (1997a, 1997b) has recently argued that all character weighting (*a priori* and *a posteriori*) should be rejected. Kluge states that all forms of differential character weighting invoke additional background knowledge about biological processes that are untestable. While such an affirmation regarding the use of biological processes or models of evolution are debated (e.g., Swofford et al., 1996), one should always be cautious of the assumptions that are being made in any phylogenetic analysis. In our study we use successive approximations to test the sensitivity of the most parsimonious unweighted trees(s) to differential character weighting based on inferred levels of homoplasy (Farris, 1969; Kluge, 1997a). Clade stability during successive approximations (= clades congruent with tree(s) based on uniform weighting) instills us with additional confidence for those relationships inferred in the uniformly weighted analysis (Carpenter et al., 1993).

A common criticism or concern of successive approximations is that the final inferred tree may be largely dependent on the initial starting tree from which weights were determined (Swofford et al., 1996). To test how robust inferred clades were to initial starting trees, we generated 20 random trees in MacClade v3.07 (Maddison and Maddison, 1992) and performed successive approximations on each of the random trees. Congruence among the final trees from the 20 completed successive approximation analyses was summarized with a 50% majority-rule consensus tree.

The number of taxa scored for the mtDNA (n = 44) and morphological (n = 43) data far exceeded the number available for the allozyme (n = 19) data. Thus, some taxa are incomplete for a subset of the total combined data. However, these incomplete taxa (missing ~8% of informative characters) were still included in the phylogenetic analyses (see Wiens and Reeder, 1995; Reeder and Wiens, 1996). Also, two taxa (*Cnemidophorus murinus* and *C. ocellifer*) were coded for only the 10 morphological characters (representing ~3% of the total informative characters), since we lacked tissue samples for molecular analysis. While these highly incomplete taxa (missing ~97% of informative characters) were included in certain phylogenetic analyses, their impact on tree stability was assessed by bootstrapping (see below) the combined data with and without these two species. The phylogenetic placement of *C. murinus* is of special significance because it is the type species of *Cnemidophorus*.

Support for individual clades was assessed by nonparametric bootstrapping (Felsenstein, 1985). Bootstrap analyses were based on 500 heuristic tree searches (with TBR branch swapping). Because of computational constraints, only three random taxon additions per pseudoreplicate were performed in each of the heuristic tree searches. Bootstrapping was performed in both the uniformly weighted and successive approximation analyses. Sullivan et al. (1997) have noted that weighted parsimony analyses often significantly increase bootstrap values (relative to their values in uniformly weighted analyses of the same data). However, because of the inherent properties of parsimony, the elevated bootstrap values in weighted parsimony analyses probably represent overestimates of the amount of support for the inferred clades (Yang et al., 1995; Sullivan et al., 1997). Therefore, we cautiously interpret the bootstrap results of the successively weighted data, and base most of our conclusions of relative support from the unweighted bootstrap analysis. For the uniformly weighted data, clades with bootstrap values of ≥70% were considered strongly supported (following Hillis and Bull, 1993).

RESULTS

Uniformly Weighted Analysis

Phylogenetic analysis of the 317 uniformly weighted phylogenetically informative characters (235 informative characters among teiine taxa) resulted in four shortest trees (L = 1539; CI = 0.39; RI = 0.61). The strict consensus of these four trees is shown in figure 2A. The numbers of unambiguous synapomorphies supporting the unambiguously resolved branches of the strict consensus tree are given in table 2. All inferred teiine clades were supported by unambiguously placed synapomorphies. However, the vast majority of the clades were supported only by mtDNA character state transformations. In all, only four of the 36 teiine clades were unambiguously supported by mtDNA, morphological, and allozymic synapomorphies (table 2), possibly because allozyme data were coded for only 19 taxa.

Monophyly of the Teiidae (excluding Gymnophthalmidae) is not supported by this analysis. However, teiid paraphyly is only weakly supported, with the gymnophthalmid (= microteiid) *Pholidobolus* being placed with *Tupinambis* (bootstrap = 57%). Teiini (Clade 1) monophyly is strongly supported (80%) by 11 synapomorphies, with *Teius* and *Dicrodon* representing the most basal lineages. Within the teiine clade, 18 of the 34 unambiguously resolved clades are strongly supported (bootstraps ≥70%) by the combined data. Within the Teiini, the cnemidophorine taxa are also supported as a clade (Clade 3). However, cnemidophorine monophyly is only weakly supported (<70%).

While cnemidophorine monophyly is supported, monophyly of *Cnemidophorus* is rejected. All of the South American *Cnemidophorus* species (except *C. longicaudus*) are more closely related to species of other genera of Central and South American cnemidophorines (i.e., *Ameiva* and *Kentropyx*) than to the North American species of *Cnemidophorus*. However, this neotropical clade (Clade 4) is only weakly supported by these data. Within Clade 4 *C. lacertoides* is weakly placed as the sister species of the remaining taxa. Monophyly of the *lemniscatus* complex (i.e., *C. arenivagus*, *C. gramivagus*, and *C. lemniscatus*; Clade 10) is strongly supported (100%), with this clade being placed as the sister taxon of a strongly supported *Kentropyx* (100%; Clade 13). In addition to 12 mtDNA synapomorphies, the *lemniscatus* complex is also supported by one morphological synapomorphy (basal tongue sheath absent [character state 1.b]). *Kentropyx* monophyly is supported by 19 synapomorphies: 12 mtDNA, four morphological (keeled ventral scutes [3.b], 14 rows of ventral scutes [4.c], two enlarged anal spurs per side in males [6.c], abruptly enlarged mesoptychial scales [8.c]), and three allozymes. Within *Kentropyx*, it is equally parsimonious to place *K. calcarata* as the sister taxon of all remaining *Kentropyx*, or as the sister species to the *K. altamazonica* + *K. pelviceps* clade.

Analysis of these data also rejects the monophyly of *Ameiva*. Within Clade 4, *A. undulata* is more closely related to the *lemniscatus* group + *Kentropyx* clade than to the small clade containing *A. ameiva*, *A. bifrontata*, and *A. quadrilineata*. Also, the West In-

dian species (*A. auberi* and *A. chrysolaema*) are strongly supported as a clade (98%), but they are distantly related to mainland ''*Ameiva*''. The West Indian clade is weakly placed (55%) as the sister taxon to a large clade containing all of the North American *Cnemidophorus* (Clade 20) and the South American *C. longicaudus*.

The monophyly of a large North American clade of *Cnemidophorus* (Clade 20) is strongly supported (84%) in this analysis by 10 mtDNA synapomorphies. This clade contains the bisexual *deppii*, *sexlineatus*, and *tigris* groups, each of whose monophyly is strongly supported (89%, 80%, and 100%, respectively). Within the North American clade, the *deppii* group and *tigris* group are strongly supported (85%) as sister taxa (Clade 21). While *deppii* group (Clade 22) monophyly is well supported, the inferred relationships within this group are weak, with the Baja California *C. hyperythrus* being placed as the sister species of the *C. deppii* + *C. guttatus* clade of mainland Mexico. The phylogenetic relationships within the *tigris* group (Clade 24) are well supported, except for the interrelationships among the following three taxa: *C. tigris punctilinealis*, *C. t. aethiops*, and the *C. t. septentrionalis* + *C. t. tigris* clade.

The monophyly of the *sexlineatus* group (Clade 29) is strongly supported by eight synapomorphies: six mtDNA, one morphological (enlarged postantebranchial scales [7.c]), and one allozyme. Only two of the seven resolved clades within the *sexlineatus* group are strongly supported by this analysis. One of these is the clade containing *C. gularis gularis*, *C. g. scalaris*, and *C. g. septemvittatus* (85%; Clade 31), which is weakly placed as the sister taxon to *C. costatus costatus*. The other strongly supported clade is the sister group relationship between *C. inornatus* and *C. sexlineatus*. The *C. inornatus* + *C. sexlineatus* clade is supported by 18 or 20 synapomorphies (depending on resolution of *C. burti* taxa): 13 or 15 mtDNA, one morphological (slightly enlarged postantebrachial scales [7.b]), and four allozymes. The only ambiguity within the *sexlineatus* group is the phylogenetic affinity of *C. burti burti* and *C. b. stictogrammus* (fig. 2A, B). Both of these taxa are weakly placed in a clade containing *C. costatus griseocephalus*, *C. inornatus*, and *C. sexlineatus*. However, it is equally parsimonious to place *C. b. burti* and *C. b. stictogrammus* as sister taxa, or to place *C. b. burti* as the most basal taxon within its clade. And finally, the two *C. costatus* taxa included (*C. c. costatus* and *C. c. griseocephalus*) are not supported as each other's closest relative.

Successive Approximations Analysis

Phylogenetic analysis of the 317 successively weighted phylogenetically informative characters (235 informative characters among teiine taxa) resulted in a single shortest tree (fig. 3; L = 43,281) with a CI of 0.61 and RI of 0.79. The numbers of unambiguous synapomorphies supporting the unambiguously resolved branches of the strict consensus tree are given in table 3. As in the uniformly weighted analysis, all clades are supported by unambiguous synapomorphies, with most clades being unambiguously supported only by mtDNA character state transformations.

Successive weighting (based on the four fundamental phylogenies from the unweighted analysis; two iterations) of these data resulted in a phylogeny that is very similar to the phylogenies inferred in the uniformly weighted analysis, with *Cnemidophorus* and *Ameiva* both being paraphyletic. Besides greater resolution in the successive approximations analysis, the only differences between the unweighted and the successive approximations analyses involve the following relationships: (1) *Dicrodon* and *Teius* have switched positions, with *Dicrodon* now being the sister taxon to the remaining teiines; and (2) interrelationships within the *sexlineatus* group of North America. Within the *sexlineatus* group, the *C. inornatus* + *C. sexlineatus* clade is now the sister taxon to the remaining *sexlineatus* group species. While the *C. inornatus* + *C. sexlineatus* clade still appears to be strongly supported, the number of unambiguously placed synapomorphies supporting this group is about half of that from the uniformly weighted analysis (11 vs. 20). Also, the single morphological synapomorphy (i.e., slightly enlarged postantebrachial scales [7.b]) in the uniformly weighted

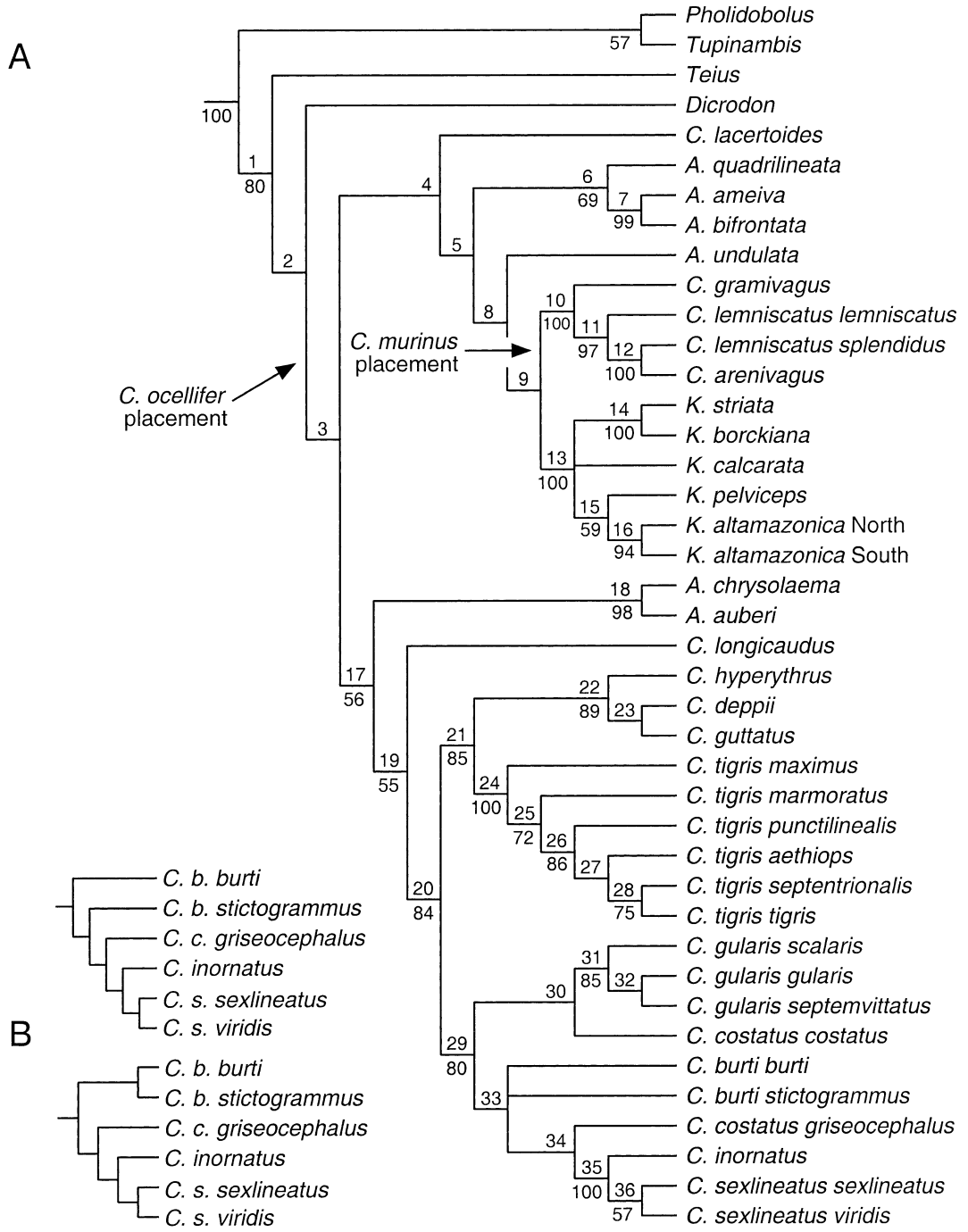

Fig. 2. Teiini phylogeny inferred from the uniformly weighted combined analysis of the mtDNA, morphological, and allozymic data. **A.** Strict consensus of four equally parsimonious shortest phylogenies (L = 1542, CI = 0.39, RI = 0.61). The phylogenetic placements of *Cnemidophorus ocellifer* and *C. murinus* (based on morphology only) are indicated by arrows. The numbers above the branches denote the different clades of the strict consensus tree. The numbers below the branches are bootstrap values. Branches without bootstrap values were supported in <50% of the pseudoreplicates. Number of

analysis no longer diagnoses the *C. inornatus* + *C. sexlineatus* clade, but instead becomes a synapomorphy of the *sexlineatus* group as a whole. In the unweighted analysis, enlarged postantebrachial scales (7.c) was a *sexlineatus* group synapomorphy, with a reversal to slightly enlarged postantebrachial scales (7.b) diagnosing the *C. inornatus* + *C. sexlineatus* clade. The two *C. burti* taxa are now unambiguously supported as sister taxa by a single mtDNA synapomorphy. And finally, while the specific placement of *C. costatus griseocephalus* has changed relative to the unweighted analysis (figs. 2, 3), this taxon and *C. c. costatus* are still not each other's closest relatives.

Bootstrap analysis resulted in 25 teiine clades with bootstrap values ≥70% (compared to only 18 clades in the unweighted analysis) (fig. 2 vs. fig. 3). The increase in bootstrap support in the successively weighted analysis is consistent with the results from other recent empirical studies (see Phylogenetic Analysis under Materials and Methods). Ten inferred clades remain weakly supported (bootstrap <70%) in the weighted analysis. These clades may represent the poorest supported relationships of the study. And finally, the level of support for the *sexlineatus* group (bootstrap = 65%) appears to have decreased in the weighted analysis, relative to its strong support (80%) in the unweighted analysis.

Effects of Initial Starting Tree in Successive Approximations

Twenty random trees were generated, which were 14–32 steps longer than the original four equally parsimonious unweighted trees. Application of successive approximations on these random trees indicated that the initial starting tree did influence the final inferred tree. None of these analyses on random trees resulted in a phylogeny completely congruent with our preferred successive approximations phylogeny (fig. 3). However, when the results of the 20 successive approximation analyses are summarized with a majority-rule consensus tree (fig. 4), it is clear that most of the inferred relationships in figure 3 are being recovered through successive approximations, regardless of the starting tree. Twenty-six clades were recovered in ≥90% of the random tree analyses, and these clades are supported in the preferred successive approximations analysis.

Phylogenetic Placement of *Cnemidophorus murinus* and *Cnemidophorus ocellifer*

Because of the lack of tissue, *Cnemidophorus murinus* and *C. ocellifer* were coded for only the 10 morphological characters. However, while lacking 97% (307 of 317) of the phylogenetically informative characters, analysis of the complete data set containing *C. murinus* and *C. ocellifer* unambiguously places these two species within the teiine phylogeny (figs. 2A, 3). The inclusion of these two species did not alter the previously inferred interrelationships among the other teiine species. Also, the placement of these two species is identical in the uniformly and successively weighted analyses. The most parsimonious placement of *C. ocellifer* is as the sister species of the large clade (Clade 3; figs. 2A, 3) containing all the remaining cnemidophorines. *Cnemidophorus murinus* is nested further in the cnemidophorine clade, being placed as the sister species of the *lemniscatus* complex (Clade 10; figs. 2A, 3). While *C. murinus* and *C. ocellifer* are unambiguously placed by the morphological data, these specific placements are weakly supported. In fact, the relative support throughout the phylogeny generally decreases when these taxa are included in a bootstrap analysis. The decrease in tree support is attributed to the largely incomplete nature of the data for *C. murinus* and *C. ocellifer*.

DISCUSSION

"*Cnemidophorus*" Phylogeny

"*Cnemidophorus*" Paraphyly: One of the primary goals of this study was to rigorously

←

synapomorphies supporting inferred clades is given in table 2. **B.** The two equally parsimonious arrangements of taxa within the *sexlineatus* group.

TABLE 2
Number of Unambiguously Placed Synapomorphies Supporting the Clades of the Teiine Phylogeny Inferred from the Uniformly Weighted Phylogenetic Analysis

Node	No. of synapomorphies (DNA:morphology:allozyme)
1 (Teiini)	11:0:0
2	8:0:0
3 (“*Ameiva*”/“*Cnemidophorus*”[a])	8:0:0
4	5:0:0
5	5:1:1
6	9:0:0
7	12:0:0
8	5:0:0
9	7:1:0
10 (*lemniscatus* complex)	12:1:0
11	7:0:0
12	10:0:0
13 (*Kentropyx*)	13:4:3
14	15:0:0
15	6:0:0
16	6:0:0
17	7:0:0
18	7:2:0
19	7:0:0
20 (North American clade[b])	10:0:0
21	7:0:0
22 (*deppii* species group)	8:0:0
23	6:0:0
24 (*tigris* species group)	12:0:0
25	3:1:0
26	5:0:0
27	1:0:0
28	4:0:0
29 (*sexlineatus* species group)	6:1:1
30	3:0:1
31 (*gularis* complex)	3:0:1
32	2:0:0
33	4–8:0:0
34	3–4:0:1
35	13–15:1:4
36	5–6:0:0

[a]This node represents the most recent common ancestor of the “*Ameiva*” and “*Cnemidophorus*” species included in the present study.

[b]This node represents the most recent common ancestor of the North American “*Cnemidophorus*” clade (i.e., *deppii*, *sexlineatus*, and *tigris* species groups).

test *Cnemidophorus* monophyly and infer the interrelationships among the bisexual species groups. Equal weighting of the combined mtDNA, allozymic, and morphological data resulted in four equally parsimonious phylogenies (strict consensus in fig. 2), and successive weighting resulted in a completely resolved phylogenetic hypothesis (fig. 3) for teiine lizards. The higher-level teiine relationships inferred in these two analyses are essentially identical, with these data not supporting *Cnemidophorus* monophyly. Such a conclusion should come as no surprise. While *Cnemidophorus* monophyly has long been assumed, no apomorphies have ever been proposed, and its monophyly has never been explicitly tested. In fact, ‘‘*Cnemidophorus*’’ (we use quotation marks in reference to the broader paraphyletic group) has historically been defined by the absence of presumably derived character states exhibited by the other teiine teiids (*Ameiva*, *Dicrodon*, *Kentropyx*, and *Teius*). Our data support at least four distinct clades or lineages of ‘‘*Cnemidophorus*’’: (1) North American ‘‘*Cnemidophorus*’’ clade (*deppii*, *sexlineatus*, and *tigris* species groups) + ‘‘*C.*’’ *longicaudus*; (2) ‘‘*C.*’’ *lacertoides*; (3) ‘‘*C.*’’ *lemniscatus* complex + ‘‘*C.*’’ *murinus*; and (4) ‘‘*C.*’’ *ocellifer*.

‘‘*Cnemidophorus*’’ *lemniscatus* Group: Except for ‘‘*Cnemidophorus*’’ *longicaudus* and ‘‘*C.*’’ *ocellifer* (placement based on morphology only), all members of the traditional *lemniscatus* group are more closely related to other neotropical cnemidophorines (i.e., *Ameiva* and *Kentropyx*) than they are to the North American ‘‘*Cnemidophorus*’’. Such a conclusion is consistent with the hypothesis put forth by Burt (1931), who proposed that the *lemniscatus* group was derived from an *Ameiva*-like ‘‘*Cnemidophorus*’’ ancestor, although he visualized the *lemniscatus* group subsequently giving rise to the ancestor of the North American ‘‘*Cnemidophorus*’’.

Specifically, ‘‘*Cnemidophorus*’’ *lacertoides* and the ‘‘*C.*’’ *lemniscatus* complex (Clade 10) are placed within a more inclusive clade (Clade 4; figs. 2A, 3) that contains *Kentropyx* and mainland neotropical *Ameiva*. However, even within this neotropical clade, the *lemniscatus* complex does not form a clade with ‘‘*C.*’’ *lacertoides*. The combined data strongly support a clade containing those *lemniscatus* group species (i.e., ‘‘*C.*’’ *arenivagus*, ‘‘*C.*’’ *gramivagus*, ‘‘*C.*’’ *lemniscatus*, ‘‘*C.*’’ *murinus*) that possess anal spurs, and this clade is placed as the sister taxon to

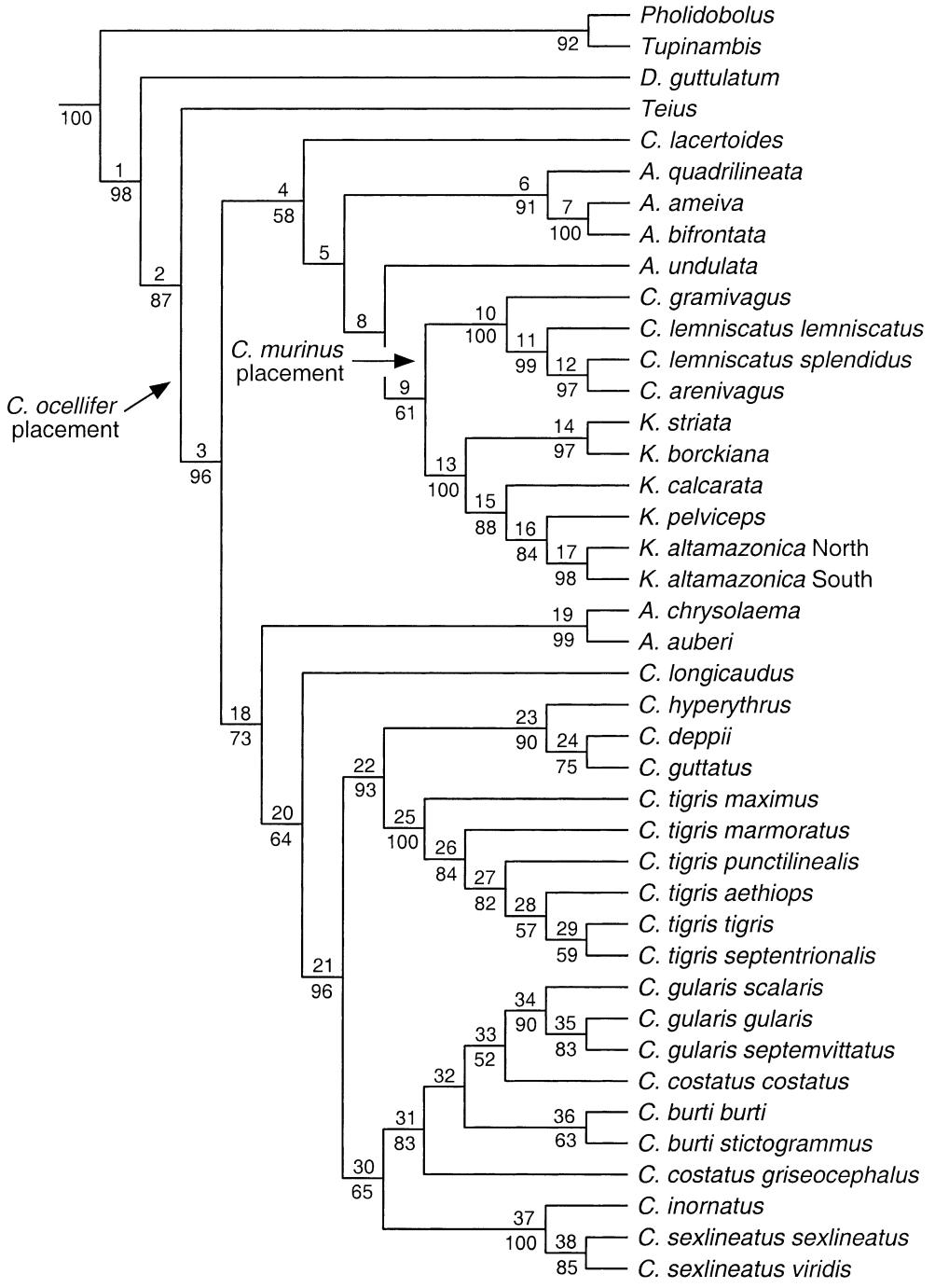

Fig. 3. Teiini phylogeny inferred from the successively weighted combined analysis of the mtDNA, morphological, and allozymic data (L = 43,489, CI = 0.61, RI = 0.79). The phylogenetic placements of *Cnemidophorus ocellifer* and *C. murinus* (based on morphology only) are indicated by arrows. The numbers above the branches denote the different clades. The numbers below the branches are bootstrap values. Branches without bootstrap values were supported in <50% of the pseudoreplicates. Number of synapomorphies supporting inferred clades (and branch lengths) is given in table 3.

TABLE 3

Number of Unambiguously Placed Synapomorphies Supporting the Clades of the Teiine Phylogeny Inferred from the Successively Weighted Phylogenetic Analysis

Node	Number of synapomorphies[a] (DNA:morphology:allozyme)	Weighted branch lengths
1 (Teiini)	9:0:0	408
2	7:0:0	250
3 ("*Ameiva*"/"Cnemidophorus"[b])	11:0:0	276
4	6:0:0	115
5	5:1:1	161
6	8:0:0	161
7	12:0:0	356
8	5:0:0	91
9	7:1:0	222
10 (*lemniscatus* complex)	12:1:0	444
11	7:0:0	292
12	10:0:0	147
13 (*Kentropyx*)	13:4:3	883
14	15:0:0	246
15	4:0:0	225
16	6:0:0	94
17	6:0:0	264
18	6:0:0	130
19	6:2:0	110
20	7:0:0	102
21 (North American clade[c])	9:0:0	331
22	8:0:0	217
23 (*deppii* species group)	7:0:0	217
24	5:0:0	88
25 (*tigris* species group)	11:0:0	484
26	3:1:0	90
27	5:0:0	93
28	1:0:0	25
29	4:0:0	44
30 (*sexlineatus* species group)	7:1:0	169
31	2:1:1	213
32	1:0:1	54
33	6:0:1	144
34 (*gularis* complex)	2:0:1	64
35	2:0:0	12
36	1:0:0	28
37	10:0:1	400
38	4:0:0	91

[a]Characters down-weighted to zero in the successively weighted analysis are not included.

[b]This node represents the most recent common ancestor of the "*Ameiva*" and "*Cnemidophorus*" species included in the present study.

[c]This node represents the most recent common ancestor of the North American "*Cnemidophorus*" clade (i.e., *deppii*, *sexlineatus*, and *tigris* species groups).

Kentropyx. Traditionally "*C.*" *lacertoides* has been included as a member of the *lemniscatus* group (Wright, 1993). However, our data do not support a close relationship between these taxa. In fact, the generic assignment of "*C.*" *lacertoides* has been controversial (Cole et al., 1979), as the species has been alternatively placed in *Ameiva* (Vanzolini and Valencia, 1966). Note also that our analyses place "*C.*" *lemniscatus splendidus*

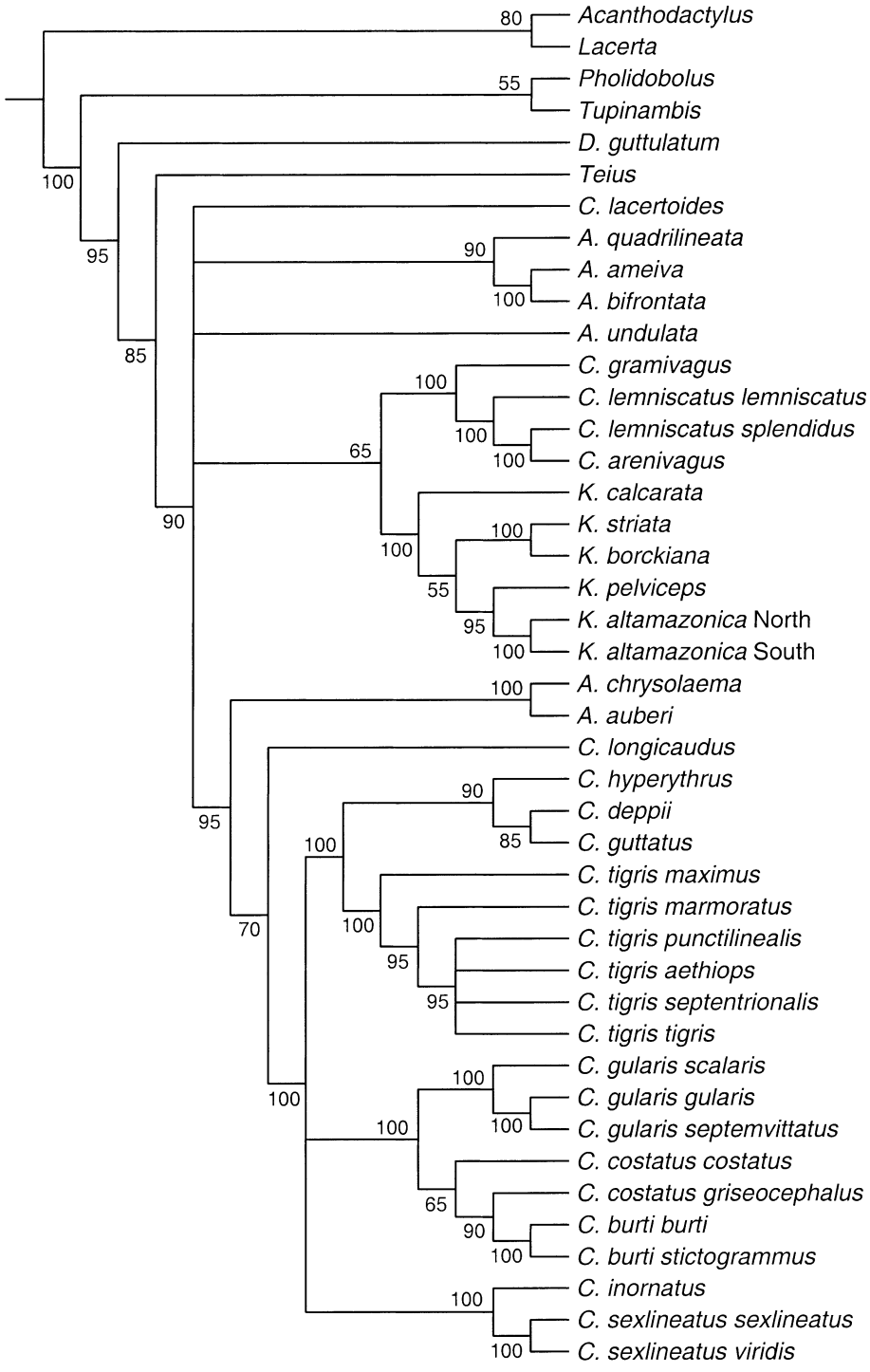

Fig. 4. Majority-rule consensus tree depicting shared clades from the 20 random-tree successive approximation analyses. Numbers along the branches denote the percentage a given clade was recovered in the analyses.

and ''*C.*'' *arenivagus* as sister taxa (figs. 2A, 3), suggesting that the specific status of ''*C.*'' *lemniscatus splendidus* merits reevaluation (Markezich et al., 1997).

Two additional species that have traditionally been placed in the ''*lemniscatus* group'' are ''*Cnemidophorus*'' *longicaudus* and ''*C.*'' *ocellifer* (Wright, 1993). Our combined analysis places ''*C.*'' *longicaudus* as the sister species of the North American ''*Cnemidophorus*'' clade. While we find this possible relationship perplexing considering that ''*C.*'' *longicaudus* is found in south-central South America, our current analysis suggests this inferred relationship is weakly supported. ''*Cnemidophorus*'' *ocellifer* was scored only for the 10 morphological characters, but it is unambiguously placed as the sister species to all remaining cnemidophorines (Clade 3; figs. 2A, 3). However, like the placement of ''*C.*'' *longicaudus*, this specific placement of ''*C.*'' *ocellifer* is very weakly supported. Therefore, we do not have great confidence in the placement of these two species, and their inferred relationships will likely change with the addition of new data (Bell and Reeder, unpubl. data).

NORTH AMERICAN ''*CNEMIDOPHORUS*'' CLADE: Our current study strongly supports the monophyly of a group of North American ''*Cnemidophorus*'', composed of the *deppii*, *sexlineatus*, and *tigris* species groups (each of which is also strongly supported). Such a hypothesis is consistent with Burt (1931), although he had also postulated that the neotropical ''*lemniscatus* group'' gave rise to the ancestor of the North American ''*Cnemidophorus*''. Within this clade there appears to be relatively strong support for a sister group relationship between the *deppii* and *tigris* species groups. Such a relationship has not been previously proposed. Lowe et al. (1970) hypothesized that the *sexlineatus* and *tigris* groups (each of which possesses uniquely derived karyotypes; see Karyotype Evolution Revisited below) were each other's closest relatives, with this clade potentially supported by a single centric fusion. A *sexlineatus* group + *tigris* group relationship was also strongly supported by mitochondrial restriction site data in Moritz et al. (1992a). Thus, there appears to be strong conflict between our mitochondrial rDNA sequences and the mitochondrial restriction site data of Moritz et al. (1992a). Since the mitochondrial genome is inherited as a single, nonrecombining unit (Brown, 1981, 1983), these two mtDNA data sets might be expected to yield the same result. Nevertheless, the nature of the restriction sites and the nucleotide gene sequences are quite different data sets, based on different details in the mtDNA.

Based on shared identical karyotypes, Lowe et al. (1970) and Robinson (1973) proposed that the Baja California ''*Cnemidophorus*'' *ceralbensis* and ''*C.*'' *hyperythrus* (sensu lato; see Grismer, 1999) were closely related to the mainland Mexico *deppii* group (''*C.*'' *deppii*, ''*C.*'' *guttatus*, and ''*C.*'' *lineatissimus*). However, since Lowe et al. (1970) also hypothesized that the *deppii* group possessed the ancestral karyotype of ''*Cnemidophorus*'', it was possible that the Baja taxa were being placed within the *deppii* group by the possession of a shared primitive trait. Also, members of the ''*C.*'' *hyperythrus* complex (Grismer, 1999) and ''*C.*'' *ceralbensis* share a uniquely derived feature (i.e., undivided frontoparietal scale; Walker et al., 1966; Walker and Taylor, 1968), but evidence supporting a specific relationship of the Baja clade to the remaining *deppii* group taxa has been lacking. The results of our current study corroborate and strongly support a close relationship between the Baja California ''*C.*'' *hyperythrus* and the mainland Mexico *deppii* group, with these data supporting the placement of ''*C.*'' *hyperythrus* as the sister taxon to the ''*C.*'' *deppii* + ''*C.*'' *guttatus* clade.

Species limits within the *tigris* group are controversial, with recent checklists recognizing anywhere from a single, widespread polytypic species (Wright, 1993) to eight species (Maslin and Secoy, 1986). Also, the phylogenetic relationships among the >20 named taxa (i.e., subspecies and species) are largely unknown, with only the recent molecular study by Radtkey et al. (1997) providing a preliminary hypothesis of relationships for the Baja taxa. The goal of our study was not to rigorously evaluate the relationships within the *tigris* group. However, even with this limited sampling, significant preliminary results are evident. ''*Cnemidopho-*

rus'' *tigris maximus* (''*C.*'' *maximus* of Maslin and Secoy [1986]) of the Cape Region of Baja California is placed as the sister taxon of all remaining *tigris* group taxa in our study. This finding is consistent with Radtkey et al. (1997), whose mitochondrial cytochrome *b* data suggested that a clade of southern Baja California ''*C.*'' *tigris* populations (including ''*C.*'' *t. maximus*) was the sister taxon to a clade containing the northern Baja taxa and the few non-Baja California populations they studied. Our data also strongly support the placement of ''*C.*'' *t. marmoratus* as the sister taxon to the remaining western U.S. ''*C.*'' *tigris* taxa. Such a finding is significant, because it demonstrates that the ongoing and evidently unrestricted hybridization between the geographically proximate ''*C.*'' *t. marmoratus* and ''*C.*'' *t. punctilinealis* (see Dessauer et al., 2000) is between relatively distantly related ''*C.*'' *tigris* lineages.

With >20 recognized species, the *sexlineatus* group is the largest species group within the North American ''*Cnemidophorus*'' clade. While we excluded the unisexual taxa and included only seven bisexual species in our study (thus limiting what can be hypothesized regarding *sexlineatus* group evolution), our results are reasonably congruent with some past hypotheses of *sexlineatus* group relationships. Our data strongly support a clade containing ''*C.*'' *inornatus* and ''*C.*'' *sexlineatus*. However, the placement of this clade within the *sexlineatus* group is ambiguous. The uniformly weighted analysis weakly supported its placement within a clade containing ''*C.*'' *burti* and ''*C.*'' *costatus griseocephalus* (fig. 2), whereas the successively weighted analysis placed the ''*C.*'' *inornatus* + ''*C.*'' *sexlineatus* clade as the sister taxon to all remaining *sexlineatus* group taxa (fig. 3). Moritz et al. (1992a) hypothesized a relationship similar to that inferred in the successive weighted analysis, with the ''*C.*'' *inornatus* + ''*C.*'' *sexlineatus* clade being relatively basal within the *sexlineatus* group.

Much taxonomic confusion exists within the ''*Cnemidophorus*'' *gularis* complex. Walker (1981a, 1981b) concluded that ''*C.*'' *septemvittatus* and ''*C.*'' *scalaris* were conspecific (but heterosubspecific) with ''*C.*'' *gularis*. More recently, Wright (1993) (without comment) elevated ''*C.*'' *g. gularis* to specific status and treated ''*C.*'' *scalaris* as a subspecies of ''*C.*'' *septemvittatus* (see Crother et al., 2001, regarding taxonomic uncertainty as to correct specific epithet for ''*C.*'' *scalaris*/*septemvittatus*). While our sampling is inadequate to address the species limits problems within the ''*C.*'' *gularis* complex, the results of our data analysis are consistent with these three taxa being very closely related. For now, we have followed the taxonomic recommendation of Walker (1981a, 1981b), but acknowledge that additional work is needed in this group.

Within the *sexlineatus* species group, the species complex involving the polytypic ''*Cnemidophorus*'' *burti* and ''*C.*'' *costatus* has also bewildered past ''*Cnemidophorus*'' systematists. While we made no rigorous attempt to thoroughly resolve these uncertainties, our data provide new insight into the potential magnitude of the problem. For example, our data do not support the supposedly conspecific ''*C.*'' *costatus costatus* and ''*C.*'' *c. griseocephalus* as being each other's closest relatives. The placement of ''*C.*'' *c. costatus* as being closely related to the ''*C.*'' *gularis* complex (figs. 2A, 3) is consistent with the findings of Duellman and Zweifel (1962). Duellman and Zweifel (1962) commented on southern Mexico populations tentatively assigned to ''*C.*'' *costatus*. They noted that these populations were similar to ''*C.*'' *c. costatus*, but also had attributes likening them to ''*C.*'' *septemvittatus*. As for ''*C.*'' *c. griseocephalus*, Dessauer and Cole (1989) provided evidence (allozymes) that this taxon was genetically more similar to ''*C.*'' *burti* than to ''*C.*'' *c. costatus* (misidentified as ''*C.*'' *deppii* in Dessauer and Cole, 1989). Without comment, Wright (1993) considered ''*C.*'' *c. griseocephalus* to be conspecific with ''*C.*'' *burti* (his ''*C.*'' *burti griseocephalus*), an action possibly prompted by the data of Dessauer and Cole (1989). The results of this phylogenetic analysis do not support a particularly close relationship of this taxon to ''*C.*'' *burti* or ''*C.*'' *c. costatus* (figs. 2, 3). Our study further reinforces the complexity of the problems within the ''*C.*'' *burti*/*costatus* complex, and suggests that future endeavors to resolve

their species limits may require the consideration of the ''*C.*'' *gularis* complex as well.

''*Ameiva*'' Phylogeny

Compared to ''*Cnemidophorus*'', our taxon sampling within *Ameiva* was not extensive, with two species from each of the following areas: West Indies (*A. auberi*, *A. chrysolaema*), Central America (*A. quadrilineata*, *A. undulata*), and South America (*A. ameiva*, *A. bifrontata*). Even with this limited sampling, our data show that *Ameiva* is paraphyletic. The West Indian clade is placed as the sister taxon of the clade containing ''*C.*'' *longicaudus* and the North American ''*Cnemidophorus*''. The other ''*Ameiva*'' species are more closely related to the neotropical ''*C.*'' *lemniscatus* group (sensu stricto) and *Kentropyx*. However, most of these inferred relationships for ''*Ameiva*'' are weakly supported, with strong support for only two small clades: ''*A.*'' *auberi* + ''*A.*'' *chrysolaema* and ''*A.*'' *ameiva* + ''*A.*'' *bifrontata*. While ''*Ameiva*'' phylogeny was not one of the main foci of this study, it is evident that additional phylogenetic studies of ''*Ameiva*'' are needed.

Evolution of Tongue Characters Traditionally Used in Cnemidophorine Systematics

Historically, finding characters to diagnose ''*Cnemidophorus*'' from ''*Ameiva*'' has been problematic. Burt (1931) used attributes of the tongue as the only real basis for differentiating these genera: (1) ''*Ameiva*'' possesses a sheath at the base of the tongue (visibly separating it from the glottis) and has the posterior margin of the tongue not forked (or only slightly so); and (2) ''*Cnemidophorus*'' lacks a basal tongue sheath and has the posterior margin of the tongue clearly forked (possessing an arrowhead- or heart-shaped tongue, according to Burt [1931]). However, not all species have perfectly fit this scheme, with ''*C.*'' *lacertoides* being a species of taxonomic instability. Without comment, Burt (1931) transferred this species to ''*Ameiva*'' (leaving one to assume that this species possessed the two lingual characteristics of ''*Ameiva*''). Milstead (1961) and Presch (1971) noted that this species exhibited the ''*Cnemidophorus*'' tongue type and recommended that this species be placed back in ''*Cnemidophorus*'', whereas Vanzolini and Valencia (1966) believed the tongue structure was more similar to ''*Ameiva*''. The confusion largely stems from the fact that ''*C.*'' *lacertoides* does not perfectly fit the diagnosis developed by Burt (1931). ''*Cnemidophorus*'' *lacertoides* possesses a distinctly forked posterior edge of the tongue (as in other ''*Cnemidophorus*''), but also exhibits the tongue sheath characteristic of ''*Ameiva*''. The results of our phylogenetic analysis shed some light on the evolution of these tongue characters in teiines and help determine which teiines can be diagnosed by derived character states.

The absence of a tongue sheath appears to be the ancestral condition for teiines (absent in the most recent common ancestor of Teiini; Clade 1 of figs. 2, 3). However, the ancestral condition for cnemidophorines (Clade 3 of figs. 2, 3) is ambiguous, with each of the following evolutionary scenarios being equally parsimonious: (1) The absence of a tongue sheath is ancestral for cnemidophorines, with independent origins of a tongue sheath in the ancestor of the neotropical clade (Clade 4 of figs. 2, 3; reversal in ''*Cnemidophorus*'' *lemniscatus* complex) and the West Indian ''*Ameiva*'' (Clade 18 of fig. 2; Clade 19 of fig. 3); or (2) presence of tongue sheath is a synapomorphy of cnemidophorines, with independent losses in the ''*C.*'' *lemniscatus* complex and the ''*C.*'' *longicaudus* + North American ''*Cnemidophorus*'' clade (Clade 19 of fig. 2 or Clade 20 of fig. 3). While the evolution of this character among cnemidophorines is largely ambiguous, under both scenarios the ''*C.*'' *lemniscatus* complex has secondarily lost the tongue sheath.

A distinctly forked posterior edge of the tongue is the ancestral condition for Teiini, as well as the cnemidophorines. The derived loss of the forking occurred independently at least twice among cnemidophorines: (1) Once in the West Indian ''*Ameiva*'' (Clade 18 of fig. 2; Clade 19 of fig. 3); and (2) one or two times among the neotropical cnemidophorines. Within the neotropical cnemidophorine clade, the distinctive forking of the posterior edge of the tongue was either

lost once in the ancestor of Clade 5 (figs. 2, 3) or lost twice (independently in Clade 6 and ''*A.*'' *undulata*). If the forking was lost only once among the neotropical cnemidophorines, then a reversal must have occurred in the ancestor of the ''*Cnemidophorus*'' *lemniscatus* complex + *Kentropyx* clade (Clade 9 of figs. 2, 3). Under any of the above evolutionary scenarios, it is apparent that the ''diagnostic'' distinctly forked posterior edge of the tongue is the plesiomorphic condition for all ''*Cnemidophorus*''. Unfortunately, the basal teiine and cnemidophorine relationships are weakly supported, with some of these currently inferred relationships likely to change with the addition of more data (e.g., placement of ''*C.*'' *longicaudus* and the West Indian ''*Ameiva*''; see Taxonomic Implications and Nomenclatural Recommendations). Thus, any future phylogenetic rearrangements will likely require a reassessment of the evolution of these two tongue characters that historically have played an important part in cnemidophorine systematics.

Taxonomic Implications and Nomenclatural Recommendations

One of the main goals of this study was to test ''*Cnemidophorus*'' monophyly, as well as the monophyly of the currently recognized bisexual ''*Cnemidophorus*'' species groups. Our study demonstrates that ''*Cnemidophorus*'' is paraphyletic with respect to ''*Ameiva*'' and *Kentropyx*. Given this result, nomenclatural changes are needed in order to maintain a classification that more accurately reflects the evolutionary relationships within the cnemidophorine clade (Clade 3; figs. 2, 3). Within this large assemblage exists a strongly supported clade that has informally been referred to as the North American ''*Cnemidophorus*'' clade (Clade 20 of fig. 2; Clade 21 of fig. 3). This clade contains the monophyletic *deppii*, *sexlineatus*, and *tigris* species groups and their associated unisexual taxa. Except for ''*C.*'' *longicaudus* and ''*C.*'' *ocellifer*, all other species of the ''*Cnemidophorus lemniscatus* group'' (i.e., the ''*C.*'' *lemniscatus* complex, ''*C.*'' *murinus*, and ''*C.*'' *lacertoides*) are more closely related to Central and South American ''*Ameiva*'' and *Kentropyx* than to members of the North American ''*Cnemidophorus*'' clade. ''*Cnemidophorus*'' *ocellifer* was weakly placed as the sister species to the large clade containing ''*Ameiva*'', *Kentropyx*, and all other ''*Cnemidophorus*'', and ''*C.*'' *longicaudus* was weakly placed as the sister species of the North American ''*Cnemidophorus*'' clade.

If our goal is to recognize monophyletic groups, then widespread nomenclatural change is required. One option would be to classify all cnemidophorine species of Clade 3 (figs. 2, 3) into a single large taxon. In this case, *Ameiva* Meyer, 1795, would have priority over *Cnemidophorus* Wagler, 1830, and *Kentropyx* Spix, 1825. A second option would be to name the more exclusive well supported cnemidophorine clades (within Clade 3) that are morphologically distinct and/or geographically coherent. We do not favor the first alternative for two reasons. First, this former option would subsume long-recognized and morphologically distinctive groups (e.g., *Kentropyx*) under a single name. Second, we feel that the recognition of a single taxon (i.e., an expanded *Ameiva*) would obscure the true phyletic diversity within this large and diverse assemblage. Given this, we find it necessary to resurrect *Aspidoscelis* as the available generic name for species of the North American ''*Cnemidophorus*'' clade (Clade 20 of fig. 2; Clade 21 of fig. 3). As the type species of *Cnemidophorus* is ''*C.*'' *murinus*, that generic name remains with the South American taxa (see additional details below).

Aspidoscelis Fitzinger, 1843

Aspidoscelis Fitzinger, 1843: 20.
Verticaria Cope, 1870: 158 (type species, *Cnemidophorus hyperythrus* Cope).

Type Species: *Lacerta sexlineata* Linnaeus, 1758, is the nominal type species.

Etymology: *Aspidoscelis* was first named by Fitzinger (1843). He merely listed it as a subgenus of *Cnemidophorus*, with the comment that the type species is *Lacerta 6-lineata* Linnaeus (= *Cnemidophorus sexlineatus*). No etymology was presented.

The name probably was derived from two Greek nouns, *aspido*, meaning ''shield'', and *scelis*, meaning ''rib'' or ''leg''. This seems appropriate, because it could refer to the

large scales on the legs and has a meaning similar to that of *Cnemidophorus*: ''equipped with leggings''.

According to the International Code of Zoological Nomenclature (1999, art. 30), gender of a compound word is that of the final component if it is a noun, so *Aspidoscelis* is feminine, although *Cnemidophorus* is masculine. Consequently, in the list of taxa below, we emend the specific and subspecific epithets for agreement with the feminine gender (ICZN, 1999, art. 31.2). Special thanks are due to Darrel Frost for providing these emendations.

CONTENT: The genus *Aspidoscelis* contains at least 87 currently recognized bisexual and unisexual taxa. The following list of taxa is a blend of those recognized by Grismer, 1999; Maslin and Secoy, 1986; Taylor and Walker, 1996; Walker, 1981a, 1981b; Walker et al., 1997; Wright, 1993; and Wright and Lowe, 1993. Given the complex nature of the interrelationships among the described taxa of the *A. burti*, *A. costata*, and *A. gularis* complexes, many additional evolutionary species may exist within *Aspidoscelis*. We realize that no two individuals or teams of herpetologists would independently come up with the same list of species and subspecies recognized these days for such a large and complex genus (especially given the insular forms), but this is our best working hypothesis for now.

The *Aspidoscelis cozumela* Group: *A. cozumela*; *A. maslini*; *A. rodecki*.

The *Aspidoscelis deppii* Group: *A. carmenensis*; *A. ceralbensis*; *A. danheimae*; *A. deppii*; *A. d. deppii*; *A. d. infernalis*; *A. d. schizophora*; *A. espiritensis*; *A. franciscensis*; *A. guttata*; *A. g. guttata*; *A. g. immutabilis*; *A. g. flavilineata*; *A. hyperythra*; *A. h. hyperythra*; *A. h. beldingi*; *A. lineatissima*; *A. l. lineatissima*; *A. l. duodecemlineata*; *A. l. exorista*; *A. l. livida*; *A. picta*.

The *Aspidoscelis sexlineata* Group: *A. angusticeps*; *A. a. angusticeps*; *A. a. petenensis*; *A. burti*; *A. b. burti*; *A. b. stictogramma*; *A. b. xanthonota*; *A. calidipes*; *A. communis*; *A. c. communis*; *A. c. mariarum*; *A. costata*; *A. c. costata*; *A. c. barrancorum*; *A. c. griseocephala*; *A. c. huico*; *A. c. mazatlanensis*; *A. c. nigrigularis*; *A. c. occidentalis*; *A. c. zweifeli*; *A. exsanguis*; *A. flagellicauda*; *A. gularis*; *A. g. gularis*; *A. g. colossus*; *A. g. pallida*; *A. g. scalaris*; *A. g. septemvittata*; *A. g. semifasciata*; *A. g. semiannulata*; *A. innotata*; *A. inornata*; *A. i. inornata*; *A. i. arizonae*; *A. i. cienegae*; *A. i. chihuahuae*; *A. i. gypsi*; *A. i. heptagramma*; *A. i. juniperus*; *A. i. llanuras*; *A. i. octolineata*; *A. i. pai*; *A. i. paulula*; *A. labialis*; *A. laredoensis*; *A. mexicana*; *A. motaguae*; *A. opatae*; *A. parvisocia*; *A. sacki*; *A. s. sacki*; *A. s. gigas*; *A. sexlineata*; *A. s. sexlineata*; *A. s. viridis*; *A. sonorae*; *A. uniparens*; *A. velox*.

The *Aspidoscelis tesselata* Group: *A. dixoni*; *A. neomexicana*; *A. neotesselata*; *A. tesselata*.

The *Aspidoscelis tigris* Group: *A. tigris*; *A. t. tigris*; *A. t. aethiops*; *A. t. disparilis*; *A. t. marmorata*; *A. t. maxima*; *A. t. multiscutata*; *A. t. pulchra*; *A. t. punctilinealis*; *A. t. rubida*; *A. t. septentrionalis*; *A. t. stejnegeri*; *A. t. undulata*; *A. t. variolosa*.

DEFINITION AND DIAGNOSIS: *Tongue morphology*: Basal tongue sheath absent and posterior portion of tongue clearly forked. *Scutellation*: Smooth ventral scutes; eight rows of ventral scutes across midbody; granular dorsal scales; anal spurs in males absent; mesoptychial scales abruptly enlarged over scales in gular fold, more anterior ones becoming smaller; three parietal scales; three or four supraocular scales on each side.

The above combination of traits distinguishes *Aspidoscelis* from all other cnemidophorine teiid genera. *Aspidoscelis* differs from *Kentropyx* by the absence of keeled ventral scutes and the absence of enlarged anal spurs in males (presence of keeled ventral scutes in *Kentropyx* is unique among teiids). *Aspidoscelis* can also be differentiated from all species currently placed in ''*Ameiva*'' by the absence of a basal tongue sheath (present in ''*Ameiva*'') and the possession of a distinctly forked posterior portion of the tongue (not clearly forked in ''*Ameiva*'').

Species of *Aspidoscelis* are easily distinguished from *Cnemidophorus murinus* and the *C. lemniscatus* complex by the following attributes: (1) lack of anal spurs in males (present in *C. murinus* and the *C. lemniscatus* complex); (2) presence of abruptly enlarged mesoptychial scales, with more anterior scales becoming smaller (somewhat enlarged in *C. murinus* and the *C. lemniscatus* com-

plex, with more anterior mesoptychials becoming abruptly enlarged); and (3) presence of three parietal scales (five in *C. murinus* and the *C. lemniscatus* complex).

Aspidoscelis differs from ''*Cnemidophorus*'' *ocellifer* by the presence of three parietal scales (five in ''*C.*'' *ocellifer*). Also, most species of *Aspidoscelis* possess slightly to greatly enlarged postantebrachial scales (most species within the *A. sexlineata* group), whereas the postantebrachials are granular in ''*C.*'' *ocellifer*. Species of *Aspidoscelis* can be differentiated from ''*C.*'' *lacertoides* by the following traits: (1) absence of a basal tongue sheath (present in ''*C.*'' *lacertoides*); (2) eight rows of ventral scutes across midbody (10–12 in ''*C.*'' *lacertoides*); and (3) presence of three parietal scales (five in ''*C.*'' *lacertoides*). Also, as in ''*C.*'' *ocellifer*, ''*C.*'' *lacertoides* possesses granular postantebrachial scales. And finally, *Aspidoscelis* can be distinguished from ''*C.*'' *longicaudus* by the presence of eight rows of ventral scales across midbody (10–12 in ''*C.*'' *longicaudus*) and abruptly enlarged mesoptychial scales over the gular fold scales (somewhat enlarged in ''*C.*'' *longicaudus*). Some populations of *A. tigris* have secondarily reduced mesoptychials, thus resembling ''*C.*'' *longicaudus*. However, all *A. tigris* typically have only eight ventral scutes across the midbody.

DISTRIBUTION: *Aspidoscelis* occurs throughout most of North America (except Canada), reaching the East and West Coasts of the United States, and ranging south through all of Mexico into Central America. Its southern limit is in extreme northwestern Costa Rica. Range maps for the species groups are provided in Wright (1993).

COMMENT: Our data place the South American ''*Cnemidophorus*'' *longicaudus* as the sister species of *Aspidoscelis*, and its inclusion in *Aspidoscelis* would be consistent with the phylogeny (figs. 2, 3). However, this placement of ''*C.*'' *longicaudus* is very weakly supported. We suspect that the true affinities of ''*C.*'' *longicaudus* lie with the other ''*lemniscatus* group'' species and ''*Ameiva*'' in South America. Preliminary sequence data from additional mitochondrial genes (Bell and Reeder, unpubl. data) lend support to this suspicion. Therefore, the exclusion of ''*C.*'' *longicaudus* from *Aspidoscelis* in this paper probably prevents the demonstration of paraphyly of *Aspidoscelis* in future studies. As currently defined, *Aspidoscelis* is a strongly supported and geographically coherent clade. Within *Aspidoscelis*, there is strong support for the monophyly of the *deppii*, *sexlineata*, and *tigris* species groups; thus, we advocate the continued recognition of these informal supraspecific groups formerly associated with ''*Cnemidophorus*''. While our present phylogenetic analysis did not include all of the described bisexual species of the aforementioned species groups, we are confident of their proposed group membership (based largely on karyotypic data; see Karyotype Evolution Revisited), and strongly doubt that their inclusion in future phylogenetic studies will render *Aspidoscelis* paraphyletic. And finally, the species of the unisexual *cozumela* and *tesselata* species groups are also included in the genus *Aspidoscelis*, as these unisexuals are derived from hybridization events within *Aspidoscelis*.

The removal of all of the North American taxa from *Cnemidophorus* leaves only the ''*lemniscatus* group'' species within *Cnemidophorus* (sensu stricto). However, the recognition of *Aspidoscelis* still does not make *Cnemidophorus* monophyletic (due to ''*lemniscatus* group'' paraphyly). Within Clade 3 (figs. 2, 3) there exists a strongly supported clade that corresponds to the ''*C.*'' *lemniscatus* complex (Clade 10). Based on only morphological data, ''*C.*'' *murinus* is placed as the sister species of the *lemniscatus* complex. Also, all males of this clade (''*C.*'' *murinus* + *lemniscatus* complex) possess two anal spurs (one per side), while all remaining species of the ''*lemniscatus* group'' lack anal spurs. Since the type species of *Cnemidophorus* is *C. murinus*, *Cnemidophorus* could be made monophyletic by restricting this name to the strongly supported and morphologically distinct clade containing *C. murinus* and the *C. lemniscatus* complex. However, that still leaves us with the problem of what to do with the remaining ''*lemniscatus* group'' species lacking anal spurs (i.e., *C. lacertoides*, *C. longicaudus*, and the *C. ocellifer* complex). To maintain *Cnemidophorus* monophyly, each of these taxa would have

to be removed from *Cnemidophorus* and placed into other taxa (e.g., ''*Ameiva*'').

The phylogenetic placements of *Cnemidophorus longicaudus*, *C. lacertoides*, and *C. ocellifer* suggest erecting monotypic genera for each species. *Cnemidophorus ocellifer* was originally described and placed in *Teius*. However, because of the pentadactyl condition of the hind foot of *C. ocellifer* and its resemblance to *Cnemidophorus*, Burt (1931) transferred this species to *Cnemidophorus*. Our current data do not support a close relationship between *C. ocellifer* and *Teius*; thus, a new generic name is needed for *C. ocellifer* (and probably to include the other members of the *C. ocellifer* complex; see Rocha et al., 1997, 2000). *Cnemidophorus longicaudus* was originally placed in *Ameiva*, and *C. lacertoides* has had an unstable taxonomic history, with *C. lacertoides* being repeatedly shifted between *Cnemidophorus* and *Ameiva* (Burt, 1931; Vanzolini and Valencia, 1966; Cole et al., 1979). Initially, it may appear that the appropriate action would be to return *C. longicaudus* and *C. lacertoides* to *Ameiva*. However, these two species are not closely related, nor are they closely related to any *Ameiva*. Furthermore, *Ameiva* is also paraphyletic, so no benefit would result by moving these two *Cnemidophorus* species from one paraphyletic taxon to another.

As previously mentioned, the phylogenetic placements of *C. longicaudus*, *C. lacertoides* and *C. ocellifer* are weakly supported. Given this, we prefer to tentatively leave these three species within *Cnemidophorus*, even though such an action renders *Cnemidophorus* paraphyletic. We feel that a better understanding of the phylogenetic relationships among the South American ''*Cnemidophorus*'' species is needed before additional taxonomic changes (e.g., transfer of taxa to existing genera and/or the proposal of new genera) should be made. Ultimately, we suspect that *Cnemidophorus* will be restricted to those species possessing anal spurs in males (i.e., *C. murinus* and the *C. lemniscatus* complex). However, such a conclusion requires that additional data and taxa (i.e., *C. ocellifer* complex species and additional species of *Ameiva*) be included in future studies before final taxonomic recommendations are proposed.

Maternal Ancestor of *Kentropyx borckiana*

As *Kentropyx borckiana* was known only from female specimens, Hoogmoed (1973) and Gallagher and Dixon (1992) were the first to suggest that it was yet another unisexual teiid species. Gallagher and Dixon (1992) hypothesized that *K. borckiana* (like other unisexual teiids) was of hybrid origin, with the bisexual *K. calcarata* and *K. striata* being the ancestor species. Based upon an extensive analysis of morphology and allozymes, Cole et al. (1995) confirmed that *K. borckiana* was of hybrid origin involving *K. calcarata* and *K. striata*. Cole et al. (1995) were also able to exclude *K. altamazonica* (a third bisexual species occurring near *K. borckiana*) of any involvement in the hybridization event giving rise to *K. borckiana*. While both ancestral species had been determined with confidence, it was not known which of the two bisexual species had been the maternal ancestor.

Karyological (e.g., Cole, 1979) and allozymic (e.g., Cole et al., 1988; Dessauer and Cole, 1989) studies have been successful in determining the ancestral species involved in the hybrid origins of many unisexual lizards. However, such methods could not elucidate which was the maternal and which was the paternal ancestor. With the advent of methods to effectively assay mitochondrial DNA, this maternally inherited molecular marker has been instrumental in elucidating the maternal ancestral species in numerous unisexual teiid species (e.g., Brown and Wright, 1979; Densmore et al., 1989a, 1989b; Moritz et al., 1989b). In our phylogenetic study, the *Kentropyx borckiana* mtDNA strongly grouped (bootstrap 97–100%) with *K. striata*. Overall, the single *K. borckiana* mtDNA sequence differed from the *K. striata* mtDNA by only 0.9%. Using allele-specific oligonucleotides (see Dessauer et al., 1996) designed for the detection of *K. calcarata* and *K. striata* 12S mtDNA, we determined that an additional *K. borckiana* individual also possesses *K. striata*-like mtDNA (fig. 5). Thus, we provide strong evidence implicating *K. striata* as the maternal ancestor of the unisexual *K. borckiana*.

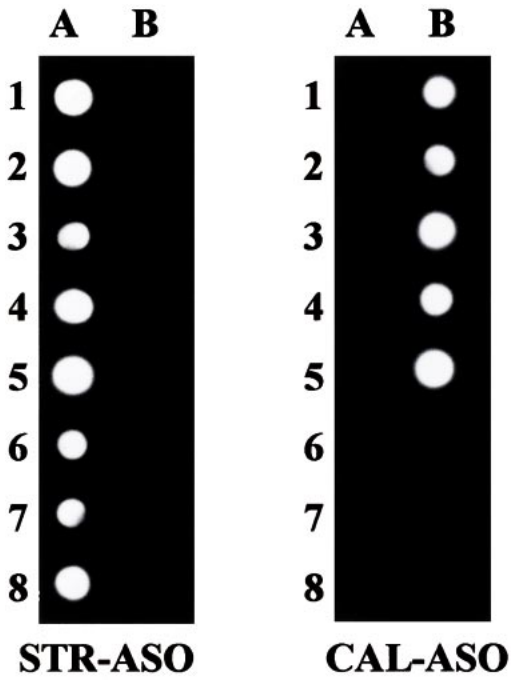

Fig. 5. Dot-blot illustrating specificity of the allele-specific oligonucleotide probes (ASOs). DNA samples from 16 lizards of the genus *Kentropyx* from Ecuador, Guyana, Surinam, and Venezuela were applied in rows A and B of a strip of nitrocellulose paper. After heat denaturation, the blot was hybridized successively with the STR-ASO probe (specific for *K. striata*; **left**), and, after stripping, with the CAL-ASO probe (specific for *K. calcarata*; **right**). Lizards in row A, positions 1–6 were specimens of *K. striata*, and lizards in row A, positions 7 and 8 were specimens of *K. borckiana*, showing that the probe binds with the mtDNA of these two species (i.e., the mtDNA of the unisexual *K. borckiana* is similar to that of *K. striata*). Lizards in row B, positions 1–5 were specimens of *K. calcarata*; row B, positions 6 and 7 were specimens of *K. altamazonica*; and row B, position 8 was a specimen of *K. pelviceps*. Note that only individuals of *K. calcarata* bind with the CAL-ASO probe, and in particular, individuals of the unisexual *K. borckiana* do not. See Dessauer et al. (1996) for details on the ASO methodology.

Unisexual Species: An Overview

Teioid Unisexual Species: There are numerous unisexual species within the Teiidae, and two or more occur among their closest relatives, the microteiids or Gymnophthalmidae. All of the unisexual taxa that have been studied in detail consist of parthenogens with a clonal pattern of inheritance, and they had a hybrid origin. Figure 6 illustrates the reticulate phylogeny of the teioid unisexual species, in which the numbered nodes indicate the following:

1. The Gymnophthalmidae is a diverse and understudied neotropical group. To date, one confirmed and two apparent unisexual lineages have been discovered. In the northern part of its range, *Gymnophthalmus underwoodi* is a diploid clonal parthenogen of hybrid origin (Cole et al., 1990, 1993; Kizirian and Cole, 1999). However, some Brazilian populations assigned to *G. underwoodi* are morphologically and genetically distinct and apparently represent a different lineage (Yonenaga-Yassuda et al., 1995), which requires additional research. In addition, *Leposoma percarinatum* probably is at least one unisexual lineage also (Uzzell and Barry, 1971; Hoogmoed, 1973; Avila-Pires, 1995).

2. *Teius suquiensis* is known on the basis of more than 160 specimens, all females (Avila and Martori, 1991). No genetic data are available for comparing this taxon with bisexual species of *Teius*.

3. ''*Cnemidophorus*'' *cryptus* is a diploid clonal parthenogen of hybrid origin (Dessauer and Cole, 1989; Sites et al., 1990). Two clones probably originated from separate F_1 hybrid zygotes (Cole and Dessauer, 1993), although it is not known whether these were produced by the same individual parents or in the same clutch of eggs. The current working hypothesis is that ''*C.*'' *gramivagus* and ''*C.*'' *lemniscatus* are the two ancestral species (Cole and Dessauer, 1993).

4. ''*Cnemidophorus*'' *pseudolemniscatus* is a triploid clonal parthenogen of hybrid origin, which is hypothesized to have been ''*C.*'' *cryptus* × ''*C.*'' *lemniscatus* (Dessauer and Cole, 1989; Cole and Dessauer, 1993).

5. *Kentropyx borckiana* is a diploid clonal parthenogen of hybrid origin (Hoogmoed, 1973; Cole et al., 1995). In this study we have determined that *K. striata* was the maternal ancestor (see above).

6. *Aspidoscelis rodecki* and the *A. cozumela* complex are diploid unisexuals of the *cozumela* species group. Both taxa are of hybrid origin, with *A. deppii* and *A. angusticeps* being the probable bisexual ancestors (Fritts,

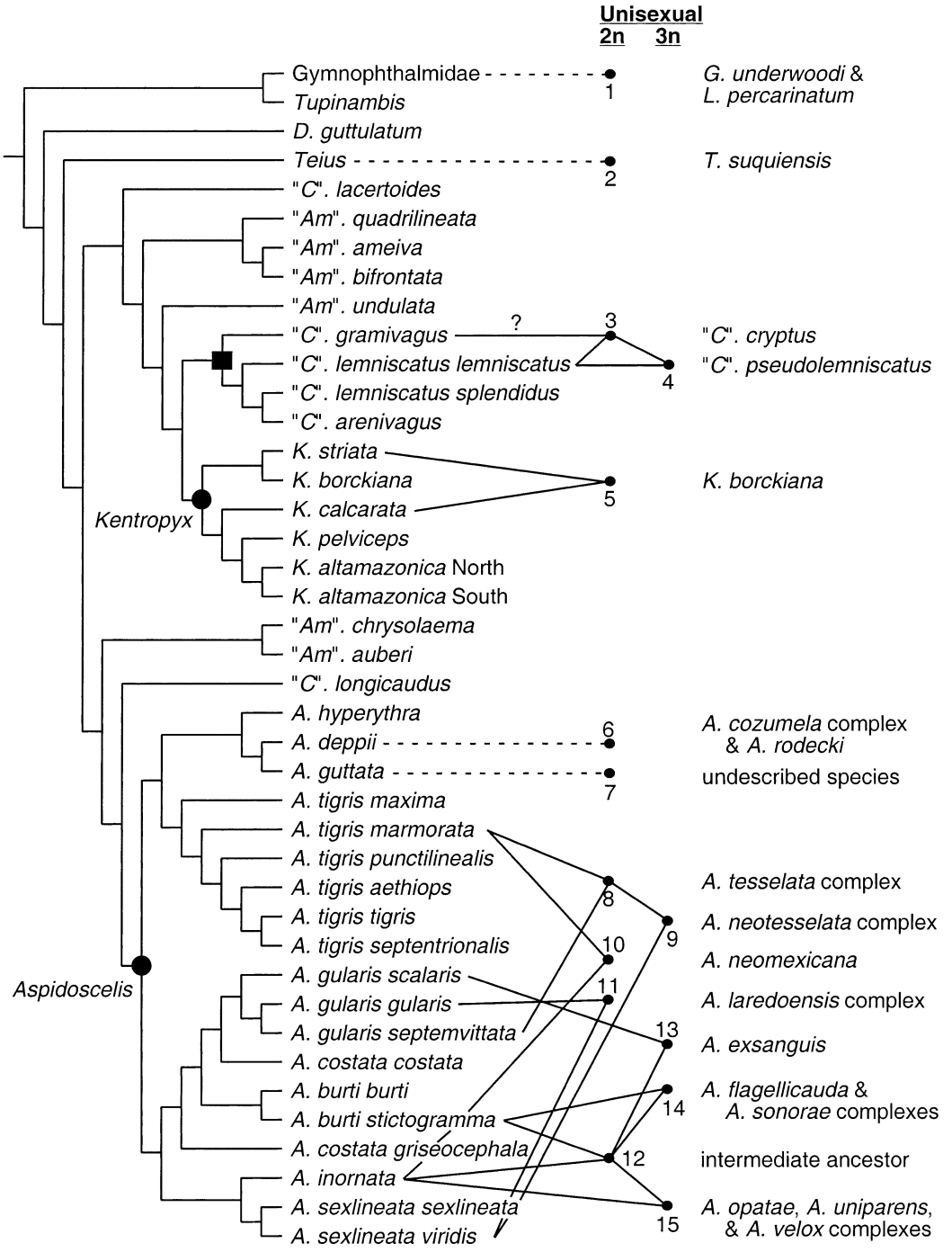

Fig. 6. Phylogeny depicting the hybrid origins of teiid unisexual species. Dashed lines indicate that not all relevant taxa are included in the given phylogeny. The solid square denotes the true ''*Cnemidophorus*'' clade (those taxa possessing anal spurs in males; see text).

1969; Moritz et al., 1992b; Hernandez-Gallegos et al., 1998). Based on mtDNA evidence, Moritz et al. (1992b) determined that *A. rodecki* and the *A. cozumela* complex were independently derived from an *A. angusticeps* maternal ancestor. The *A. cozumela* complex includes several distinct clonal lineages (Fritts, 1969; Moritz et al., 1992b; Hernandez-Gallegos et al., 1998).

7. The third member of the *cozumela* species group is an undescribed diploid unisexual species (Moritz et al., 1992b; Wright, 1993). Based on unpublished data, John Wright speculated that *Aspidoscelis guttata* and *A. motaguae* were the parental species. Moritz et al. (1992b) provided mtDNA evidence supporting *A. motaguae* as the maternal ancestor.

8. The *Aspidoscelis tesselata* complex includes diploid clonal parthenogens that may be derived from more than one F_1 hybrid zygote (Parker and Selander, 1976; Densmore et al., 1989b; Dessauer and Cole, 1989, work in progress). It is not known whether these were produced by the same individual parents or in the same clutch of eggs. Mitochondrial DNA evidence has confirmed *A. tigris marmorata* as the maternal ancestor (Brown and Wright, 1979; Densmore et al., 1989b; Dessauer et al., 1996). Walker et al. (1997) provided rationale for using the specific epithet *tesselata* for the unisexual species comprising most of the diploid populations in this complex (contra Wright, 1993). Walker et al. (1997) also recognized the isolated diploid populations in southwest New Mexico and southwest Texas as *A. dixoni* (originally described by Scudday, 1973; pattern class ''F'' of Zweifel, 1965).

9. The *Aspidoscelis neotesselata* complex includes triploid clonal parthenogens of hybrid origin(s) involving three different species of diploid bisexual ancestors (Parker and Selander, 1976; Densmore et al., 1989b; Dessauer and Cole, 1989; Walker et al., 1997), with *A. tigris marmorata* being the maternal species of the intermediate ancestor, *A. tesselata* (Densmore et al., 1989b; Dessauer et al., 1996).

10. *Aspidoscelis neomexicana* is a diploid parthenogen with several clones that may or may not have diverged from a single F_1 hybrid female (Parker and Selander, 1984; Cole et al., 1988; Cordes et al., 1990). Mitochondrial DNA evidence has shown that *A. tigris marmorata* was the maternal ancestor of this unisexual form (Brown and Wright, 1979; Densmore et al., 1989b; Dessauer et al., 1996).

11. The *Aspidoscelis laredoensis* complex includes diploid clonal parthenogens of hybrid origin(s) (McKinney et al., 1973; Bickham et al., 1977; Dessauer and Cole, 1989; Abuhteba et al., 2000), with *A. gularis* being the bisexual maternal ancestor (Wright et al., 1983; Parker et al., 1989).

12. This node in figure 6 represents an intermediate parthenogenetic ancestor(s) of certain triploid taxa (nodes 13–15). The two bisexual species involved in the original hybridization event(s) were *Aspidoscelis inornata* and *A. burti stictogramma* (or possibly *A. costata barrancorum*), with the intermediate ancestor originally occurring in both forms of reciprocal hybridizations. For the unisexual *A. flagellicauda, A. opatae, A. sonorae*, and *A. uniparens* complexes, the bisexual *A. inornata* was the maternal parent of this intermediate ancestor (Densmore et al., 1989a). For the unisexual *A. exsanguis* and *A. velox* complex, identity of the intermediate ancestor's maternal species is ambiguous. Based on mtDNA data, Moritz et al. (1989b) hypothesized that either *A. burti stictogramma* or *A. costata barrancorum* were equally likely to have been the maternal species of this diploid intermediate ancestor. The intermediate ancestor of *A. opatae* may or may not still survive today in northeastern Sonora (Dessauer and Cole, 1989; Wright, 1993). If it does, then this diploid species requires a new name (following the recommendations of Cole, 1985; Frost and Wright, 1988), since the original description of *A. opatae* applies to the triploid populations (node 15; see below). And finally, it has been suggested that diploid individuals of *A. velox* may exist in some populations of northern New Mexico (Cuellar and Wright, 1992) and southern Utah (Wright, 1993 [based on unpubl. data]). If such individuals and/or populations do occur, then the name *A. innotata* potentially could be applied to this diploid species. We feel the existence of these diploid *A. velox* populations need to be verified by investigating the possibility that they actually rep-

resent ''cryptic'' populations of the bisexual *A. inornata*.

13. *Aspidoscelis exsanguis* is a triploid clonal parthenogen of hybrid origin in which an intermediate diploid parthenogen (node 12; see above) backcrossed with a third bisexual ancestor. Two similar hypotheses have been proposed for its bisexual ancestors. Based on allozyme data, Good and Wright (1984) hypothesized that *A. inornata*, *A. costata barrancorum*, and *A. gularis septemvittata* were the bisexual ancestors. However, they did acknowledge that *A. burti stictogramma* was almost equally as likely as *A. c. barrancorum*. Dessauer and Cole (1989) postulated that *A. inornata*, *A. b. stictogramma*, and *A. g. scalaris* were involved in the hybrid origin of this species. The disagreement between these two studies is partially the result of different population and taxon sampling: (1) The *A. g. septemvittata* in the two studies were from different populations; (2) *A. g. scalaris* was not included in Good and Wright (1984); and (3) *A. c. barrancorum* was not included in Dessauer and Cole (1989). The allozymic similarities among the members of the *A. gularis* complex and among members of the *A. burti*/*costata* complex (Dessauer and Cole, 1989) also contributes to the difficulty of determining the parental species when these bisexuals were involved.

14. The *Aspidoscelis flagellicauda* and *Aspidoscelis sonorae* complexes include multiple triploid clones that are of hybrid origin(s) in which an intermediate diploid parthenogen (node 12; see above) backcrossed with its paternal bisexual ancestor, *Aspidoscelis b. stictogramma* (Dessauer and Cole, 1989).

15. The *Aspidoscelis uniparens* and *Aspidoscelis velox* complexes include multiple triploid clones that are of hybrid origin(s) in which an intermediate diploid parthenogen (node 12; see above) backcrossed with one of its bisexual ancestors, *A. inornata* (Dessauer and Cole, 1989).

In addition, ''*Cnemidophorus*'' *nativo*, a unisexual taxon of the ''*C.*'' *ocellifer* complex from Brazil was recently described (Rocha et al., 1997). The genetics, reproduction, mode of origin, and ancestry of this species remain to be investigated in detail.

Below we address the following two issues concerning the evolution of unisexual species: Our ability to know their bisexual ancestors, and the extent and origin of parthenogenetic cloning in vertebrates.

KNOWING ANCESTORS: It is generally accepted that one cannot truly discover ancestors in the process of reconstructing bifurcating phylogenies. We agree that this is generally true. However, in the case of unisexual lineages that are the result of recent hybridization events, it is possible that the derived forms of the ancestral bisexual species still exist. For example, the mitochondrial DNAs of some populations of the bisexual *Aspidoscelis tigris marmorata* are more closely related to the unisexuals *A. neomexicana* and *A. tesselata* than to some other *A. t. marmorata* populations (Densmore et al., 1989b). Whether or not these individual ancestral demes/populations are extant or extinct, the taxon *A. t. marmorata* still exists today, with geographic variation. In addition, when an F_1 hybrid female clones herself at an age of one or two years, both of her parents (of different species) may still be alive. However, those individual parents did not change into different species during their lifetimes. Thus, we have indicated ancestors by name for parthenogenetic species in figure 6. However, as noted elsewhere, the indicated ancestral species for some unisexuals is still in question, with additional taxon sampling and/or molecular markers being needed to further resolve these issues.

As yet there is no credible method for estimating ages of parthenogenetic lineages. However, those that have been studied in detail appear to be very young, based on the remarkable integrity maintained in the ancestral genomes they clone. Biogeographic, mitochondrial, and allozyme data suggest that essentially all unisexual *Aspidoscelis* lineages originated during or since the Pleistocene (Moritz et al., 1989a). These ancestral genomes are often so well preserved that in one analysis of a diploid parthenogen, detailed predictions could be made about the karyotype and protein mobilities of an unknown bisexual ancestor, which was later discovered (Cole et al., 1993). In general, the origin of the unisexual lineages was such a short time ago that their ancestors are best considered

as being represented by populations surviving today, although some allele frequencies and distributions may have shifted.

EXTENT AND ORIGIN OF PARTHENOGENETIC CLONING IN VERTEBRATES: All genetic data available for unisexual species of lizards indicate that females clone the F_1 hybrid state, excepting rare mutations (Dessauer and Cole, 1986, 1989). One possible exception may exist within *Lepidophyma* of the Xantusiidae (*L. flavimaculatum obscurum*; Bezy and Sites, 1987). The phylogeny of the teioid unisexual species (fig. 6) and their perpetuation of the F_1 hybrid state in lineages suggest that there is an instantaneous switch from sperm-dependent to sperm-independent reproduction in one generation of hybridization (Neaves, 1971; Cole, 1975, 1985; Darevsky et al., 1985; Moritz et al., 1989a). Although it is possible that a rare mutation affecting the reproductive mode could occur in an F_1 hybrid individual, the high frequency with which F_1 hybrids have established clones independently suggests a cause-and-effect relationship between hybridization and the origin of parthenogenesis in squamates, perhaps through genetic dysfunction in the control of meiosis in hybrids (Neaves, 1971; Cole, 1975; Moritz et al., 1989a, 1992a; Darevsky, 1992; Cole and Dessauer, 1995). For the unisexual taxa discussed in the literature cited above, this sudden switch happened at least 12 times among F_1 hybrids represented by the diploid nodes of figure 6. The hypothesis of cause-and-effect is also supported by the way hybrid origins of parthenogens span the phylogenetic breadth of the Teiidae and occur broadly in other squamates within the Gymnophthalmidae, Lacertidae, and Gekkonidae, and (if a hybrid origin is demonstrated in the future) possibly also the unisexual Chamaeleoninae, Agaminae, Xantusiidae, and Serpentes (*Ramphotyphlops*). The ability to produce parthenogenetic hybrids may extend back throughout the >200 million year history of the squamates.

It may appear paradoxical that the ability to spawn parthenogens instantly could have lasted for hundreds of millions of years, yet the recent unisexual clones are among the youngest of all lineages. A unisexual lineage may well experience a brief existence, being more prone to extinction than are bisexual lineages (White, 1970; Maynard Smith, 1978; but see Moritz et al., 1989a). If so, we would expect that throughout the history of the squamates unisexual lineages have originated repeatedly, appearing briefly in certain places in the phylogeny where bisexual taxa underwent interspecific hybridization. These hybridizing species are generally not closely related to one another. Evidence for such a conclusion is supported by two general observations: (1) Hybridization between closely related *Aspidoscelis* taxa is not uncommon, but unisexual clones are not always produced (e.g., Walker, 1981a, 1981b; Dessauer et al., 2000); and (2) the bisexual ancestral species of unisexual clones are genetically divergent (Cole, 1985; Dessauer and Cole, 1989; Moritz et al., 1992a). Hybridization events may have been most frequent during times of environmental changes and shifting habitats, which could have brought together populations that had been previously isolated from each other. We will never know how many of the squamate taxa known only from fossils were actually unisexual species, but we would not be surprised if it is on the order of 0.5% (as it is today), the number varying with the extent of environmental disturbances. As with other forms of life, we think that more unisexual lineages of vertebrates have gone extinct than survive today.

SUCCESSIVE APPROXIMATIONS AND INITIAL STARTING TREES

It has been a major concern of successive approximations that the final inferred phylogeny may be largely dependent on which initial tree(s) is used to successively weight the characters. Our results based on successive approximations on 20 randomly selected trees indicate that the initial starting tree does influence the outcome, with each analysis yielding a slightly different final tree. However, the vast majority of the inferred clades (fig. 4) were also evident in our successive approximations phylogeny (fig. 3). Those clades that were consistently recovered in the random tree successive approximation analyses also represent those groups that are strongly supported by our data (based on bootstrap analysis of the unweighted data). In general, at least for our data, it appears

that those relationships that are strongly supported are also robust to starting tree selection during successive approximations. These results give us additional confidence that those relationships that we determined to be strongly supported are not sensitive to the starting tree.

Similar analyses on mitochondrial rDNA sequences in *Phrynosoma* (Reeder, unpubl.) and mitochondrial ND4 sequences in Australian *Sphenomorphus* group skinks (Reeder, unpubl.) yield similar results. Recently, Kluge (1997a) has rejected reliability weighting because it invokes some unknown biological process that differentially commits some characters to higher degrees of homoplasy. However, for some molecular data sets it appears that some nucleotide positions (at least in the mitochondrial genome) are evolving at such a rate that they will be highly homoplastic (= large number of changes) on essentially any tree. When this is the case, such characters will be greatly down-weighted in all successive approximation analyses. Discovering this phenomenon does not require any specific knowledge of the biological process affecting the evolution of these characters, only that the characteristics of the data be thoroughly examined. How general these results are to other data sets is unknown. However, if one is to use successive approximations for phylogeny estimation, we recommend that individuals assess the sensitivity of their results to initial starting trees.

Karyotype Evolution Revisited

Considerable new data have appeared since initial hypotheses on karyotype evolution in teiid lizards were presented (Gorman, 1970; Lowe et al., 1970). Now we have karyotypic data for 66% of the taxa in the phylogeny presented here (figs. 2, 3). However, nearly all of the observations are based on standard, Giemsa stained chromosome preparations, in which homology of chromosome arms is not sufficiently clear for unambiguous coding for phylogenetic analysis. Consequently, we excluded the karyotypic data from our analyses, and now we can use the phylogenies (figs. 2, 3) to review hypotheses on karyotype evolution, which are identical for both phylogenies. We begin at the terminal nodes of the North American *Aspidoscelis* and work backward down toward the base of the teiine phylogeny. Terminology of chromosome shape based on centromere position follows Cole (1970), and we have reinterpreted illustrations of some other authors to be consistent with our terminology and assignment of chromosomes into groups (Set I–Set III), following Lowe et al. (1970). Figure 7 provides a summary and phylogenetic perspective of these major karyotypic events that have occurred during teiine evolution.

The 10 taxa representing the *sexlineata* species group of *Aspidoscelis* all share one basic karyotype (Lowe et al., 1970: 131, their fig. 2B). This is consistent with their representing one clade (fig. 7; Clade 29 of fig. 2, or Clade 30 of fig. 3), particularly as their karyotype appears nowhere else in the phylogeny. The Set I chromosomes include only one pair of large metacentric macrochromosomes. These have a subterminal secondary constriction on one arm, the nucleolar organizer region, or NOR (Ward and Cole, 1986), which sets off an elongate satellite. The Set II chromosomes include 12 pairs of smaller macrochromosomes, which are all telocentric to subtelocentric. The Set III chromosomes include 10 pairs of microchromosomes. Sex chromosomes are not recognizable. This karyotype has a diploid number (2n) of 46 and can be referred to as 2n = 46 with 2 + 24 + 20 chromosomes. Only two basic variants are known within the *sexlineata* group: (1) In *A. sexlineata*, chromosomes of the fourth largest pair of Set II have a longer short arm than in the other species (fig. 7) (Bickham et al., ''1976'' [1977]; Cole et al., 1988); and (2) most of the parthenogenetic species of this group are triploids, and many of these perpetuate minor chromosomal mutations through cloning (3n = 69 or so). Consequently, we conclude that the basic *sexlineata* group karyotype, 2n = 46 with 2 + 24 + 20 chromosomes, was present in the common ancestor of this group.

The six taxa representing the *tigris* species group of *Aspidoscelis* also all share one basic, unique karyotype (Cole et al., 1969; Lowe et al., 1970: 134, their fig. 3A), which is consistent with them representing a monophyletic group (Clade 24 of fig. 2, or Clade 25 of fig. 3). There are three pairs of large

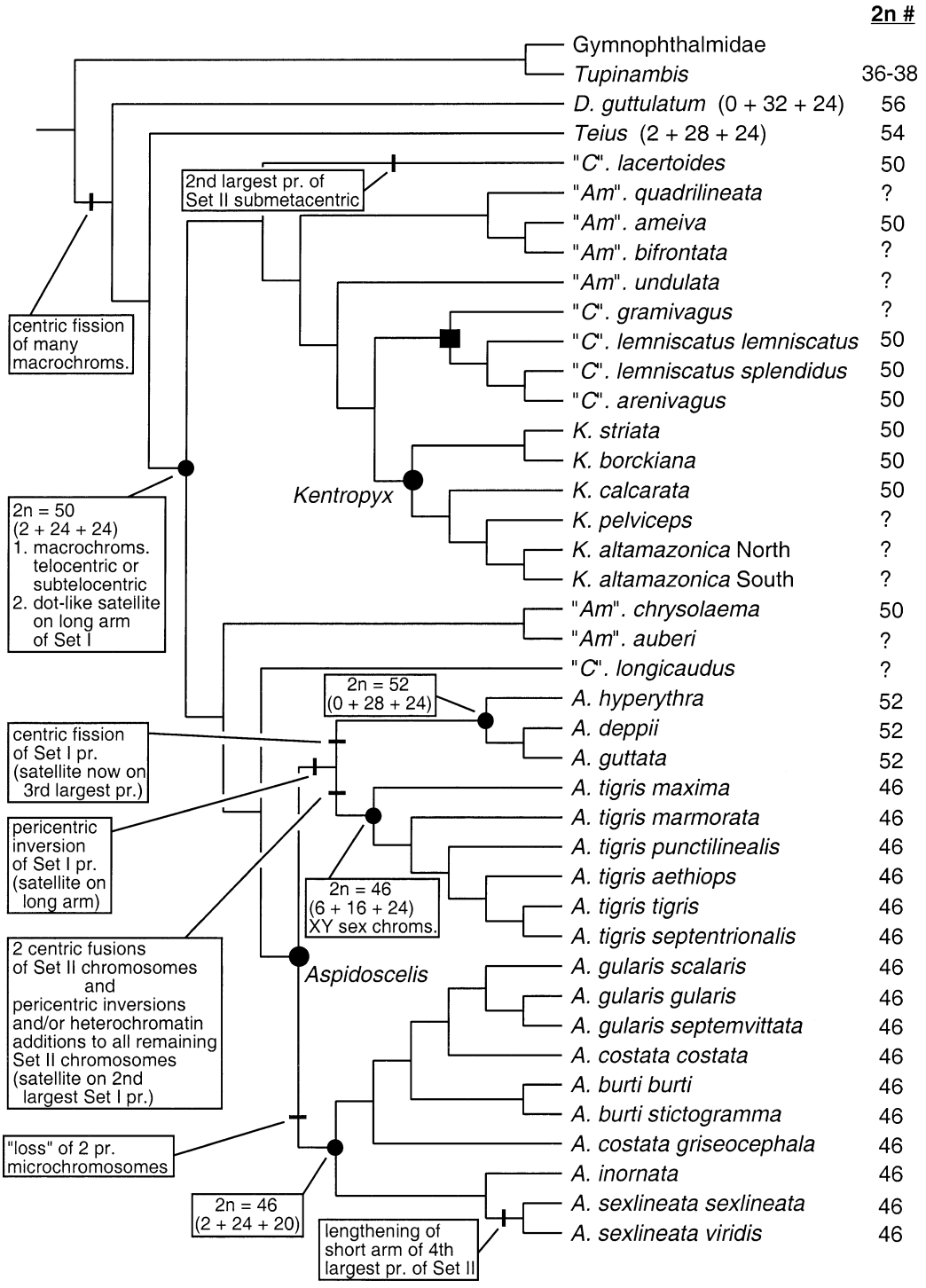

Fig. 7. Phylogeny depicting major events in karyotypic evolution among cnemidophorine lizards. Karyotypes are not known for those taxa denoted with ''?''. The solid square denotes the true *Cnemidophorus* clade (those taxa possessing anal spurs in males; see text).

biarmed Set I macrochromosomes, of which the first pair is metacentric, the second largest pair (also metacentric) has a subterminal NOR (Ward and Cole, 1986) that sets off a dot-like satellite, and the third largest pair is the sex chromosomes (fig. 7) (Cole et al., 1969; Bull, 1978). The male is the heterogametic sex (XY sex determination). The Set II chromosomes include eight pairs of smaller macrochromosomes, which are all subtelocentric to submetacentric. Set III includes 12 pairs of microchromosomes. This karyotype can be abbreviated as 2n = 46 with 6 + 16 + 24 chromosomes, and, considering that it occurs in all of the taxa, must have occurred in the ancestor of this clade.

The three taxa representing the *deppii* species group of *Aspidoscelis* also all share one basic karyotype (Lowe et al., 1970: 129, their fig. 1; Robinson, 1973) that is unique to their clade (fig. 7; Clade 22 of fig. 2, or Clade 23 of fig. 3). There are no large Set I macrochromosomes. The Set II chromosomes include 14 pairs of telocentric macrochromosomes, the second or third pair of which has an inconspicuous dot-like satellite distal to a nearly terminal secondary constriction. Set III includes 12 pairs of microchromosomes. This karyotype has 2n = 52 with 0 + 28 + 24 chromosomes, and most likely occurred in the common ancestor of this clade.

There are no karyotypic data for ''*Cnemidophorus*'' *longicaudus* or for ''*Ameiva*'' *auberi*, but there are for ''*A.*'' *chrysolaema* (Gorman, 1970: 237, his fig. 4d; De Smet, 1981). ''*Ameiva*'' *chrysolaema* has 2n = 50 with 2 + 24 + 24 chromosomes (fig. 7). De Smet (1981) reported that all macrochromosomes were telocentric, whereas Gorman (1970) showed the largest one to be subtelocentric, as well as two among the Set II chromosomes, the latter of which looks to us as the normal variation one sees from cell to cell among telocentric to subtelocentric chromosomes. Nevertheless, the Set I chromosomes illustrated by Gorman (1970) looked identical, or nearly so, to that which characterizes the *lemniscatus* species group (sensu stricto) of *Cnemidophorus*, as do all of the other features of this karyotype. This karyotype is also the same as the basic karyotype hypothesized to be present in the common ancestor of Clade 4 (figs. 2, 3; no data are available for *Kentropyx altamazonica*, *K. pelviceps*, ''*A.*'' *bifrontata*, ''*A.*'' *quadrilineata*, ''*A.*'' *undulata*, and *Cnemidophorus gramivagus*, although lizards designated as ''*lemniscatus* class E'' from Brazil may be *C. gramivagus* [Cole and Dessauer, 1993]).

Kentropyx calcarata, *K. striata*, *K. borckiana*, *Cnemidophorus arenivagus*, *C. lemniscatus lemniscatus*, *C. l. splendidus*,''*C.*'' *lacertoides*, and ''*Ameiva*'' *ameiva* all have similar karyotypes of 2n = 50 with 2 + 24 + 24 chromosomes (fig. 7) (Gorman, 1970; Lowe et al., 1970: 131, their fig. 2A; Cole et al., 1979, 1995; and Markezich et al., 1997). All of these species also have a dot-like satellite on the long (or only) arm of the Set I pair of chromosomes. Karyotypic differences among these species are minor, involving only two points: (1) The Set I chromosomes are either telocentric (usually) or subtelocentric; and (2) the Set II chromosomes usually are all telocentric, but some species have one or two subtelocentric chromosomes, and the second largest pair of Set II in ''*C.*'' *lacertoides* is uniquely submetacentric. These differences are readily explained by recent derivations, possibly through unequal pericentric inversions or addition of heterochromatin. Because ''*C.*'' *lacertoides*, ''*Ameiva*'' *ameiva*, and the three species of *Kentropyx* karyotyped all share the telocentric Set I pair of chromosomes, we suggest that this is the ancestral state for this clade (Clade 4; figs. 2, 3). This, taken together with the similar karyotypic data for ''*A.*'' *chrysolaema* (described above) suggests that the ancestor of Clade 3 (figs. 2, 3) had the following karyotype: 2n = 50 with 2 + 24 + 24 chromosomes (fig. 7), and all of the macrochromosomes were telocentric or subtelocentric.

Given the karyotypic similarities and nearly complete information available for the taxa discussed so far, we now review karyotype evolution with a scenario that begins at the node that represents the common ancestor of *Aspidoscelis* and ''*Cnemidophorus*'' (fig. 7; Clade 3 of figs. 2, 3). That ancestor probably had a karyotype of 2n = 50 with 2 + 24 + 24 chromosomes, and all of the macrochromosomes were telocentric or subtelocentric. Evolution in Clade 4 (figs. 2, 3) and in the lineage leading to ''*Ameiva*'' *chryso-*

laema only involved minor changes in centromere positions of from zero to two or three macrochromosomes. This hypothesis predicts that the species in Clade 4 (and ''*A.*'' *auberi* and ''*C.*'' *longicaudus*) that have not been karyotyped yet will be found to have basically the same ancestral karyotype or one readily derived therefrom (fig. 7).

Evolution in the lineage leading to the *Aspidoscelis deppii* species group involved the addition of two pairs of Set II telocentric chromosomes while losing the Set I pair, and a change in occurrence of the satellites from being on the largest to the third largest pair. Although other possibilities exist, this could have happened in two steps: (1) unequal pericentric inversion on the ancestral Set I chromosome to produce a large metacentric or submetacentric chromosome with the dot-like satellite on the long arm; (2) centric fission of this derived chromosome, resulting in simultaneous loss of the Set I pair and addition of two pairs of Set II telocentric chromosomes. It is conceivable and parsimonious to suggest that the derived Set I macrochromosome prior to the centric fission just mentioned occurred in the most recent common ancestor of the *deppii* and *tigris* groups (fig. 7), and that today this chromosome is represented in *A. tigris* by the second largest metacentric chromosome that bears the NOR and dot-like satellite. Additional evolution to the karyotype of *A. tigris* could have involved two centric fusions of Set II chromosomes to form the rest of the Set I condition of *tigris* plus unequal pericentric inversions and/or addition of heterochromatin on each of the Set II pairs of chromosomes (fig. 7).

Evolution of the karyotype of the *Aspidoscelis sexlineata* species group from that of their ancestor shared with ''*Ameiva*'' *chrysolaema* involved a change in the position of both the centromere and secondary constriction of the Set I chromosomes, little to no conspicuous changes in Set II, and an apparent loss of two pairs of microchromosomes, which, through translocations, could have become incorporated into other chromosomes (fig. 7). Future analyses of chromosome banding patterns could reveal whether there are arm homologies among the satellite chromosomes of the *deppii*, *tigris*, and *sexlineata* groups, which could indicate whether the Set I pair of biarmed chromosomes with satellites occurred in the ancestor represented by the node that ties together these three groups.

Now we turn to the karyotype evolution in the far more distant past, involving the other macroteiids, including *Tupinambis*, *Dicrodon*, and *Teius*. The most basal lineage among these is that which leads to *Tupinambis* (figs. 2, 3). The *Tupinambis* that have been karyotyped to date (Gorman, 1970: 236, his fig. 2d; De Smet, 1981) have been reported to represent two species, *T. teguixin* and *T. nigropunctatus*, but details on individuals examined were not always cited; at least we know that Gorman's were from Trinidad and Brazil. These lizards had either 2n = 36 or 38 with 12 macrochromosomes (6 pairs) and either 24 or 26 microchromosomes (fig. 7). The six pairs of macrochromosomes, from largest to smallest, appear as follows: number 1, large metacentric; number 2, large submetacentric with subterminal secondary constriction and dot-like satellite on the long arm; numbers 3 and 4, somewhat smaller, metacentric, similar to each other; number 5, somewhat smaller metacentric; and number 6, significantly smaller subtelocentric. This is or approximates in close detail (but with no. 6 submetacentric) the karyotype hypothesized to have occurred in the common ancestor of Iguania and possibly all lizards (Gorman, 1970, 1973; Paull et al., 1976; Sites et al., 1992). This karyotype is shared by additional South American macroteiids, including *Callopistes*, *Dracaena*, and *Crocodilurus* (which has chromosome no. 6 larger than in the other species and one pair fewer of microchromosomes evident; Gorman, 1970: 236, his fig. 2). Centric fissioning of all of the macrochromosomes in this karyotype would result in a karyotype approximating that of ''*Ameiva*'' *ameiva* (fig. 7; Gorman, 1970), although additional changes in details would have been involved also.

Dicrodon and *Teius* remain to be discussed, two species of lineages that diverged possibly before, during, or after the extensive fissioning of the large ancestral macrochromosomes as represented in *Tupinambis* (fig. 7). According to Gorman (1970: 238, his fig. 5a), *D. guttulatum* has a karyotype of 2n =

56 with 0 Set I chromosomes, 32 telocentric Set II chromosomes, and 24 microchromosomes, so the extensive fissioning of macrochromosomes occurred after it shared a common ancestor with *Tupinambis*. The karyotype known for *Teius* is rather similar to that of *D. guttulatum*, with *Teius* having 2n = 54 with two large Set I macrochromosomes + 28 Set II macrochromosomes (mostly telocentric) + 24 microchromosomes (Gorman, 1970: 238, his fig. 5b; Hernando, 1994). The Set I chromosome is submetacentric and appears similar to chromosome number 2 of the ancestral state as represented in *Tupinambis*, so this could be one ancestral biarmed chromosome that was not yet fissioned in the common ancestor of *Teius* and *Dicrodon*, or it could represent a new centric fusion that occurred in *Teius*. If the former, this chromosome became fissioned in both the *Dicrodon* and between the *Teius* and *Ameiva* clades (fig. 7).

SUMMARY AND CONCLUSIONS

1. Whiptail lizards of the genus *Cnemidophorus* range widely in the New World. This group has been extensively studied and much is known about its biology, ecology, and natural history.

2. Historically, *Cnemidophorus* has been diagnosed from other teiine teiids by the lack of derived character states. While it has been generally assumed, *Cnemidophorus* monophyly has never been rigorously tested.

3. Mitochondrial 12S and 16S rDNA (491 bp and 581 bp, respectively), allozymes (31 loci), and morphology (10 characters) were used to infer the phylogenetic relationships among 27 *Cnemidophorus* taxa, as well as to determine the phylogenetic placement of *Cnemidophorus* among other teiine genera (*Ameiva*, *Dicrodon*, *Kentropyx*, and *Teius*).

4. Phylogenies based on uniformly weighted and successively weighted phylogenetic analyses were nearly identical, with *Dicrodon* and *Teius* representing basal teiines.

5. The cnemidophorines (= *Ameiva*, *Cnemidophorus*, and *Kentropyx*) were supported as a monophyletic group.

6. The monophyly of *Cnemidophorus* was not supported, with the *lemniscatus* group taxa being more closely related to other neotropical cnemidophorines (i.e., *Ameiva* and *Kentropyx*) than to a strongly supported North American clade of *Cnemidophorus* (consisting of the *deppii*, *sexlineatus*, and *tigris* groups). The traditional *lemniscatus* group is also paraphyletic.

7. There was strong support for the monophyly of the *deppii*, *sexlineatus*, and *tigris* groups of the North American ''*Cnemidophorus*'' clade.

8. Only two clades within the *sexlineatus* group are strongly supported: the ''*Cnemidophorus*'' *gularis* complex, and the ''*C.*'' *inornatus* + ''*C.*'' *sexlineatus* clade.

9. Based only on morphological data, ''*Cnemidophorus*'' *murinus* was placed as the sister species of the ''*C.*'' *lemniscatus* complex and ''*C.*'' *ocellifer* was placed as the sister species to all remaining cnemidophorines.

10. The monophyly of *Ameiva* is rejected.

11. Because of the paraphyly of ''*Cnemidophorus*'', taxonomic changes were recommended. The name *Aspidoscelis* Fitzinger, 1843, is resurrected to accommodate the taxa of the North American clade of ''*Cnemidophorus*''.

12. The type species of *Cnemidophorus* is *C. murinus*, a member of the ''*lemniscatus* group''. Because of the paraphyly of the ''*lemniscatus* group'', restricting *Cnemidophorus* to this group still leaves the genus paraphyletic. However, because of the weakly supported relationships among the neotropical cnemidophorines and paraphyletic nature of ''*Ameiva*'', further nomenclatural changes within the ''*lemniscatus* group'' would be premature. Until additional data (i.e., taxa and characters) are collected, we prefer to apply the name ''*Cnemidophorus*'' to the ''*lemniscatus* group'', but acknowledge its paraphyly. Ultimately, *Cnemidophorus* will likely be restricted to the clade containing *C. murinus* and the *C. lemniscatus* complex.

13. The maternal ancestor of the unisexual *Kentropyx borckiana* was the bisexual *K. striata*.

14. Diploid and triploid unisexual species of recent hybrid origin are numerous within the Teiidae. The vast majority of these are in the genus *Aspidoscelis*, of which approximately one-third of the species are parthen-

ogens. In comparison with the bisexual species, the unisexuals have had an instantaneous origin in one generation, but they are prone to extinction.

15. An extensive karyotypic database exists for teiine lizards. Using our inferred phylogeny, karyotypic evolution was reevaluated from an evolutionary perspective. The chromosomes reflect a history consistent with the phylogeny. In particular, the three monophyletic species groups in *Aspidoscelis* all have unique karyotypes.

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APPENDIX 1

Specimens Examined

The specimens are referred to by their individual catalog numbers, and initials for their respective collections are as follows: ALM (field series of Allan L. Markezich, Black Hawk College, Moline, IL); AMNH (American Museum of Natural History); CRE (Costa Rica Expedition collection of Jay Savage; to be accessioned into the Los Angeles County Museum of Natural History); DMH (uncataloged specimen in the CRE collection collected by David M. Hillis); KU (Natural History Museum, University of Kansas); LACM (Los Angeles County Museum of Natural History); LSUMZ (Museum of Natural Science, Louisiana State University); LVT (Tissue Collection, University of Nevada–Las Vegas); MZFC (Museo de Zoologia, Universidad Nacional Autonoma de Mexico); OMNH (Oklahoma Museum of Natural History, University of Oklahoma); REE (private collection of Robert Espinoza; eventually to be deposited at California State University, Northridge); RWM (Robert W. Murphy, Royal Ontario Museum); SDNHM (San Diego Natural History Museum); SDSU (San Diego State University); TNHC (Texas Natural History Collection of the Texas Memorial Museum, University of Texas at Austin); USNM (National Museum of Natural History, Washington, DC). The lowercase letters following the catalog numbers indicate the type of data taken from each specimen, as follows: d, DNA; m, morphology; p, ASO probes.

Acanthodactylus cantoris

Genbank accession numbers AF080298 and AF080300.

''Ameiva'' ameiva

GUYANA: Northern Rupununi Savanna; Karanambo (on Rupununi River), McTurk Ranch (AMNH R-137907–137914, m); Mackiedon (ranch), 3 mi (linear) WNW Karanambo (AMNH R-138119, m).

PERU: Madre de Dios; Cuzco Amazonico, 15 km E Puerto Maldonado (KU 205000, d).

''Ameiva'' auberi

CUBA: Habana; 2 mi E Playa de Guanabo, Cueba de Rincon de Guanabo (AMNH R-78021–78022, m); 2 mi E Boca de Jaruco (AMNH R-78023–78025, m; AMNH R-96330, m); Provincia Matanzas, Playa Larga (USNM 498139, d).

''Ameiva'' bifrontata

COLOMBIA: Guajira; Merochon, 5 km SE Uribia (AMNH R-106053, m; AMNH R-106065–106066, m; AMNH R-106079, m; AMNH R-106081, m).

NO DATA: SDSU 3899 (d).

''Ameiva'' chrysolaema

DOMINICAN REPUBLIC: Monte Cristi; 1.5 mi NE Monte Cristi (AMNH R-42478, m); Monte Cristi (AMNH R-42480–42481, m; AMNH R-42486, m); 1.5 mi W Monte Cristi (AMNH R-42485, m); Monte Cristi; 0.25 mi beyond bridge at La Barca on Copey Rd (AMNH R-42487, m); Monte Cristi; 3 km SE Monte Cristi (SDNHM 67040, d).

''Ameiva'' quadrilineata

COSTA RICA: Boca Sacati (AMNH R-16306, m); Colorado Bar (AMNH R-16754–16757, m); Limon: 17.3 km W Guapiles (CRE 4807, d).

''Ameiva'' undulata

MEXICO: Oaxaca; Colonia Rodolfo Figueroa, Cerro Baul, Rancho Vicente (AMNH R-100665, m); Colonia Rodolfo Figueroa, Rancho Vicente, Cerro Baul, 18 km NW Rizo de Oro (Chiapas) (AMNH R-100666–100668, m).

COSTA RICA: Puntarenas; nr mouth Rio Barranca, 10 km E Puntarenas (DMH 86–220, d).

Aspidoscelis burti burti

MEXICO: Sonora; 2.3 mi (by rd) NE Guaymas (AMNH R-80598, m); Bahia de San Carlos (AMNH R-131433, d; AMNH R-131433–131436, m).

Aspidoscelis burti stictogramma

USA: Arizona; Cochise Co.; Bass Canyon, ca. 0.5 mi from Hot Springs Canyon, 31.1 mi (by rd) WNW Willcox (AMNH R-126768, d; AMNH R-126767–126782, m).

Aspidoscelis costata costata

MEXICO: Morelos; El Rodeo (AMNH R-93289–93296, m); Morelos; 13.5 km S Puente de Ixtla (MZFC 811, d).

Aspidoscelis costata griseocephala

MEXICO: Sonora; El Caracol Trailer Park, 9 mi (by Sonora Hwy 001) WNW Alamos (AMNH R131442, d; AMNH R-131439–131444, m).

Aspidoscelis deppii

MEXICO: Guerrero; 1 mi SW Tierra Colorada (AMNH R-106549–106551, m); Guerrero; 14.7 mi N Zumpango del Rio on Hwy 95 (MZFC 7046, d).

Aspidoscelis gularis gularis

USA: Texas; McCulloch Co., 1.2 mi N FM 2028, on unnumbered N-S farm rd, at Brady Reservoir, ca. 6 mi W Brady (TNHC 53222, d); Webb Co.; 15 mi (by I-35) NNE Laredo (AMNH R-134950, m); Reeves Co.; 2.7 mi (by TX Hwy 17) SW Balmorhea (AMNH R-134952–134953, m); Brewster Co.; 30.6 km N Marathon, foothills Glass Mtns (AMNH R-135465, m).

Aspidoscelis gularis scalaris

MEXICO: Chihuahua; 2 mi (by Mex. Hwy 45) NW Bachimba (AMNH R-129175, d); Coahuila; Las Delicias, Sierra del Sobaco (AMNH R-67392–67396, m); Durango; Rio Florido nr Canutillo (bridge for Mex. Hwy 45) (AMNH R-129178, karyotyped).

Aspidoscelis gularis septemvittata

USA: Texas; Brewster Co.; Stillwell Ranch, 75 km SSE from Marathon by hwy (AMNH R-135745–135746, m); Brewster Co.; Marathon (TNHC 53902, d).

Aspidoscelis guttata

MEXICO: Oaxaca; 4.5 mi E jct Hwys 185 and 200 (MZFC 7044, d); Veracruz; Mandinga (AMNH R-15454–15460, m); sand dunes, 2 mi S Veracruz (AMNH R-15461–15462, m).

Aspidoscelis hyperythra

MEXICO: Baja California; Mulege (AMNH R-5523, m); Castro Rancho (AMNH R-5524, m); San Pedro (AMNH R-20434, m); 2 mi N Punta Hughes, Isla Magdalena (AMNH R-77387, m); Espiritu Santo Island, Bahia San Gabriel (SE side) 2 mi E Punta Prieta (AMNH R-78919, m); Espiritu Santo Island, SE side 0.5–1.5 mi N Bonanza Point (AMNH R-78921, m); Baja California Sur; arroyo San Miguel, 14.2 mi W of Mulege (RWM 1025, d).

Aspidoscelis inornata

USA: Arizona; Coconino Co.; 9.3 mi (by US Hwy 89) S Gray Mountain (AMNH R-126861, d); New Mexico; Hidalgo Co.; 16.9 mi (by US Hwy 70) NW Lordsburg (AMNH R-131060, m); 16.7 mi NW Lordsburg on US Hwy 70 (AMNH R-131061–131064, m).

Aspidoscelis sexlineata sexlineata

USA: Florida; Okaloosa Co.; Destin, on beach (LSUMZ 49566, d); Georgia; Liberty Co.; St Catherine's (= Catherines) Id (AMNH R-122825–122827, m).

Aspidoscelis sexlineata viridis

USA: New Mexico; Chaves Co.; 6.2 mi W Caprock (Lea Co.) (AMNH R-130295, m); San Miguel Co.; Conchas Lake at South State Park campground (AMNH R-135193–135196, m); Texas; Brooks Co.; 7.1 mi (by US Hwy 281) S Falfurrias (AMNH R-126901, d). The Texas specimen was referred to *C. s. stephensi* by Trauth (1992).

Aspidoscelis tigris tigris

USA: California; Inyo Co.; 0.5 mi W Independence (AMNH R-110676, m; AMNH R-115556, m); Los Angeles Co.; Lovejoy Spgs Antelope Valley (AMNH R-42772, m); Riverside Co.; Piñon Flats, San Jacinto Mtns (AMNH R-60509, m); Riverside Co.; Indian Wells (AMNH R-60526, m); Nevada; Henderson (LVT 00007, d).

Aspidoscelis tigris aethiops

MEXICO: Sonora; 30.8 mi S Santa Ana (AMNH R-80761, m); 2 mi W Mazatán (AMNH R-84929, m); 7 mi N (Hwy 15) Hermosillo (AMNH R-84939, m); 36 mi SE Hermosillo, on Rte 16 (AMNH R-84945, m); Bahia San Carlos (AMNH R-131430, m); 4 mi (by rd) NE Bahia de San Carlos (AMNH R-129164–129165, m); along Rio Mayo, Navojoa (AMNH R-131432, d; AMNH R-131431–131432, m).

Aspidoscelis tigris marmorata

USA: New Mexico; Hidalgo Co.; 10.1 mi (by US Hwy 70) NW Lordsburg (AMNH R-131082–131088, m); Hidalgo Co.; 0.6 mi (by rd) E and 9.6 mi (by rd) N Animas (AMNH R-127072, d).

Aspidoscelis tigris maxima

MEXICO: Baja California Sur; Miraflores (AMNH R-5542, m; AMNH R-5570, m); San Bernardo Mtn (AMNH R-5549, m; AMNH R-5656, m); La Paz (AMNH R-15233, m); Espiritu Santo Island, NW side opposite Isla Partida (AMNH R-78933–78934, m); Hwy 1, 7 mi S San Antonio (LACM 128251, d).

Aspidoscelis tigris punctilinealis

USA: Arizona; Cochise Co.; 3 mi (linear) E and 10 mi (linear) S San Simon (AMNH R-127052, d); Pima Co.; Huerfano Butte, Santa Rita Experimental Range, 27 mi (air) SSE Tucson (AMNH R-127056–127066, m).

Aspidoscelis tigris septentrionalis

USA: Arizona; Apache Co.; Many Farms (AMNH R-136798, d; AMNH R-136796–136800, m).

''Cnemidophorus'' arenivagus

COLOMBIA: Guajira; Merochon, 5 km SE Uribia (AMNH R-106221, m); Merochon, ca 5 km SE Uribia (AMNH R-109995, m; AMNH R-109998, m).

VENEZUELA: Falcon; Paraguana Peninsula, 6 km S Adicora on Coast Rd (AMNH R-142582, m); Paraguana Peninsula, ca. 4 km N Moruy (AMNH R-142583, d; AMNH R-142583–142586, m); Paraguana Peninsula, W edge Adicora (AMNH R-142587–142588, m).

''Cnemidophorus'' gramivagus

COLOMBIA: Arauca; Cravo Norte (AMNH R-97415–97424, m).

VENEZUELA: Portuguesa; 9.7 km (by rd) SW Guanarito (ALM 8199, d).

''Cnemidophorus'' lacertoides

URUGUAY: Maldonado; Abra de Perdomo (AMNH R-115938, d; AMNH R-115938–115939, m); Rocha; Cabo Polonio (AMNH R-116321, m).

''Cnemidophorus'' lemniscatus lemniscatus

GUYANA: Dubulay Ranch on Berbice River (AMNH R-140862, d; AMNH R-140862–140872, m).

''Cnemidophorus'' lemniscatus splendidus

VENEZUELA: Falcon; Paraguana Peninsula, on gravel rd nr Capuchino radar base (AMNH R-142589, m); Paraguana Peninsula, 2 km S Miraca nr Agua Sabrida area (AMNH R-142590, m; AMNH R-142592, d, m; AMNH R-142595, m); Paraguana Peninsula, SW of San Jose de Cocodite (nr El Pizarral) (AMNH R-142591, m; AMNH R-142593–142594, m; AMNH R-142596, m).

''Cnemidophorus'' longicaudus

ARGENTINA: Buenos Aires; Bahia Blanca (AMNH 17020, m); La Rioja; Famatina; 9.9 km W Antinaco (AMNH R-144524–144525, m); Tucuman; btwn Santa Maria and Amaicha del Valle (AMNH R-144526–144527, m); Mendoza Prov.; Depto. San Rafael; rd behind Pueblo de Nihuil along NE side Embalse Nihuil (REE 130, d).

''Cnemidophorus'' murinus

DUTCH WEST INDIES: Curacao; Round Cliff (AMNH R-118623, m; AMNH R-118625, m; AMNH R-118627, m; AMNH R-73290, m); Curacao (AMNH R-13538, m); Curacao; nr Piscadera Bay (AMNH R-73293–73294, m; AMNH R-73296, m); Bonaire (AMNH R-73297–73299, m).

''Cnemidophorus'' ocellifer

BRAZIL: Bahia (AMNH R-36372–36374, m); Mato Grosso; confluence of Rio Araguaia and Tapirapé, Tapirapé village (AMNH R-87903, m).

BOLIVIA: Santa Cruz; San Antonio de Parapetí (AMNH R-141482, m; AMNH R-141484, m); La Brecha, ca 104–120 km NE Charagua, Izozog Region (AMNH R-141485, m; AMNH R-141497, m).

Dicrodon guttulatum

ECUADOR: Santa Clara Island, Gulf of Guayaquil (AMNH R-28977–28981, m); Santa Elena (AMNH R-21875, m).

NO DATA: SDSU 3906 (d).

Eumeces septentrionalis

USA: Kansas; Sumner Co.; Sec 15, T35S, R3W (KU 211138, d).

Kentropyx altamazonica

PERU: Loreto; Moyobamba Trail, Cahuapanas (AMNH R-65373, m); Madre de Dios; Cuzco Amazonico, 15 km E Puerto Maldonado (KU 205015, d).

VENEZUELA: Amazonas; Neblina Base Camp on Rio Mawarinuma (AMNH R-127818–127821, m; AMNH R-129243, m; AMNH R-133667–133669, m); Amazonas; Tapirapeco Expedition Base Camp, upper Rio Mavaca (AMNH R-134174, p; AMNH R-134175, d, p).

Kentropyx borckiana

GUYANA: Georgetown, Botanical Gardens (AMNH R-138111, p; AMNH R-138112, d, p).

Kentropyx calcarata

GUYANA: Dubulay Ranch on Berbice River (AMNH R-141858–141859, m); Warniabo Creek, 4 mi (by rd) SW Dubulay Ranch house (AMNH R-141864–141865, m; AMNH R-140967, d; AMNH R-140967–140968, m).

SURINAM: Brokopondo; Mazaroni Top, Brownsberg Nature Reserve (AMNH R-133347–133350, p); Surinam; Paramaribo, grounds of Paramaribo Zoo (AMNH R-133351, p).

Kentropyx pelviceps

ECUADOR: Morona-Santiago; Cusuime, Rio Cusuime (60 km airline SE Macas) (AMNH R-113767–113772, m); Sucumbios Prov., Reserva Faunistica Cuyabeno (RPF-Cuyabeno), Estacion Biologia da Universidad Catolica (OMNH 36502, d, p).

Kentropyx striata

GUYANA: Northern Rupununi Savanna, vicinity Cajueiro, 8 mi WNW Karanambo (AMNH R-138088, m, p); Northern Rupununi Savanna, pd 5 mi (airline) SW Karanambo (AMNH R-138089–138090, m, p; AMNH R-138091–138094, m; AMNH R-138097–138098, m); Northern Rupununi Savanna, Yupukari (on Rupununi River), 7 mi (airline) SSW Karanambo (AMNH R-138057, p); Northern Rupununi Savanna, Simoni area, ca. 10 mi (by trail) E Yupukari (AMNH R-138083–138084, p); Southern Rupununi Savanna, Aishalton (on Kubanawau Creek) (AMNH R-139881, d).

Lacerta agilis

Genbank accession numbers AF080344 and AF080346.

Pholidobolus montium

ECUADOR: Quito (AMNH R-28772–28780, m); Cotopaxi; 7 km N Latacunga (KU 196355, d).

Teius teyou

ARGENTINA: Córdoba; Cruz del Eje (AMNH R-21093–21098, m); La Roija Prov.; Depto. Castro Barros, CRILAR Institute (REE 150, d).

Tupinambis nigropunctatus

GUYANA: Warniabo Creek, 4 mi (by rd) SW Dubulay Ranch house (AMNH R-140938, m).

SURINAM: Brokopondo; Mazaroni Top, Brownsberg Nature Reserve (AMNH R-133345, m).

Tupinambis teguixin

PERU: Madre de Dios; Cuzco Amazonico, 15 km E Puerto Maldonado (KU 205023, d).

APPENDIX 2
MITOCHONDRIAL DNA DATA

The following aligned nucleotide positions correspond to given gene regions: 1–337 = 12S rDNA; 338–841 = 16S rDNA; and 842–876 = recoded gap characters (see Wiens and Reeder, 1997). The asterisks (*) above sequences denote those nucleotide positions that were considered ambiguously aligned and excluded from all phylogenetic analyses (see Materials and Methods). Taxon abbreviations are as follows: Eumeces = *Eumeces septentrionalis*; Lacerta = *Lacerta agilis*; Acanth = *Acanthodactylus cantoris*; Pholio = *Pholidobolus montium*; Tuptex = *Tupinambis teguixin*; Ameame = *Ameiva ameiva*; Ameaub = *Ameiva auberi*; Amebif = *Ameiva bifrontata*; Amechr = *Ameiva chrysolaema*; Amequa = *Ameiva quadrilineata*; Ameund = *Ameiva undulata*; Cneare = *Cnemidophorus arenivagus*; Cneburbur = *Cnemidophorus burti burti*; Cnebursti = *Cnemidophorus burti stictogrammus*; Cnecoscos = *Cnemidophorus costatus costatus*; Cnecosgri = *Cnemidophorus costatus griseocephalus*; Cnedep = *Cnemidophorus deppii*; Cnegra = *Cnemidophorus gramivagus*; Cnegul = *Cnemidophorus gularis gularis*; Cnegut = *Cnemidophorus guttatus*; Cnehyp = *Cnemidophorus hyperythrus*; Cneino = *Cnemidophorus inornatus*; Cnelac = *Cnemidophorus lacertoides*; Cnelemlem = *Cnemidophorus lemniscatus lemniscatus*; Cnelemspl = *Cnemidophorus lemniscatus splendidus*; Cnelon = *Cnemidophorus longicaudus*; Cnesca = *Cnemidophorus gularis scalaris*; Cnesep = *Cnemidophorus gularis septemvittatus*; Cnesexsex = *Cnemidophorus sexlineatus sexlineatus*; Cnesexvir = *Cnemidophorus sexlineatus viridis*; Cnetigaet = *Cnemidophorus tigris aethiops*; Cnetigpun = *Cnemidophorus tigris punctilinealis*; Cnetigmar = *Cnemidophorus tigris marmoratus*; Cnetigmax = *Cnemidophorus tigris maximus*; Cnetigsep = *Cnemidophorus tigris septentrionalis*; Cnetigtig = *Cnemidophorus tigris tigris*; Dicgut = *Dicrodon guttulatum*; KenaltN = *Kentropyx altamazonica* North (Venezuela); KenaltS = *Kentropyx altamazonica* South (Peru); Kenbor = *Kentropyx borckiana*; Kencal = *Kentropyx calcarata*; Kenpel = *Kentropyx pelviceps*; Kenstr = *Kentropyx striata*; Teitey = *Teius teyou.*

DNA data matrix:

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                                                                      50
Eumeces         CACTACCCGCCAGAGAACTACAAGTGAAAAGCTTAAAACTCTAAGGACTT
Lacerta         NNNNNNCCGCCAGAGAACTACAAGTGAAAAACTTGAAACTCAAAGGACTT
Acanth          NNNNNNCCGCCAGAGAACTACTAGTGAAA-ACTTAAAACTCAAAGGACTT
Pholio          CCATATTCGCCAGAAAATTACGGGCGAAA-GCCTAAAACTCAGAAGACTT
Tuptex          AAATGTCCGCCAGAGAATTACGGGTGAAA-ACCTAAAACTCAAAAGACTT
Ameame          GTTTATCCGCCAGAGGATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
Ameaub          ACTTGTCCGCCAGAGGATTACGGGTGAAA-ACCTAAAACTCAAAAGACTT
Amebif          ATCTGTCCGCCAGAGGATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
Amechr          ACTTGTCCGCCAGAGAATTACGGGTGAAA-ACCTAAAACTCAAAAGACTT
Amequa          ATTAATCCGCCAGAGAATTACGGGTGAAA-GCCTAAAACTCAAAAGACTT
Ameund          ACCTGTCCGCCAGAGAATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
Cneare          ACTTGTCCGCCAGAAAATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
Cneburbur       ATTTGTCCGCCAGAAAATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
Cnebursti       ATTTGTCCGCCAGAAAATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
Cnecoscos       ATTTGTCCGCCAGAGAATTACGGGCGAAA-GTCTAAAACTCAAAAGACTT
Cnecosgri       ATTTGTCCGCCAGAAGATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
Cnedep          ATCTGTCCGCCAGAGGATTACGGGTGAAA-ACCTAAAACTCAAAAGACTT
Cnegra          ACTCGTCCGCCAGAAAATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
Cnegul          ATTTGTCCGCCAGAAAATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
Cnegut          ATTTGTCCGCCAGAAAATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
Cnehyp          ATTTGTCCGCCAGAAGATTACGGGTGAAA-ACCTAAAACTCAAAAGACTT
Cneino          ATTTGTCCGCCAGAAAATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
Cnelac          ACTTGTCCGCCAGAGAATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
Cnelemlem       ACTTGTCCGCCAGAAAATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
Cnelemspl       ACTTGTCCGCCAGAAAATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
Cnelon          ATTTGTCCGCCAGAGAATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
Cnesca          ATTTGTCCGCCAGAAGATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
Cnesep          ATTTGTCCGCCAGAAAATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
Cnesexsex       ATTTGTCCGCCAGAAAATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
Cnesexvir       ATTTGTCCGCCAGAAAATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
Cnetigaet       ATTTGTCCGCCAGAAGATTACGGGCGAGA-GCCTAAAATTCAAAAGACTT
Cnetigpun       ATTTGTCCGCCAGAAGATTACGGGCGAGA-GCCTAAAATTCAAAAGACTT
Cnetigmar       ATTTGTCCGCCAGAAGATTACGGGCGAGA-GCCTAAAATTTAAAAGACTT
Cnetigmax       ACTTGTCCGCCAGAAGATTACGGGCGAGA-GCCTAAAATTCAAAAGACTT
Cnetigsep       ATTTGTCCGCCAGAAGATTACGGGCGAGA-GCCTAAAATTCAAAAGACTT
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APPENDIX 2
(*Continued*)

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Cnetigtig     ATTTGTCCGCCAGAAGATTACGGGCGAGA-GCCTAAAATTCAAAAGACTT
Dicgut        ACTTGTCCGCCAGAGAATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
KenaltN       ACTTGTTCGCCAGAATATTACGGGCGAAA-GCCTAAAATTCAAAAGACTT
KenaltS       ACTTGTTCGCCAGAATATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
Kenbor        ACTTGTTCGCCAGAAAATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
Kencal        ACTTGTCCGCCAGAAAATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
Kenpel        AATTGTTCGCCAGAAAATTACGGGTGAAA-ACCTAAAACTCAAAAGACTT
Kenstr        ACTTGTTCGCCAGAAAATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT
Teitey        AATTGTCCGCCAGAGAATTACGGGCGAAA-GCCTAAAACTCAAAAGACTT

                                                            100
Eumeces       GGCGGTGCCCCACATC-AACCTAGAGGAGCCTGTCCTATAATCGATAATC
Lacerta       GACGGTGTCCCATATC-GACCTAGAGGAGCCTGTCCTATAATCGATACCT
Acanth        GGCGGTGTCCCATTTC-GACCTAGAGGAGCCTGTCCTATAATCGATGCCC
Pholio        GACGGTGTCCCAAC-C-CCCCTAGAGGAGCCTGTTCCATAATCGACAACC
Tuptex        GACGGTGTTCCAACCC-TGCCTAGAGGAGCCTGTTCCATAATCGATAATC
Ameame        GACGGTGTCCCAACCC-TGCCTAGAGGAGCCTGTTTCATAATCGATAACC
Ameaub        GACGGTGTCCCAATTC-TACCTAGAGGAGCCTGTTTCATAATCGATAACC
Amebif        GACGGTGTCCCAACCC-TGCCTAGAGGAGCCTGTTTCATAATCGATAACC
Amechr        GACGGTGTCCCAATTC-TACCTAGAGGAGCCTGTTTCATAATCGATAATC
Amequa        GACGGTGTCCCAATTC-TGCCTAGAGGAGCCTGTTTCATAATCGATAACC
Ameund        GACGGTGTCCCAATCC-TGCCTAGAGGAGCCTGTTTCGTAATCGATAACC
Cneare        GACGGTGTCCCACTCC-TGCCTAGAGGAGCCTGTTTCATAATCGATAATC
Cneburbur     GACGGTGTCCCACTTC-TACCTAGAGGAGCCTGTTTCATAATCGATAACC
Cnebursti     GACGGTGTCCCACTTC-TACCTAGAGGAGCCTGTTTCATAATCGATAACC
Cnecoscos     GACGGTGCCCCACTTC-TACCTAGAGGAGCCTGTTTCATAATCGATAACC
Cnecosgri     GACGGTGTCCCACTTC-TACCTAGAGGAGCCTGTTTCATAATCGATAACC
Cnedep        GACGGTGTTCCACC-C-TACCTAGAGGAGCCTGTTCCATAATCGATAATC
Cnegra        GACGGTGTCCCAATCC-TGCCTAGAGGAGCCTGTTTCATAATCGATAACC
Cnegul        GACGGTGTCCCACTTC-TACCTAGAGGAGCCTGTTTCATAATCGATAACC
Cnegut        GACGGTGTTCCACC-C-TACCTAGAGGAGCCTGTTTCATAATCGATAATC
Cnehyp        GACGGTGTTCCACC-C-TACCTAGAGGAGCCTGTTTCATAATCGATAACC
Cneino        GACGGTGTTCCACTCC-TACCTAGAGGAGCCTGTTTCATAATCGATAACC
Cnelac        GACGGTGTCCCACCCC-TGCCTAGAGGAGCCTGTTTCATAATCGATAACC
Cnelemlem     GACGGTGCCCCAATCC-TACCTAGAGGAGCCTGTTTCATAATCGATAACC
Cnelemspl     GACGGTGTCCCACTCC-TGCCTAGAGGAGCCTGTTTCATAATCGATAATC
Cnelon        GACGGTGTCCCAATAC-TACCTAGAGGAGCCTGTTTCATAATCGATAATC
Cnesca        GACGGTGTCCCACTTC-TACCTAGAGGAGCCTGTTTCATAATCGATAACC
Cnesep        GACGGTGTCCCACTTC-TACCTAGAGGAGCCTGTTTCATAATCGATAACC
Cnesexsex     GACGGTGTTCCACCCCCTACCTAGAGGAGCCTGTTTCATAATCGATAACC
Cnesexvir     GACGGTGTTCCACCCC-TACCTAGAGGAGCCTGTTTCATAATCGATAACC
Cnetigaet     GACGGTGTCCCACTTC-TACCTAGAGGAGCCTGTTCCATAATCGATATTC
Cnetigpun     GACGGTGTCCCACTTC-TACCTAGAGGAGCCTGTTCCATAATCGATACTC
Cnetigmar     GACGGTGTCCCACTTC-TACCTAGAGGAGCCTGTTCCATAATCGATAATC
Cnetigmax     GACGGTGTCCCACTTC-TACCTAGAGGAGCCTGTTTCATAATCGATAATC
Cnetigsep     GACGGTGTCCCACTTC-TACCTAGAGGAGCCTGTTCCATAATCGATATTC
Cnetigtig     GACGGTGTCCCACTTC-TACCTAGAGGAGCCTGTTCCATAATCGATATTC
Dicgut        GACGGTGTCCCAACCC-TGCCTAGAGGAGCCTGTTACATAATCGATAATC
KenaltN       GACGGTGTCCCAATCC-TGCCTAGAGGAGCCTGCTTCATAATCGATAACC
KenaltS       GACGGTGTCCCAATCC-TGCCTAGAGGAGCCTGCTTCATAATCGATAACC
Kenbor        GACGGTGTCCCAATCC-TGCCTAGAGGAGCCTGCTTCATAATCGATAACC
Kencal        GACAGTGTCCTA--TC-TGCCTAGAGGAGCCTGCTTCATAATCGATAAAC
Kenpel        GACGGTGTCCCAATCC-TGCCTAGAGGAGCCTGCTTCATAATCGATAACC
Kenstr        GACGGTGTCCCAATCC-TGCCTAGAGGAGCCTGCTTCATAATCGATAACC
Teitey        GACAGTGTCCCAACCC-TGCCTAGAGGAGCCTGTTTCATAATCGATAACC
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APPENDIX 2
(*Continued*)

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                                                  ************                150
Eumeces       CA-CGCTCCACCCAACCATCTTTTGCCA-------TCAGCCTATATACCG
Lacerta       CCACGTTTCACCCAACCTTAACTAGCAAAATA---TCAGCCTATATACCG
Acanth        CC-CGTTCCACCCAACCTTTACTTGCACAT-----TCAGCCTATATACCG
Pholio        CC-CGATACACCTAACCACCCCTAGACCAAA----CCAGCCTATATACCG
Tuptex        CC-CGATCAACCCGACCACCTATTGAAATA----CTCAGCCTATATACCG
Ameame        CC-CGTTCAACCCAACCTTCCCTCGAACATCC----CAGCCTATATACCG
Ameaub        CC-CGCTCCACCCAACCTCTTCTTGAAATCC---TTCAGCCTATATACCG
Amebif        CC-CGCTCAACCTTACCCCCCCTCGAACATCTT---CAGCCTATATACCG
Amechr        CC-CGCTCCACCCGACCCCTTCTTGAAATAC---TTCAGCCTATATACCG
Amequa        CC-CGTTCAACCCAACCCCTCCTTGTAAATCCC-CTCAGCCTATATACCG
Ameund        CC-CGCTCAACCCGACCTCTCCTTGTAAC-----CCCAGCCTATATACCG
Cneare        CC-CGCTCAACCCGACCTTTCCTTGAAAT---TATCCAGCCTATATACCG
Cneburbur     CC-CGCTCAACCCGACCTCTCCTTGAAACCAT-ACTCAGCCTATATACCG
Cnebursti     CC-CGCTCAACCCAACCTCCCCTTGAAACCAT-ATTCAGCCTATATACCG
Cnecoscos     CC-CGATCAACCCGACCCCTCCTTGAA-TCAC-ATTCAGCCTATATACCG
Cnecosgri     CC-CGCTCAACCCGACCTCTCCTTGAAACCAT-ATTCAGCCTATATACCG
Cnedep        CC-CGATCAACCCGACCTTTCCTTGAAATACA-ATTCAGCCTATATACCG
Cnegra        CC-CGTTCAACCCGACCTTTCCTTGAAAT---ATTTCAGCCTATATACCG
Cnegul        CC-CGCTCAACCCGACCCCTCCTTGAA-TCAC-ATTCAGCCTATATACCG
Cnegut        CC-CGATCAACCCGACCTCTCCTTGAAATACT--AACAGCCTATATACCG
Cnehyp        CC-CGATCAACCCGACCTTTCCTTGAAATATA--TTCAGCCTATATACCG
Cneino        CC-CGATCAACCCAACCTCCCCTTGAA-CCAC-ATTCAGCCTATATACCG
Cnelac        CC-CGTTCAACCCGACCTCTCCTTGAAATA-CTTCTCAGCCTATATACCG
Cnelemlem     CC-CGTTCAACCCGACCTTTCCTTGAAAT---TACCCAGCCTATATACCG
Cnelemspl     CC-CGCTCAACCCGACCTTTCCTTGAAAT---TACCCAGCCTATATACCG
Cnelon        CC-CGCTCAACCCAACCCCTTCTCGCAAATC---TTCAGCCTATATACCG
Cnesca        CC-CGCTCAACCCGACCCCTCCTTGAA-TCAC-ATTCAGCCTATATACCG
Cnesep        CC-CGCTCAACCCGACCCCTCCTTGAA-TCAC-ATTCAGCCTATATACCG
Cnesexsex     CC-CGCTCAACCCAACCTCTCCTTGAA-TCAC-ATTCAGCCTATATACCG
Cnesexvir     CC-CGTTCAACCCAACCTCCCCTTGAA-TCAC-ATTCAGCCTATATACCG
Cnetigaet     CC-CGATCAACCCGACCTCTCCTTGAAACCC--ATCCAGCCTATATACCG
Cnetigpun     CC-CGATCAACCCGACCTCTCCTTGAAACCCC-ATTCAGCCTATATACCG
Cnetigmar     CC-CGATCAACCCGACCTCTCCTTGAAA-TT--ATTCAGCCTATATACCG
Cnetigmax     CC-CGATCAACCCGACCTCTCCTTGAAACTT--TTTCAGCCTATATACCG
Cnetigsep     CC-CGATCAACCCGACCTCTCCTTGAAACCC--ATTCAGCCTATATACCG
Cnetigtig     CC-CGATCAACCCGACCTCTCCTTGAAACCCC-ATTCAGCCTATATACCG
Dicgut        CC-CGATCAACCCGACCCTTTCTTG--TAAAC-CTTCAGCCTATATACCG
KenaltN       CC-CGCTTAACCCAACCTTCCCTTGAAACC-ATTTTCAGCCTATATACCG
KenaltS       CC-CGTTCAACCCAACCTTCCCTTGAAATTTATTTTCAGCCTATATACCG
Kenbor        CC-CGTTCAACCCTACCTTCCCTCGAAATC-----CCAGCCTATATACCG
Kencal        CC-CGTTCAACCCAACCCTCCCTCGAAATCCACTTTCAGCCTATATACCG
Kenpel        CC-CGTTCAACCTAACCTTCCCTTGAAACCTACTTTCAGCCTATATACCG
Kenstr        CC-CGTTCAACCCTACCTCCCCTCGAAATC-----CCAGCCTATATACCG
Teitey        CC-CGATCAACCTAACCTTCCCTTGCTTAAACACTTCAGCCTATATACCG

                    ******                                        200
Eumeces       CCGTCGT-----CAACCCACCCTATGAAAGAGG-CAC-AGTGAGTGAAAT
Lacerta       CCGTCGA-----CAGCCTACCCTATGAAGGTCT-AAC-AGTAGACTCAAT
Acanth        CCGTCGA-----CAGTCTACCCCATGAGGGCTC-ATT-AGTAGACACAAT
Pholio        CCGTCGA----ACAGCTTACCTT-TAAAAGACT-ACA-AGTAAGCCAAAT
Tuptex        CCGTCAC----CACGCCTACCCTTTGAAAGACA-CAC-AGTAGGCACAAT
Ameame        CCGTCTTACTTCTAGCTTACCTTCTGAAAGAAA-CAC-AGTAAGCACAAT
Ameaub        CCGTCCTT-CTTCCGCTTACCTTTTGAAAGACA-AAC-AGTAAGCCCAAT
Amebif        CCGTCTTAC--CCAGCTTACCTTCTGAAAGAATT-AT-AGTAAGCACAAT
Amechr        CCGTCCT--CTTCCGCTTACCTTTTGAAAGACA-AAC-AGTAAGCCCAAT
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APPENDIX 2
(*Continued*)

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Amequa      CCGTCTTTACTCTAGCTTACCTTATGAAAGACT-AAC-AGTAAGCTTAAT
Ameund      CCGCCCCCT--TCTGCTTACCTTCTGAAAGACA-AAG-AGTAAGCCCAAC
Cneare      CCGTCCTTT--TCCGCCTACCTTTTGAAAGATTT-AC-AGTAGGCTCAAC
Cneburbur   CCGTCCT----CTCGCTTACCCTTTGAAAGACC-AAC-AGTAAGCTCAAT
Cnebursti   CCGTCCT----CTCGCTTACCCTTTGAAAGACC-AAC-AGTAAGCTCAAT
Cnecoscos   CCGTCCT----CCTGCTTACCCTTTGAAAGACA-AAC-AGTAAGCCCAAT
Cnecosgri   CCGTCCT----CTCGCTTACCCTTTGAAAGATC-AAC-AGTAAGCTCAAT
Cnedep      CCGTCTCC-----CGCTTACCCTTTGAAAGATACAAC-AGTAAGCCTAAT
Cnegra      CCGTCCTTT--TCCGCCTACCTTCTGAAAGACCT-AC-AGTAGGCCTAAT
Cnegul      CCGTCCT----CTTGCTTACCCTTTGAAAGACACAAC-AGTAAGCCCAAT
Cnegut      CCGTCCTTTT---CGCTTACCTTCTGAAAGACATAAC-AGTAAGCCTAAT
Cnehyp      CCGTTCTTTTTTACGCTTACCTTTTGAAAGATATAAC-AGTAAGCCTAAT
Cneino      CCGTCCT----CTTGCTTACCCTTTGAAAGATC-AAT-AGTAAGCCCAAC
Cnelac      CCGTCCCTC--CCCGCTTACCTTCTGAAAGACGC-AC-AGTAAGCCCAAT
Cnelemlem   CCGTCCCTT--CCCGCCTACCTTTTGAAAGATTT-AC-AGTAGGCCTAAT
Cnelemspl   CCGTCCTTT--TCCGCCTACCTTTTGAAAGATTT-AC-AGTAGGCTCAAT
Cnelon      CCGTTCTTT--CCCGCTTACCTTCTGAAAGAAA-AAC-AGTAAGCCCAAT
Cnesca      CCGTCCTT---CTTGCTTACCCTTTGAAAGACATAAC-AGTAAGCCCAAT
Cnesep      CCGTCCT----CTTGCTTACCCTTTGAAAGACACAAC-AGTAAGCCCAAT
Cnesexsex   CCGTCCT----CCTGCTTACCCTTTGAAAGATC-AAT-AGTAAGCCCAAC
Cnesexvir   CCGTCCT----CCTGCTTACCCTTTGAAAGATT-AAT-AGTAAGCCCAAT
Cnetigaet   CCGTCCTTT--CCCGCTTACCTTCTGAAAGATT-AAC-AGTAAGCCCAAT
Cnetigpun   CCGTCCTTT--CCCGCTTACCTTTTGAAAGATT-AAC-AGTAAGCCTAAT
Cnetigmar   CCGTCCT----CCCGCTTACCTTTTGAAAGATT-AAC-AGTAAGCCCAAT
Cnetigmax   CCGTCCTT---CCAGCTTACCTTTTGAAAGACT-AAC-AGTAAGCCTAAT
Cnetigsep   CCGTCCTT---CCCGCTTACCTCTTGAAAGACT-AAC-AGTAAGCCTAAT
Cnetigtig   CCGTCCTT---CCCGCTTACCTCTTGAAAGACT-AAC-AGTAAGCCTAAT
Dicgut      CCGTCTCTC--TTAGCCTACCTTTTGAAAGATATAAC-AGTAAGCCAAAA
KenaltN     CCGTCCTTT--ACCGCTTACCTTCTGAAAGTCAC-ACTAGTAAGCCTAAT
KenaltS     CCGTCCTTT--ACCGCTTACCTTCTGAAAGAAAT-ACTAGTAAGCCTAAT
Kenbor      CCGTCATAT--ACCGCTTACCTTCTGAAAGACAT-AC-AGTAAGCCTAAT
Kencal      CCGTCCTTCT-TGCGCTTACCTTCTGAAAGATCT-ATTAGTAAGCCCAAT
Kenpel      CCGTCCTT---ACCGCTTACCTTCTGAAAGATGT-ACTAGTAAGCTCAAC
Kenstr      CCGTCATCT--ACCGCTTACCTTCTGAAAGACAT-AC-AGTAAGCCTAAT
Teitey      CCGTCCACTTTTTTCGCTTACCTTTTGAAAGAAA-AAC-AGTAAGCCCAAT

                 *******                                    250
Eumeces     AGTTA---TTAACTAATACGTCAGGTCAAGGTGTAGCACATGAGATGGAA
Lacerta     AGCATCA--CCGCTAGTACGTCAGGTCAAGGTGTAGCAAATATTAAGGTA
Acanth      AGCAATAACTCGCTAACACGTCAGGTCAAGGTGTAGCAAATGTTAAGGTA
Pholio      AGTAA----ACACTAACAAGTCAGGTCAAGGTGTAGCTTATGGGGTGGAG
Tuptex      AGTTTC--CAAACTAACAAGTCAGGTCAAGGTGTAGCTTATTGGGTGGAG
Ameame      AGT--C--CCAACTGAAAAGTCAGGTCAAGGTGTAGCTTATGGGAAGGAG
Ameaub      AGTTTCA-ACAACTAAAAAGTCAGGTCAAGGTGTAGCTTATGAAGAGGAG
Amebif      AGTTCAC-CCAACTAAAAAGTCAGGTCAAGGTGTAGCTCATGGGGAGGAG
Amechr      AGTC-CA-ACAACTAAAAAGTCAGGTCAAGGTGTAGCTTATGAAGGGGAG
Amequa      AGTCCC--CTAACTAGTAAATCAGGTCAAGGTGTAGCTTATGGAGAGGAG
Ameund      AGCCC---CTAACTAAAAAGTCAGGTCAAGGTGTAGCTTATGGAGGGGAG
Cneare      AGTTTA--TTAACTAAAAAGTCAGGTCAAGGTGTAGCTTATGGAGAGGAG
Cneburbur   AGTTAA--TCAACTAAAAAATCAGGTCAAGGTGTAGCTTATGGAGAGGAG
Cnebursti   AGTTAA--TCAACTAAAAAATCAGGTCAAGGTGTAGCTTATGGGGAGGAG
Cnecoscos   AGTTAAA-TTAACTAAAAAATCAGGTCAAGGTGTAGCTCATGGGGGGGAG
Cnecosgri   AGTTAA--TCAACTAAAAAATCAGGTCAAGGTGTAGCTTATGGGGAGGAG
Cnedep      AGTCTA--TAAACTAATAAGTCAGGTCAAGGTGTAGCTTACGGAAAGGAG
Cnegra      AGTTCA--CCAACTAAAAAGTCAGGTCAAGGTGTAGCTTATGGAAAGGAG
Cnegul      AGTTAA--TTAACTAAAAAATCAGGTCAAGGTGTAGCTTATGGAGAGGAG
```

APPENDIX 2
(*Continued*)

```
Cnegut          AGTCTA--CTAACTAATAAGTCAGGTCAAGGTGTAGCTTATGGAGAGGAG
Cnehyp          AGTTTA--TTAACTAAAAAATCAGGTCAAGGTGTAGCTTATGGAGAGGAG
Cneino          AGTCTA--CCAACTAAAAAGTCAGGTCAAGGTGTAGCTTATGGGAAGGAG
Cnelac          AGTTTC--ACAACTAAAAAGTCAGGTCAAGGTGTAGCTTATGGAGAGGAG
Cnelemlem       AGTTCA--TTAACTAAAAAGTCAGGTCAAGGTGTAGCTTATGGAAAGGAG
Cnelemspl       AGTTTA--TTAACTAAAAAGTCAGGTCAAGGTGTAGCTTATGGAAAGGAG
Cnelon          AGTT-AT-ACAACTAAAAAATCAGGTCAAGGTGTAGCTTATGAAGGGGCG
Cnesca          AGTTAA--TTAACTAAAAAATCAGGTCAAGGTGTAGCTTATGGAGGGGAG
Cnesep          AGTTAA--TTAACTAAAAAATCAGGTCAAGGTGTAGCTTATGGAGAGGAG
Cnesexsex       AGTCCA--CCAACTAAAAAGTCAGGTCAAGGTGTAGCTTATGGAGAGGAG
Cnesexvir       AGTCTA--CCAACTAAAAAGTCAGGTCAAGGTGTAGCTTATGGAGAGGAG
Cnetigaet       AGTTCA--TTAACTAAAAAATCAGGTCAAGGTGTAGCTTATGGAGAGGAG
Cnetigpun       AGTTTC--TCAACTAAAAAATCAGGTCAAGGTGTAGCTTATGGAGAGGAG
Cnetigmar       AGTCCA--CCAACTAAAAAATCAGGTCAAGGTGTAGCTTATGGAGGGGAG
Cnetigmax       AGTCCA--CCAACTAAAAAATCAGGTCAAGGTGTAGCTTATGGAGAGGAG
Cnetigsep       AGTTTG--TCAACTAAAAAATCAGGTCAAGGTGTAGCTTATGGAGAGGAG
Cnetigtig       AGTTTA--TCAACTAAAAAATCAGGTCAAGGTGTAGCTTATGGAGAGGAG
Dicgut          AGTC-CT-TCAACTAAAAAGTCAGGTCAAGGTGTAGCTAATGAAAGGGAG
KenaltN         AGCCA-T--TAGCTAGAAAGTCAGGTCAAGGTGTAGCCCATGGGTAGGAG
KenaltS         AGCCC-C--TAGCTAAAAAGTCAGGTCAAGGTGTAGCCTATGGGAAGGAG
Kenbor          AGCCC----GAGCTAAAAAGTCAGGTCAAGGTGTAGCCAATGGGAAGGAG
Kencal          AGCCC-T-TAAGCTAAAAAGTCAGGTCAAGGTGTAGCCCATGGGAGGGAG
Kenpel          AGCAC-T--TAACTAAAAAGTCAGGTCAAGGTGTAGCCCATGGGAAGGAG
Kenstr          AGCCC----TAGCTAAAAAGTCAGGTCAAGGTGTAGCTAATGGGAAGGAG
Teitey          AGTCACT-ATAACTAGAAAGTCAGGTCAAGGTGTAGCTTATGAGAAGGTG

                                                                300
Eumeces         GAGATGGGCTACATTTTCTATTGC---AGAAAAC--ACGAACAGCTCAAT
Lacerta         GAGATTGGCTACATTTTTTATAAT---AAAAAAC--ACGAAAAGTACTAT
Acanth          GTGATTGGCTACATTTTTTATTTT---AAAACAA--ACGAAATGCAACAT
Pholio          GAAATGGGCTACATTATTTAATGT---AAATTAC--ACGAACTACCCCAT
Tuptex          GAAATGGGCTACATTTTCTACGAC---AGATCACCTACGGACTTCGCTCT
Ameame          AAAATGGGCTACATTTTCTGTCAC---AGAACACCCACGGAAAATATTCT
Ameaub          AAAATGGGCTACATTTTCTATTAT---AGAACACCTACGGAAAGTATTCT
Amebif          AAAATGGGCTACATTTTCTGCCAC---AGAACACCAACGGAAAATATTCT
Amechr          AAAATGGGCTACATTTTCTATCCT---AGAACACCCACGGAAAGTTTTCT
Amequa          AAAATGGGCTACATTTTCTACCAC---AGAATAC-TACGAAAAATATTCT
Ameund          AAAATGGGCTACATTTTCTAGTAT---AGAACAC-TACGAAAAATATTCT
Cneare          AAAATGGGCTACATTTTCTTCCAC---AGAATAC-TACGAAATGTTTTCT
Cneburbur       AAAATGGGCTACATTCTCTATTAT---AGACCAT-CACGGAAAGTACTCT
Cnebursti       AAAATGGGCTACATTCTCTATTAT---AGACCAT-CACGGAAAGTACCCT
Cnecoscos       AAAATGGGCTACATTATCTATTAT---AGATCACTCACGGAAAGTACCCT
Cnecosgri       AAAATGGGCTACATTCTCTACTATT--AGACCAT-CACGGAAAGTACTCT
Cnedep          AGAATGGGCTACATTTTCTACAA-CCTAGACCAC--ACGAAAAGTATTCT
Cnegra          AAAATGGGCTACATTTTCTACTAT---AGAACAC-CACGAAATACTTTCT
Cnegul          AAAATGGGCTACATTCTCTATTAT---AGAGCAC-CACGGAAAGTACCCT
Cnegut          AAAATGGGCTACATTTTCTATAGTCTTAGACCAT--ACGAAAAGTATTCT
Cnehyp          AAAATGGGCTACATTTTCTAT---CATAGATAAC--ACGAAAAGTATTCT
Cneino          AAAATGGGCTACATTTTCTATTATT--AGACTAT-TACGGAAAGTACCCT
Cnelac          AAAATGGGCTACATTTTCTACCACT--AGAACAC-CACGAAAAATATTCT
Cnelemlem       AAAATGGGCTACATTTTCTTCTAC---AGAACAC-CACGAAATGTTTTCT
Cnelemspl       AAAATGGGCTACATTTTCTTCCAC---AGAATAC-TACGAAATGTTTTCT
Cnelon          AAAATGGGCTACATTTTCTATTAT---AGAACAC-CACAGACAGTACTCT
Cnesca          AAAATGGGCTACATTCTCTATTAT---AGATCAC-CACGGAAAGTACCCT
Cnesep          AAAATGGGCTACATTCTCTATTAT---AGATCAC-CACGGAAAGTACCCT
Cnesexsex       AAAATGGGCTACATTTTCTATTATT--AGACCAT-CACGGAAAGTACTTT
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APPENDIX 2
(*Continued*)

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Cnesexvir       AAAATGGGCTACATTTTCTATTATT--AGACCAT-CACGGAAAGTACCTT
Cnetigaet       AAAATGGGCTACATTTTCTATAA---TAGAAAAT-CACGGAAAGTATTCT
Cnetigpun       AAAATGGGCTACATTTTCTACAA---TAGAAAAC-CACGGAAAGTATTCT
Cnetigmar       AAAATGGGCTACATTTTCTACAA---TAGACAAC--ACGGAAAGTATTCT
Cnetigmax       AAAATGGGCTACATTTTCTATAA---TAGACAAC--ACGGAAAGTATTCT
Cnetigsep       AAAATGGGCTACATTTTCTACAA---TAGAAAAT-TACGGAAAGTATTCT
Cnetigtig       AAAATGGGCTACATTTTCTACAA---TAGAAAAC-TACGGAAAGTATTCT
Dicgut          ATAATGGGCTACATTTTCTACAAT---AGAACAT-AACGAAAAACACTCT
KenaltN         AAAGTGGGCTACATTTTCTACTTCT--AGAACAC--ACGAAACATACTCT
KenaltS         AAAGTGGGCTACATTTTCTACTTCT--AGAACAC--ACGAAATATACTCT
Kenbor          AAAGTGGGCTACATTTTCTACTCA---AGAACAC--ACGAAACTTATCCT
Kencal          AAAGTGGGCTACATTTTCTACCTT---AGAACAC--ACGAAATATATTCT
Kenpel          AAAGTGGGCTACATTTTCTACTTC---AGAATAC--ACGAAATATACTCT
Kenstr          AAAGTGGGCTACATTTTCTACTCA---AGAACAC--ACGAAACTTATCCT
Teitey          AAAATGGGCTACATTTTCTATATT---AGAACAC-TACGAAAAGCATCCT

                                                              350
Eumeces         GAAACT--TGGGC-TAAAAGGCGGATTTAGAAGTCAGAACGGCCGCGGTA
Lacerta         GAAAC---TGTAC-ATGAAGGTGAATTTAGTAGTTAANNNNNNNNNNNNN
Acanth          GAAAC--ACTTGC-ACGAAGGTGAATTTAGCAGTAAANNNNNNNNNNNNN
Pholio          GAAAA--AGATAA--TGAAGGCGGATTTAGCAGTAAGAACGGCCGCGGGA
Tuptex          GAACC--AAGCAA---CAAGGAGGATTTAGCAGTAAGAACGGCCGCGGGA
Ameame          GAAAT-AAAATAT-ATAAAGGCGGATTTAGCAGTAAGAACGGCCGAGGGA
Ameaub          GAAAT-AAAATAC-ACAAAGGCGGATTTAGTAGTAAGAACGGCCGCGGGA
Amebif          GAAAT-AAAATAC-AAAAAGGCGGATTTAGTAGTAAGAACGGCCGCGGGA
Amechr          GAAAT-AAGAAGC-ACAAAGGAGGATTTAGTAGTAAGAACGGCCGCGGGA
Amequa          GAAAT-AAAGTAT-ATAAAGGTGGATTTAGTAGTAAGAACGGCCGCGGGA
Ameund          GAAAT-AAAATGT-ATGAAGGTGGATTTAGTAGTAAGAACGGCCGCGGGA
Cneare          GAAAT-GAT-TGC-ACGAAGGAGGATTTAGTAGTAAGAACGGCCGCGGGA
Cneburbur       GAAAC-AAAGTAC-ACAAAGGTGGATTTAGCAGTAAGAACGGCCGAGGGA
Cnebursti       GAAAC-AAAGTAC-ACAAAGGTGGATTTAGCAGTAAGAACGGCCGCGGGA
Cnecoscos       GAAAC-AAAGTAC-ACAAAGGTGGATTTAGCAGTAAGAACGGCCGCGGGA
Cnecosgri       GAAAC-AAAGTAC-ACAAAGGTGGATTTAGCAGTAAGAACGGCCGCGGGA
Cnedep          GAAAC-AAAATAC-ACGAAGGCGGATTTAGCAGTAAGAACGGCCGCGGGA
Cnegra          GAAAT-AAA-TGT-ATGAAGGAGGATTTAGTAGTAAGAACGGCCGCGGGA
Cnegul          GAAAC-AAAGTAC-ACAAAGGTGGATTTAGTAGTAAGAACGGCCGCGGGA
Cnegut          GAAAC-AAAATAC-ACAAAGGTGGATTTAGCAGTAAGAACGGCCGCGGGA
Cnehyp          GAAAT-AAAATAC-ACGAAGGTGGATTTAGCAGTAAGAACGGCCGCGGGA
Cneino          GAAAC-AAAGTAC-ACAAAGGTGGATTTAGCAGTAAGAACGGCCGCGGGA
Cnelac          GAAAT-AAAATAT-ATGAAGGCGGATTTAGTAGTGAGNNNNGCCGCGGGA
Cnelemlem       GAAAT-GAG-TGC-ATGAAGGAGGATTTAGTAGTAAGNNCGGCCGCGGGA
Cnelemspl       GAAAT-GAT-CAC-ACGAAGGAGGATTTAGTAGTAAGAACGGCCGCGGGA
Cnelon          GAAAC-AAAGTAC-ACAAAGGTGGATTTAGTAGTAAGAACGGCCGCGGGA
Cnesca          GAAAT-AAAGTAC-ACAAAGGTGGATTTAGTAGTAAGAACGGCCGCGGGA
Cnesep          GAAAC-AAAGTAC-ACAAAGGTGGATTTAGTAGTAAGAACGGCCGCGGGA
Cnesexsex       GAAAC-AAAGTAC-ACAAAGGTGGATTTAGCAGTAAGAACGGCCGCGGGA
Cnesexvir       GAAAC-AAAGTAC-ACAAAGGTGGATTTAGCAGTAAGAACGGCCGCGGGA
Cnetigaet       GAAAT-AAAATAC-ACAAAGGTGGATTTAGAAGTAAGAACGGCCGCGGGA
Cnetigpun       GAAAT-AAAATAC-ACAAAGGTGGATTTAGAAGTAAGAACGGCCGCGGGA
Cnetigmar       GAAAT-AAAATAC-ACAAAGGTGGATTTAGAAGTAAGNNNNNNNNCGGGA
Cnetigmax       GAAAT-AAAATAC-ACAAAGGTGGATTTAGAAGTAAGAACGGCCGCGGGA
Cnetigsep       GAAAT-AAAATAC-ACAAAGGTGGATTTAGAAGTAAGAACGGCCGCGGGA
Cnetigtig       GAAAT-AAAATAC-ACAAAGGTGGATTTAGAAGTAAGAACGGCCGCGGGA
Dicgut          GAAAC--AGGTGT-ATAAAGGCGGATTTAGTAGTAAGAACGGCCGCGGGA
KenaltN         GAAATCAAAGTAA-CCGAAGGCGGATTTAGTAGTAAGAACGGCCGCGGGA
KenaltS         GAAATCAAAGTAA-CTGAAGGCGGATTTAGTAGTAAGAACGGCCGCGGGA
```

APPENDIX 2
(*Continued*)

```
Kenbor      GAAAT-AAGATAA-ATGAAGGCGGATTTAGTAGTAAGNNNNGCCGCGGGA
Kencal      GAAACCAAAGTAATATGAAGGTGGATTTAGTAGTAAGAACGGCCGCGGGA
Kenpel      GAAAT-AAAGTAA-ATGAAGGCGGATTTAGTAGTAAGNACGGCCGCGGGA
Kenstr      GAAAT-AAGGTAA-ATGAAGGCGGATTTAGTAGTAAGAACGGCCGCGGGA
Teitey      GAAA--AACATGC-ACAAAGGTGGATTTAGCAGTAAGAACGGCCGCGGGA

                                                            400
Eumeces     TTCTA-ACCGTGCAAAGGTAGCGTAATCACTTGTCTTCTAAATAAAGACC
Lacerta     NNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNACT
Acanth      NNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNACT
Pholio      TCCTCCACCGTGCAAAGGTAGCATAATCACTTGTCCCCTAAATAGTGACT
Tuptex      TCCTCCACCGTGCAAAGGTAGCATAATCATTTGTCCCCTAAATAGGGACT
Ameame      TCCTACACCGTGCAAAGGTAGCATAATCATTTGTCATCTAAATAGTGACT
Ameaub      TCCTACCCCGTGCAAAGGTAGCATAATCACTTGTCACCTAAATAGTGACT
Amebif      CCCTACACCGTGCAAAGGTAGCATAATCATTTGTCATCTAAATAATGACT
Amechr      TCCTACCCCGTGCCAAGGTAGCATAATCACTTGTCATCTAAATAATGACT
Amequa      TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCATCTAAATAATGACT
Ameund      TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCACCTAAATAGTGACT
Cneare      TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCACCTAAATAGTGACT
Cneburbur   TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCATCTAAATAATGACT
Cnebursti   TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCATCTAAATAATGACT
Cnecoscos   TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCATCTAAATAATGACT
Cnecosgri   TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCATCTAAATAATGACT
Cnedep      CCCTACACCGTGCAAAGGTAGCATAATCACTTGTCATCTAAATAATGACT
Cnegra      TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCACCTAAATAGTGACT
Cnegul      TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCATCTAAATAATGACT
Cnegut      TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCATCTAAATAATGACT
Cnehyp      TCCTACCCCGTGCAAAGGTAGCATAATCACTTGTCATCTAAATAATGACT
Cneino      TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCATCTAAATAATGACT
Cnelac      TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCATCTAAATAATGACT
Cnelemlem   TCCTACACCGTGCAAAGGTAGCATAATCACTTGTTACCTAATTAGTGACT
Cnelemspl   TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCACCTAAATAGTGACT
Cnelon      TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCATCTAAATAATGACT
Cnesca      TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCATCTAAATAATGACT
Cnesep      TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCATCTAAATAATGACT
Cnesexsex   TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCATCTAAATAATGACT
Cnesexvir   TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCATCTAAATAATGACT
Cnetigaet   TCTTACACCGTGCAAAGGTAGCATAATCACTTGTCATCTAAATAATGACT
Cnetigpun   TCTTATACCGTGCAAAGGTAGCATAATCACTTGTCATCTAAATAATGACT
Cnetigmar   TCTTATACCGTGCCAAGGTAGCATAATCACTTGTCATCTAAATAATGACT
Cnetigmax   TCTTATACCGTGCAAAGGTAG-ATAATCACTTGTCATCTAAATAATGACT
Cnetigsep   TCTTACACCGTGCAAAGGTAGCATAATCACTTGTCATCTAAATAATGACT
Cnetigtig   TCTTACACCGTGCAAAGGTAGCATAATCACTTGTCATCTAAATAATGACT
Dicgut      TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCACCTAAATAGTGACT
KenaltN     TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCACCTAAATAGTGACT
KenaltS     TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCACCTAAATAGTGACT
Kenbor      TCCTACACCGTGTAAAGGTAGCATAATCACTTGTCACCTAAATAGTGACT
Kencal      TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCACCTAAATAGTGACT
Kenpel      TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCACCTAAATAGTGACT
Kenstr      TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCACCTAAATAGTGACT
Teitey      TCCTACACCGTGCAAAGGTAGCATAATCACTTGTCATCTAAATAATGACT

                                                            450
Eumeces     AGTATG-AACGGCTAAATGAGGACAAACCTGTCTCTTGCAACCAA-TCAG
Lacerta     AGAATG-AATGGCTAAATGAGGACTAAACTGTCTCTTACGGACCAGCCAA
Acanth      AGAATG-AATGGCTAAATGAAGACCCAACTGTCTCTTGCAGCCCA-CCAA
Pholio      AGTATG-AATGGCCAAATGAAGATTTTACTGTCTCTTATAGCCGA-TCTA
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APPENDIX 2
(*Continued*)

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Tuptex      AGTATG-AATGGCCCAATGAAGATTTACCTGTCTCTTGTAGCTGA-TCTA
Ameame      AGTATG-AATGGCCCAATGAGGACTTTCCTGTCTCTTGTAACCAA-TCAA
Ameaub      AGTATG-AATGGCCAAATGAGGACTTTCCTGTCTCTTGTAACCAA-TCTA
Amebif      AGTATG-AATGGCCCAATGAGGACTTTCCTGTCTCTTGTAACCAA-TCGA
Amechr      AGTATG-AATGGCCCAATGAGGACCTTACTGTCTCTTGTAACCAA-TCTA
Amequa      AGTATG-AACGGCCCAATGAGGACTTTCCTGTCTCTTATAATCAA-TCAA
Ameund      AGTATG-AATGGCCCCATGAGGACTTTCCTGTCTCTTGTAACTAA-TCAA
Cneare      AGTATG-AATGGCCCAATGAGGACTTTCCTGTCTCTTGTAACCAA-TCAA
Cneburbur   AGTATG-AATGGCCCTATGAGGACTTCCCTGTCTCTTGTAACCAA-TCAA
Cnebursti   AGTATG-AATGGCCCTATGAGGACTTCCCTGTCTCTTGTAACCAA-TCAA
Cnecoscos   AGTATG-AATGGCCCTATGAGGACTTCCCTGTCTCTTGTAACCAA-TCAA
Cnecosgri   AGTATG-AATGGCCCTATGAGGACTTCCCTGTCTCTTGTAACCAA-TCAA
Cnedep      AGTATG-AATGGCCCTATGAGGACTTCCCTGTCTCTTGTAACCGA-TCGA
Cnegra      AGTATG-AATGGCCCAATGAGGACTTTCCTGTCTCTTGTAACCAA-TCAA
Cnegul      AGTATG-AATGGCCCTATGAGGACTTCCCTGTCTCTTGTAACCAA-TCAA
Cnegut      AGTATG-AATGGCCCTATGAGGACTTCCCTGTCTCTTGTAACCAA-TCAA
Cnehyp      AGTATG-AATGGCCCTATGAGGACTTCCCTGTCTCTTGTAACCAA-TCAA
Cneino      AGTATG-AACGGCCCTATGAGGACTTCCCTGTCTCTCGTAATTAA-TCAA
Cnelac      AGTATG-AACGGTCCAATGAGGATCTTCCTGTCTCTTGTAATTAA-TCTA
Cnelemlem   AGTATG-AATGGCCAAATGAGGACTTTCCTGTCTCTTGTAACCAA-TCAA
Cnelemspl   AGTATG-AATGGCCCAATGAGGACTTTCCTGTCTCTTGTAACCAA-TCAA
Cnelon      AGCATG-AATGGTCCAATGAGGACTTTCCTGTCTCTTGTAACTAA-TCAA
Cnesca      AGTATG-AATGGCCCTATGAGGACTTCCCTGTCTCTTGTAACCAA-TCAA
Cnesep      AGTATG-AATGGCCCTATGAGGACTTCCCTGTCTCTTGTAACCAA-TCAA
Cnesexsex   AGTATG-AACGGCCCTATGAGGACTTCCCTGTCTCTTGTAACCAA-TCAA
Cnesexvir   AGTATG-AACGGCCCTATGAGGACTTCCCTGTCTCTTGTAATCAA-TCAA
Cnetigaet   AGTATGGAATGGCCCTATGAGGACTTCCCTGTCTCTTATAACCAA-TCAA
Cnetigpun   AGTATGGAATGGCCCTATGAGGACTTCCCTGTCTCTTATAACCAA-TCAA
Cnetigmar   AGTATG-AATGGCCCTATGAGGACTTCCCTGTCTCTTATAACCAA-TCAA
Cnetigmax   AGTATG-AACGGCCCTACGAGGACTTTCCTGTCTCTTATAACCAA-TCAA
Cnetigsep   AGTATGGAATGGCCCTATGAGGACTTCCCTGTCTCTTATAACCAA-TCAA
Cnetigtig   AGTATG-AATGGCCCTATGAGGACTTCCCTGTCTCTTATAACCAA-TCAA
Dicgut      AGTATG-AATGGCCAAATGAGGACTTACCTGTCTCTTATAACCAA-TCTA
KenaltN     AGTATG-AATGGCCCAATGAGGACTTTTCTGTCTCTTGTAACCAA-TCAA
KenaltS     AGTATG-AATGGCCTAATGAGGACTTTTCTGTCTCTTGTAACCAA-TCAA
Kenbor      AGTATG-AATGGCCCAATGAGGACTTTACTGTCTCTTGTAATTGA-TCAA
Kencal      AGTATG-AATGGCCCAATGAGGACCTTACTGTCTCTTGTAACCAA-TCAA
Kenpel      AGTATG-AATGGCCTAATGAGGACTTTACTGTCTCTTATAACCAA-TCAA
Kenstr      AGTATG-AATGGCCCAATGAGGACTTTACTGTCTCTTGTAATTGA-TCAA
Teitey      AGTATG-AATGGCCAAATGAAGACTTTCCTGTCTCTTGTAATCAA-TCAA

                                                          500
Eumeces     TGAAACTGATCTTCCGGTCCAAAAGCCGGAGTGCCCCCATAAGACGAGAA
Lacerta     TGAAATTGATTTCCCAGTACAAAAGCTGGGATATACTCATAAGACGAGAA
Acanth      TGAAACTGATCCCCTAGTCCAAAAGCTAGGATTTTCCCACAAGACGAGAA
Pholio      TGAAACTAAACTATCAGTACAAAAGCTGATATATTAACATAAGACGAAAA
Tuptex      TGAAACTGATCTTCCAGTACAAAAGCTGGAATAATAACACAAGACGAAAA
Ameame      TGAAACTGATCTTTCAGTCCAAAAGCTGAAATATTTACACAAGACGAAAA
Ameaub      TGAAACTGATCTTCCAGTTCAAAAGCTGGAATAAACACACAAGACGAAAA
Amebif      TGAAACTGATCTTTCAGTCCAAAAGCTGAAATGTACACACAAGACGAAAA
Amechr      TGAAACTGATCTTCCAGTTCAAAAGCTGGAATAAACACACAAGACGAAAA
Amequa      TGAAACTGATCTCTCAGTCCAAAAGCTGAAATATCCCCACAAGACGAAAA
Ameund      TGAAACTGATCTTCCAGTTCAAAAGCTGAAATAAACCCACAAGACGAAAA
Cneare      TGAAACTGATCTTCCAGTCCAAAAGCTGGGATAAAACCACAAGACGAAAA
Cneburbur   TGAAACTGATCCCCCAGTACAAAAGCTGGGATAAAATCACAAGACGAAAA
Cnebursti   TGAAACTGATCCCCCAGTACAAAAGCTGGGATAAAATCACAAGACGAAAA
```

APPENDIX 2
(*Continued*)

```
Cnecoscos       TGAAACTGATCCCCCAGTTCAAAAGCTGGGATAAAATCACAAGACGAAAA
Cnecosgri       TGAAACTGATCCCCCAGTACAAAAGCTGGGATAAAATCACAAGACGAAAA
Cnedep          TGAAACTGATCTTCCAGTCCAAAAGCTGGAATACTACCACAAGACGAAAA
Cnegra          TGAAACTGATCTCCCAGTCCAAAAGCTGGAATAAAGCCACAAGACGAAAA
Cnegul          TGAAACTGATCCCCCAGTCCAAAAGCTGGGATAAAATCACAAGACGAAAA
Cnegut          TGAAACTGATCTTCCAGTCCAAAAGCTGGAATACACCCACAAGACGAAAA
Cnehyp          TGAAACTGACCCCCCAGTTCAAAGGCTGGAATAAATTCACAAGACGAAAA
Cneino          TGAAACTGATCCCCCAGTACAAAAGCTGGGATAAAATCACAAGACGAAAA
Cnelac          TGAAACTGATCTTTCAGTCCAAAAGCTGAAATAAGCCCACAAGACGAAAA
Cnelemlem       TGAAACTGATCTTTCAGTCCAAAAGCTGGAATAAGACCACAAGACGAAAA
Cnelemspl       TGAAACTGATCTTCCAGTCCAAAAGCTGGAATAAAACCACAAGACGAAAA
Cnelon          TGAAACTGATCTCCCAGTTCAAAAGCTGGGATAATCTCACAAGACGAAAA
Cnesca          TGAAACTGATCCCCCAGTCCAAAAGCTGGGATAAAATCACAAGACGAAAA
Cnesep          TGAAACTGATCCCCCAGTCCAAAAGCTGGGATAAAATCACAAGACGAAAA
Cnesexsex       TGAAACTGATCTCCCAGTACAAAAGCTGGGATAAAACCACAAGACGAAAA
Cnesexvir       TGAAACTGATCTCCCAGTACAAAAGCTGGGATAAAACCACAAGACGAAAA
Cnetigaet       TGAAACTGATCTCCCAGTACAAAAGCTGGGATAATAACACAAGACGAAAA
Cnetigpun       TGAAACTGATCTCTCAGTACAAAAGCTGGGATAATAACACAAGACGAAAA
Cnetigmar       TGAAACTGATCTCCCAGTACAAAAGCTGGAATAATAACACAAGACGAAAA
Cnetigmax       TGAAACTGATCTCCCAGTACAAAAGCTGGGATAACAACACAAGACGAAAA
Cnetigsep       TGAAACTGATCTCCCAGTACAAAAGCTGGGATAATAACACAAGACGAAAA
Cnetigtig       TGAAACTGATCTCCCAGTACAAAAGCTGGGATAATAACACAAGACGAAAA
Dicgut          TGAAACTGATCTCTCAGTACAAAAGCTGAGATAAACACACAAGACGAAAA
KenaltN         TGAAACTGATTCCCCAGTCCAAAAGCTGGGATAAAACCACAAGACGAAAA
KenaltS         TGAAACTGATCTCCCAGTCCAAAAGCTGGGATAAAACCACAAGACGAAAA
Kenbor          TGAAACTGATCTCTCAGTCCAAAAGCTGAGATAAGACCACAAGACGAAAA
Kencal          TGAAACTGATCTTCTAGTCCAAAAGCTAGAATAAAAACACAAGACGAAAA
Kenpel          TGAAACTGATCCTCCAGTCCAAAAGCTGGGATAAAGCCACAAGACGAAAA
Kenstr          TGAAACTGATCTCTCAGTCCAAAAGCTGAGATAAAACCACAAGACGAAAA
Teitey          TGAAACTGATCTTTCAGTTCAAAAGCTGAAATAATAACACAAGACGAAAA
                                                                550
                                                                * * *
Eumeces         GACCCTGTGGAGCTTCAAACAAACTACTATGTAGTACACCAAGCCACAAC
Lacerta         GACCCTGTGGAGCTTCA---AAACCA---------AA-CCA---CCCAGC
Acanth          GACCCTGTGGAGCTTAT---AAACCA---------AAACCA---TAAAGC
Pholio          GACCCTGTGGAACTTCA---AGCACA---------AACCCA---CCATA-
Tuptex          GACCCTGTGGAACTTTT---AAACCG---------CAACCA---ACACAC
Ameame          GACCCTGTGGAACTT-T---AAGTGC---------TAATCA---ACA-C-
Ameaub          GACCCTGTGGAACTTTC---AAGTGC---------CAATCA---ACAAC-
Amebif          GACCCTGTGGAACTT-T---AAGTGT---------TAATCA---ACA-C-
Amechr          GACCCTGTGGAACTTTT---AAGTGT---------CAATCA---ATAAA-
Amequa          GACCCTGTGGAACTTCT---AAGTGC---------TAATCA---ATT-A-
Ameund          GACCCTGTGGAACTTCC---AAATAT---------TAATCA---TCAAT-
Cneare          GACCCTGTGGAACTTTT---AAGTGC---------TAGTCA---ACAAC-
Cneburbur       GACCCTGTGGAACTTAC---AAGTGT---------TAATCA---ACAAA-
Cnebursti       GACCCTGTGGAACTTAT---AAGTGC---------CAATCA---ACAAA-
Cnecoscos       GACCCTGTGGAACTTAT---AAGTGC---------TAATCA---ACAAA-
Cnecosgri       GACCCTGTGGAACTTAC---AAGTGC---------CAATCA---ACAAA-
Cnedep          GACCCTGTGGAACTTCT---AAGTGC---------TAATCA---ACAAT-
Cnegra          GACCCTGTGGAACTTTT---AAGTGT---------TAGTCA---ACAAC-
Cnegul          GACCCTGTGGAACTTAT---AAGTGC---------CAATCA---ACAAA-
Cnegut          GACCCTGTGGAACTTTC---AAGTGC---------TAATCA---ACAAC-
Cnehyp          GACCCTGTGGAACTTCC---AAGTGC---------TAATCA---ATAAC-
Cneino          GACCCTGTGGAACTTAT---AAGTAC---------CAATCA---ATAAT-
Cnelac          GACCCTGTGGAACTTTA---AAGTGC---------CAGTCA---ACAAC-
```

APPENDIX 2
(*Continued*)

```
Cnelemlem       GACCCTGTGGAACTTTT---AAGTGT---------TAGTCA---ACAAC-
Cnelemspl       GACCCTGTGGAACTTTT---AAGTGC---------TAGTCA---ACAAC-
Cnelon          GACCCTGTGGAACTTTA---AAGTGC---------CAATCA---ACA-T-
Cnesca          GACCCTGTGGAACTTAT---AAGTGC---------CAATCA---ACAAA-
Cnesep          GACCCTGTGGAACTTAT---AAGTGC---------CAATCA---ACAAA-
Cnesexsex       GACCCTGTGGAACTTAT---AAGTGC---------TAATCA---ATAAC-
Cnesexvir       GACCCTGTGGAACTTAT---AAGTGC---------TAATCA---ATAAC-
Cnetigaet       GACCCTGTGGAACTTCC---AAGTGT---------TAATCA---ACAAC-
Cnetigpun       GACCCTGTGGAACTTCC---AAGTGT---------TAATCA---ACAAC-
Cnetigmar       GACCCTGTGGAACTTCT---AAGTGC---------TAATTA---ACAAC-
Cnetigmax       GACCCTGTGGAACTTCT---AAGTGC---------TAATCA---ACAAC-
Cnetigsep       GACCCTGTGGAACTTCC---AAGTGC---------TAATCA---ACAAC-
Cnetigtig       GACCCTGTGGAACTTCC---AAGTGT---------TAATCA---ACAAC-
Dicgut          GACCCTGTGGAACTTAC---AAGTGT---------CAACCA---ACAAC-
KenaltN         GACCCTGTGGAACTTTT---AAGTGC---------TAATCA---TTA--T
KenaltS         GACCCTGTGGAACTTTT---AAGTGC---------TAGTCA---TTA--T
Kenbor          GACCCTGTGGAACTTTT---AAGTGT---------TAATCA---TCG--C
Kencal          GACCCTGTGGAACTTTT---AAGTGT---------CAATCA---TCA--T
Kenpel          GACCCTGTGGAACTTTC---AAGTAC---------CAATCA---TTA--C
Kenstr          GACCCTGTGGAACTTTT---AAGTGT---------TAATCA---TCG--C
Teitey          GACCCTGTGGAACTTTT---AAGTGA---------AAACCA---ACAATT

                                                                600
Eumeces         TAGTAGTAAACGTTTTGAGTTGGGGCGACTTCGGAAACAAAAAAAACTTC
Lacerta         ATGCTCCTTGGATTTTTAGTTGGGGCGACTTCGGAATATAAAAAAACTTC
Acanth          TTGGCCTCTTGGTTTTTAGTTGGGGCGACTTCGGAGTATAAAAACCCCTC
Pholio          ATGGCCCACCTGCTTTTAGTTGGGGCAACTTTGGAAAAAAACAAAACTTC
Tuptex          ATGGCCACGCCGCTTTTAGTTGGGGCAACTTTGGAAAAAAACACAACTTC
Ameame          ATGACACAGACACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Ameaub          ATGATATAATCACTTTTAGTTGGGGCAACTTTGGAACGAAACAAAACTTC
Amebif          ATGACATAC-CACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Amechr          ATGATACAACCACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Amequa          ATGATTAAT-CACTTTTGGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Ameund          ATGACAAAA-TATTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Cneare          ATGATAAAA-CACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Cneburbur       AATGATAAATCACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Cneburbut       ATGAATAAACCACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Cnecoscos       ATGACACAACCACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Cnecosgri       ATGATAAAACCACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Cnedep          ATGATACAACCACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Cnegra          ATGATAAAC-CACTTTTAGTTGGGGCAACTTTGGAATAAAACAAAACTTC
Cnegul          ATGACACAATCACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Cnegut          ATGACACAAACACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Cnehyp          ATGACACAACCACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Cneino          ATGATACAAGTACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Cnelac          ATGACACCACCACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Cnelemlem       ATGATTAA--CACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Cnelemspl       ATGATAAAA-CACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Cnelon          ATGACACAATCACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Cnesca          ATGACACAACCACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Cnesep          ATGACACAATCACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Cnesexsex       ATGACACAAACACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Cnesexvir       ATGATACAAACACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Cnetigaet       ATGACACAACCACTTTTAGTTGGGGCAACTTTGGAACAAAATAAAACTTC
Cnetigpun       ATGACACAACCACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Cnetigmar       ATAATACAACCACTTTTAGTTGGGGCAACTTTGGAATAAAATAAAACTTC
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APPENDIX 2
(*Continued*)

```
Cnetigmax     ATGATACAACCACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Cnetigsep     ATGACACAATCACTTTTAGTTGGGGCAACTTTGGAACAAAATAAAACTTC
Cnetigtig     ATGACACAATCACTTTTAGTTGGGGCAACTTTGGAACAAAATAAAACTTC
Dicgut        ATGGAACAACCACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
KenaltN       ATGATAAAGACACTTTTAGTTGGGGCAACTTTGGAACAAAGTAAAACTTC
KenaltS       ATGATAGAAACACTTTTAGTTGGGGCAACTTTGGAACAAAGTAAAACTTC
Kenbor        ATGACACAGCCACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Kencal        ATGATATAACCACTTTTAGTTGGGGCAACTTTGGAATAAAGAAAAACTTC
Kenpel        ATGACTAAG-CACTTTTAGTTGGGGCAACTTCGGAATAAAGTAAAACTTC
Kenstr        ATGACACAGCCACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC
Teitey        ATGGCACAACCACTTTTAGTTGGGGCAACTTTGGAACAAAACAAAACTTC

                   ****************************                  650
Eumeces       CGA-------CACAGAACCACCAGTTCTTACCAAGAC-CAACAAGTCAAA
Lacerta       CAA-------AAATGAAATAAT----TTTATTAAGGT-TAACACACCAAA
Acanth        CGA-------CATGGCACTAGC----CTGACTCAGAT-GGACACACAAAA
Pholio        CAATAAAATTAAAGATTAACACAT--------------CTATATAGTTAT
Tuptex        CAATCAAGGAGCAATTTAAAACACGCC----TTAGGC-CGACACGCCTAT
Ameame        CAATACA---AAGACCAC--CTCCGACAAACCAAGGC-CCACACGCCAAT
Ameaub        CAATTATGGGAGATAACCTAAATG-----ATCTAGGT-CAACACACCAAC
Amebif        CAATTCA---AGAACCACA-CCCCCGTAAACCAAGGC-CAACACGCCAAC
Amechr        CAATCACGGGAAATAATATAAAG--------CTAGGT-CTACACACCAAC
Amequa        CAATTTTT--AGGATTATTAAAAATTTAAACTTAGGC-CTACCTGCCAAT
Ameund        CAATTAT---AGGATTTAAGCCCACCCTAACATAGGT-CCACACACCAAA
Cneare        CAATTAAG--GA-ACAGA--CTATCATAAATCTAGGC-CCACACGCCAAA
Cneburbur     CAATC---ATGGTA-T-ATTTCGACCCAAAACTAGGT-CCACACACCAAC
Cnebursti     CAATC---ATGGTA-TTACTATAGCCCAAAACTAGGT-CCACACACCAAC
Cnecoscos     CAATT---ATGATA-ATATCTTAACCCAAAACTAGGT-CCACACACCAAC
Cnecosgri     CAATC---ATGGTA-TTATTTCAACCCAAAACTAGGT-CTACACACCAAC
Cnedep        CAATTACAT-AACA-CCCGATTAACTAAAAATTAGGT-CCACACACCAAC
Cnegra        CAATAAAG--GGTACAAC--TCACCCTAAATCTAGAC-ACACACGCCAAA
Cnegul        CAATTT--ATGATA-ATAATCTAACCCAAAATTAGGT-CCACACACCAAC
Cnegut        CAATTA----AACA-CAAAATTCACCAAAAACTAGGT-TCACACACCAAC
Cnehyp        CAATTACCG-GATA-CTACTTTAAATAAAA-CTAGGT-TCACACACCAAC
Cneino        CAAT----ATAGGA-TATACTTA-CCCAAAACTAAGT-CCACACACTAAC
Cnelac        CAAT--CAGGGCAAATCATGCTTACCCAAATCTAGGT-ATACATACCAAC
Cnelemlem     CAATTAAG--GG-ATA-A--CCATTCTAAATCTAGGC-CCACACGCCAAA
Cnelemspl     CAATTAAG--GA-ACAAA--ATATCATAAATCTAGGC-CCACACGCCAAA
Cnelon        CAATATTAGGGACCACCACAACATACCTAAGCTAGGT-CCACACACCAAC
Cnesca        CAATT---ATGATATATACCTTAACCCAAAATTAGGT-CCACACACCAAC
Cnesep        CAATTT--ATGATA-ATAATTTAACCCAAAATTAGGT-CCACACACCAAC
Cnesexsex     CAATT---ATAGGG-TATTCTTAACCCGAAACTAAGT-CCACACACTAAT
Cnesexvir     CAAT----ATAGGG-TATACTTAACCCAAAACTAAGT-CCACACACTAAC
Cnetigaet     CAATTAAAGTTACA-CCACTTTGACTAAAAACTAGGT-CCACACACCAAC
Cnetigpun     CAATTAAAGTTATA-CCACTTTAACTAAAAACTAGGT-CCACACACCAAC
Cnetigmar     CAATTAAAGTAACA-CCACTTTAACTAAAAACCAGGT-CCACACACCGAC
Cnetigmax     CAATTCAAGTAACA-CCACTTTAACTAAAAACTAGGT-CCACACACCAAC
Cnetigsep     CAATTAAAGTTATA-CCACTTTAACTAAAAACTAGGT-CCACACACCAAC
Cnetigtig     CAATTAAAGTTATA-CCACTTTAACTAAAAACTAGGT-CCACACACCAAT
Dicgut        CAATTTAGGCAAACATAAAAATTC-----AAATAGGT-ATACACACCAAA
KenaltN       CAATT------AAATTTTATTACACCTTAATCTAGGCACTACACACCAAC
KenaltS       CAATT------AAATTTTATTATACCTTAATCTAGGTATTACACACCGAC
Kenbor        CAATT------AAATTTATTATTACCTTAATTTAGGT-CCACACACCAAT
Kencal        CAATT------AT-TTTTATCTTTCCCTAATCTAGGT-CCACATACCAAA
Kenpel        CAATT------AAACTTACCCTTACCTTAATCTAGGT-TTACACACCAAC
Kenstr        CAATT------AAATTTATCATTACCTTAATTTAGGT-CCACACACCAAT
Teitey        CAATTACAG-GTTCAACGAAACAG-----TTTTAGGT-CTACACACCTTA
```

APPENDIX 2
(*Continued*)

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                   *****                                       700
Eumeces      GCCTTA--------AAACACGACCCAGTAATA----------CTGACCAA
Lacerta      ATTAGC--------CCACTAGACCCAGCAACT----------CTGATTAA
Acanth       ACA-----------CAAAAAGACCCAGTAGTT----------CTGATCAA
Pholio       ATACCC--------------GACCCAACACCTG---------TTGATCAA
Tuptex       TTTCCTC----CCCA----TGACCCAGTACAA----------CTGATTAA
Ameame       GTTTGC----CTCTTATACTGATCCAGTATTA----------CTGATCAA
Ameaub       CTTCATCTA--CCCACTATCGACCCAGTACTA----------CTGATAAA
Amebif       GTCTAC----TTCTTACACTGACCCAGTACCA----------CTGATTAA
Amechr       CTTTATTTA--CCCA-TATCGACCCAGTACTA----------CTGATAAA
Amequa       CTTTAA----GTCCTTATTCGACCCAGCACCG----------CTGATAAA
Ameund       TTTTTT-----CCTAACCTAGACCCAGCACCG----------CTGATTAA
Cneare       ATTCTA---AATCCTAAATCGACCCAGTACCA----------CTGATAAA
Cneburbur    TTTTGA-----CCAACAACTGACCCAGTATTA----------CTGATTAA
Cnebursti    TTTTGA-----CCAATAACTGACCCAGTATTA----------CTGATTAA
Cnecoscos    CTTTGA-----CCAACAATTGACCCAGTACTA----------CTGATTAA
Cnecosgri    TTCTGA-----CCACCAACTGACCCAGTATTA----------CTGATTAA
Cnedep       CTTTTAG----CCCACCATCGACCCAGTACCA----------CTGATAAA
Cnegra       ATTTAG----ACCCAGAATCGACCCAGTACCA----------CTGACAAA
Cnegul       CTTTGA-----CCAACAATTGACCCAGTATTA----------CTGATTAA
Cnegut       CTTTTA-----CCCCCCATCGACCCAGTATTA----------CTGATAAA
Cnehyp       CTTTTAA----TCCACCACCGACCCAGTACTA----------CTGATAAA
Cneino       TTTTAAC----CCACCAATTGACCCAGTATTA----------CTGACAAA
Cnelac       ATCAATCTTAACCCACACTTGACCCAGTATTA----------CTGATTAA
Cnelemlem    ATCATA----ACCCTAAATCGACCCAGTACCA----------CTGATAAA
Cnelemspl    ATTCTAG--AATCCTAAATCGACCCAGTACCA----------CTGATAAA
Cnelon       CTTAATTT--ACCCACATTTGACCCAGTACTA----------CTGATCAA
Cnesca       CTTTGA-----CCAACAATTGACCCAGTATTA----------CTGATTAA
Cnesep       CTTTG------CCAACAATTGACCCAGTATTA----------CTGATTAA
Cnesexsex    TTTTGAC----CCACCAATTGACCCAGTATTA----------CTGATAAA
Cnesexvir    TTTTGAC----CCACCAATTGACCCAGTATTA----------CTGATAAA
Cnetigaet    CTTTTAA----CTTAC-ACCGACCCAGTACTA----------CTGATAAA
Cnetigpun    CTTTTAA----CTTAC-ACCGACCCAGTACTA----------CTGATAAA
Cnetigmar    CTTTTAA----CTTAC-ACCGACCCAGTATTA----------CTGATAAA
Cnetigmax    CTTTTAA----CTTAC-ATCGACCCAGTTCTAA---------CTGATAAA
Cnetigsep    CTTTTAA----CTTAC-ACCGACCCAGTACTA----------CTGATAAA
Cnetigtig    CTTTTAA----CTTAC-ACCGACCCAGTACTA----------CTGATAAA
Dicgut       TCTGAACAG---CCATTATCGACCCAGTATTA----------CTGATAAA
KenaltN      ATTAAAAA-----TACCCTTGACCCAGTACTA----------CTGATTAA
KenaltS      ATTAAAA------TACTCTTGACCCAGTACTA----------CTGATTAA
Kenbor       ATTTTAAA-----TAATTTTGACCCAGTATTA----------CTGATTAA
Kencal       ATTAATGA-----TACTTCTGACCCAGTCCTA----------CTGATTAA
Kenpel       ATTCATAA-----CATTCTCGACCCAGTATTA----------CTGATTAA
Kenstr       ATTTTAAA-----TAATTTTGACCCAGTATTA----------CTGATTAA
Teitey       AACCCACA----CCACTATCGACCCAGTACTA----------CTGATAAA

                                                               750
Eumeces      CGAACCAAGTTACCCCAGGGATAACAGCGCTATCTTCTTCAAGAGTCCAT
Lacerta      TGAACCAAGTTACCCCAGGGATAACAGCGCAATCTCCTTTTAGAGTCCAT
Acanth       TGAACCAAGTTACCCCAGGGATAACAGCGCCATCCTCTCTTAGAGTCCCT
Pholio       AGAACCAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGCCCAA
Tuptex       AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGCCCAA
Ameame       AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCCA
Ameaub       AGAACCAAGCTACCCCAGGGATAACAGCGCCATCCCCTCCTAGAGTCCCA
Amebif       AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCAA
Amechr       AGAACCAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCCA
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APPENDIX 2
(*Continued*)

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Amequa      AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCCA
Ameund      AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCTA
Cneare      AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCCA
Cneburbur   AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGCCCAA
Cnebursti   AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGCCCAA
Cnecoscos   AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGCCCAA
Cnecosgri   AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGCCCAA
Cnedep      AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCAA
Cnegra      AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCCA
Cnegul      AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGCCCAA
Cnegut      AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCAA
Cnehyp      AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCAA
Cneino      AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCATAGAGCCCAA
Cnelac      AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCCA
Cnelemlem   AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCCA
Cnelemspl   AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCCA
Cnelon      AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCCA
Cnesca      AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGCCCAA
Cnesep      AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGCCCAA
Cnesexsex   AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCCTAGAGCCCAA
Cnesexvir   AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCCTAGAGCCCAA
Cnetigaet   AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCAA
Cnetigpun   AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGCCCAA
Cnetigmar   AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCAA
Cnetigmax   AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCAA
Cnetigsep   AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCAA
Cnetigtig   AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGCCCAA
Dicgut      AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCCC
KenaltN     AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCCA
KenaltS     AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCCA
Kenbor      AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCCA
Kencal      AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCCA
Kenpel      AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCCA
Kenstr      AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCTTAGAGTCCCA
Teitey      AGAAACAAGCTACCCCAGGGATAACAGCGCCATCCCCTCCTAGAGTCCCA

                                                          800
Eumeces     ATCGACAAG-AAGGTTTACGACCTCGATGTTGGATCAGGACACCCCAATG
Lacerta     ATCGACAAG-GAGGTTTACGACCTCGATGTTGGATCAGGACACCCCAATG
Acanth      ATCGACGAG-AGGGCTTACGACCTCGATGTTGGATCAGGACAACCTAATA
Pholio      ATCGACGAGCGGGGTTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Tuptex      ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAG-CA
Ameame      ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGCCCCCCAAACA
Ameaub      ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCACCCAAACA
Amebif      ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Amechr      ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Amequa      ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGCCCCCCAAACA
Ameund      ATCGACGAGTGGGGCTTACGACCTCGATGTTGGATCAGGCCCCCCAAACA
Cneare      ATCGACGAG-GGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Cneburbur   ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Cnebursti   ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Cnecoscos   ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Cnecosgri   ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Cnedep      ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Cnegra      ATCGACGAG-GGGGCTTACGACCTCGATGTTGGATCAGGGCACCCAAACA
Cnegul      ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Cnegut      ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
```

APPENDIX 2
(*Continued*)

```
Cnehyp      ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Cneino      ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Cnelac      ATCGACGAG-GGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Cnelemlem   ATCGACGAG-GGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Cnelemspl   ATCGACGAG-GGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Cnelon      ATCGATGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Cnesca      ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Cnesep      ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Cnesexsex   ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Cnesexvir   ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Cnetigaet   ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Cnetigpun   ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Cnetigmar   ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Cnetigmax   ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Cnetigsep   ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Cnetigtig   ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
Dicgut      ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA
KenaltN     ATCGATGAGCGGGGCTTACGACCTCGATGTTGGATCAGGCCCCCCAA-CA
KenaltS     ATCGACGAGTGGGGCTTACGACCTCGATGTTGGATCAGGCCCCCCAA-CA
Kenbor      ATCGACGAGTGGGGCTTACGACCTCGATGTTGGATCAGGCCCCCCAA-CA
Kencal      ATCGACGAGTGGGGCTTACGACCTCGATGTTGGATCAGGCCCCCCAA-CA
Kenpel      ATCGACGAGTGGGGCTTACGACCTCGATGTTGGATCAGGCCCCCCAA-CA
Kenstr      ATCGACGAGTGGGGCTTACGACCTCGATGTTGGATCAGGCCCCCCAA-CA
Teitey      ATCGACGAGCGGGGCTTACGACCTCGATGTTGGATCAGGGCCCCCAAACA

                                                          850
Eumeces     GTGCAGCCGCTATTAAAGGTTCGTTTGTTCAACGANNNNNNTTCCCTCTC
Lacerta     GTGCAGCCGCCATTAAAGNNNNNNNNNNNNNNNNNNNNNTTCTCTCTC
Acanth      GTGCAACCGCTATTAACGNNNNNNNNNNNNNNNNNNNNNCTCCCTCTC
Pholio      GTGCAACAGCTGTTAACGGTNNNNNNNNNNNNNNNNNNNNCCCCCTCTC
Tuptex      GTGCAGCAGCTGCTAACGGTTTGTTTGTTCAACAAGGAATGCTCCCTCTC
Ameame      GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAATTAATGCTCCCTCTC
Ameaub      GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAATTAATGCTCCCTCTC
Amebif      GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAATTAATGCTCCTCCTC
Amechr      GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAATTAATGCTCCCTCTC
Amequa      GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAATTAATGCTCCCTCTC
Ameund      GTGCAGCAGCTGTTAAAGGTTTGNNNNNNNNNNNNNNNNNCTCCCTCTC
Cneare      GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAATTAAAGCTCCTCCTC
Cneburbur   GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAATTAATGCTCCCTCTC
Cneburbut   GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAANNNNNNCTCCCTCTC
Cnecoscos   GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAATTAATNCTCCCTCTC
Cnecosgri   GTGCAGAAGCTGTTAAAGGTTTGTTTGTTCAACAATTAATNCTCCCTCTT
Cnedep      GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAATTAATGCCCCTTCCT
Cnegra      GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAATTAAAGCTCCTCCTC
Cnegul      GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAATTAATNCTCCTTCTC
Cnegut      GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAATTAATGCCCCTTCTT
Cnehyp      GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAATTAATNCCCCTTCCT
Cneino      GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAACTAATGCTCCCTCTT
Cnelac      GTGCAACAGCTGTTAATGGTTTGTTTGTTCAACAANNNNNNCTCCTCCTT
Cnelemlem   GTGCAGCAGCTGTTAAAGGTTTGNNNNNNNNNNNNNNNNNCTCCTCCTC
Cnelemspl   GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAATTAAANCTCCTCCTC
Cnelon      GTGCAGCAGCTGTTAATGGTTTGTTTGTTCAACAATTAATGCTCCCTCTC
Cnesca      GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAATTAATGCTCCTTCTC
Cnesep      GTGCAGCAGCTGTTAAAGGTTTGTNNNNNNNNNNNNNNNNCTCCTTCTC
Cnesexsex   GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAACTAATNCTTCCTCTT
Cnesexvir   GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAACTGATNCTCCCTCTT
Cnetigaet   GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAATTAATNCTCCCTCCC
Cnetigpun   GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAATTAATGCTCCCTCCC
```

APPENDIX 2
(*Continued*)

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Cnetigmar       GTGCAG-AGCTGTGAAAGGTTTGNNNNNNNNNNNNNNNNNNCTCCCTCCC
Cnetigmax       GTGCAG-AGCTGTTAAAGGTTTGTTTGTTCAACAATTAATGCTCCCTCCC
Cnetigsep       GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAATTAATNCTCCCTCCC
Cnetigtig       GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAATTAATGCTCCCTCCC
Dicgut          GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAATTAATGCTCCTTCTC
KenaltN         GTGCAGCAGCTGTTAAAGGTTTGTTNNNNNNNNNNNNNNNNCTCCTCTTT
KenaltS         GTGCAGCAGCTGTNNNNNNNNNNNNNNNNNNNNNNNNNNCTCCTCTTT
Kenbor          GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAATTAATGCTCCTCCTC
Kencal          GTGCAGCAGCTGCTAAAGGTTTGTTTGTTCAACAATTAATNCTCCTCTTC
Kenpel          GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAATTAATNCTCCTCTTC
Kenstr          GTGCAGCAGCTGTTAAAGGTTTGTTTGTTCAACAATTAATNCTCCTCCTC
Teitey          GTGCAGCAGCTGTTAATGGTTTGTTTGTTCAACAATTAATGCTCCCTCTC

                                                          876
Eumeces         CCCCTCCTCTTCCCTTTTTCCCCCTC
Lacerta         CCCCCCCTCTTNCTTCCCTCCCCCTC
Acanth          CCCCCCTTCTTNCCTCCCTCCCCCTC
Pholio          CCCCCCTTCCTTCCTCCCTCCCCCCT
Tuptex          CCTTCCTTCCCTCCTCCCTCCTTTCT
Ameame          CCTTCTTTCTTTCCCCCCTCTTTTTT
Ameaub          CCTTCTTTCTTTCCTCCCTCCTTTTT
Amebif          CCCTCTTTCTTTCCCCCCCCTTTTTT
Amechr          CCTTCTTTCTTTCCTCCCTCCTTTTT
Amequa          CCCTCTTTCTTTCCTCCCCCTTTTTT
Ameund          CCCTCTTTCTTTCCTCCCCCCTTTTT
Cneare          CCCTCTTCCTTTCCTCCCCCTTTTTC
Cneburbur       CCCTCTTTCTTTCCTCCCTCCTTTTT
Cnebursti       CCCTCTTTCTTTCCTCCCTCCTTTTT
Cnecoscos       CCTTCTTTCTTTCCTCCCTCCTTTTT
Cnecosgri       CCCTCTTTCTTTCCTCCCTCCTTTTT
Cnedep          TTCCCTTTCTTTCCTCCCTCCTTTTT
Cnegra          CCCTCTTCCTTTCCTCCCCCTTTTTC
Cnegul          CCCTCTTTCTTTCCTCCCTCCTTTTT
Cnegut          TTCCCTTTCTTTCCTCCCTCCTTTTT
Cnehyp          TTCCCTTTCTTTCCTCCCTCCTTTTT
Cneino          CCCTCTTTCTTTCCTCCCTCCTTTTT
Cnelac          CCCTCTTTCTTTCCTCCCTCTTTTTC
Cnelemlem       CCCTCTTCCTTTCCTCCCCCTTTTTC
Cnelemspl       CCCTCTTCCTTTCCTCCCCCTTTTTC
Cnelon          CCCTCTTTCTTTCCTCCCTCTTTTTT
Cnesca          CCCTCTTTCTTTCCTCCCTCCTTTTT
Cnesep          CCCTCTTTCTTTCCTCCCTCCTTTTT
Cnesexsex       CCCTCTTTCTTTCCTCCCTCCTTTTT
Cnesexvir       CCCTCTTTCTTTCCTCCCTCCTTTTT
Cnetigaet       CTCTCTTTCTTTTCTCCCTCCTTTCT
Cnetigpun       CTCTCTTTCTTTTCTCCCTCCTTTCT
Cnetigmar       CTCCCTTTCTTTCCTCCCTCCTTTCT
Cnetigmax       CTCCCTTTCTTTCCTCCCTCCTTTCT
Cnetigsep       CTCTCTTTCTTTTCTCCCTCCTTTCT
Cnetigtig       CTCTCTTTCTTTCCTCCCTCCTTTCT
Dicgut          CCCTCCTTCTTTCCTCCCTCCCTTTT
KenaltN         CCCCTTTTCTTTCCTCCCTTCCCTTT
KenaltS         CCCCTTTTCTTTCCTCCCTTCCCTTT
Kenbor          CCCCCTTTCTTTCCTCCCTCCCCTTT
Kencal          CCCCTTTTTTTTCCTCCCTCCCCTTT
Kenpel          CCCCCTTTCTTTCCTCCCCCCCCTTT
Kenstr          CCCCCTTTCTTTCCTCCCTCCCCTTT
Teitey          CCCTCTTTCTTTCCTCCCTCCCTTTT
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APPENDIX 3
ALLOZYME DATA

The electrophoretic allozyme data were based on tables in Dessauer and Cole (1989), Cole and Dessauer (1993), Cole et al. (1995), and Markezich et al. (1997). For more details, see Materials and Methods. The phylogenetically informative protein loci are listed below. The protein names and abbreviations are those recommended by the International Union of Biochemistry (IUBNC, 1984). Taxon abbreviations are given in appendix 2. For each locus (character), the alternate alleles (character states) are designated by letters.

1. L-Iditol Dehydrogenase (IDDH)
2. Glycerol-3-Phosphate Dehydrogenase (G3PDH)
3. L-Lactate Dehydrogenase 1 (LDH1)
4. L-Lactate Dehydrogenase 2 (LDH2)
5. s-Malate Dehydrogenase (sMDH)
6. m-Malate Dehydrogenase (mMDH)
7. Malate Dehydrogenase (NADP+) (MDHP)
8. s-Isocitrate Dehydrogenase (sIDH)
9. m-Isocitrate Dehydrogenase (mIDH)
10. Phosphogluconate Dehydrogenase (PGDH)
11. s-Superoxide Dismutase (sSOD)
12. s-Aspartate Aminotransferase (sAAT)
13. m-Aspartate Aminotransferase (mAAT)
14. Phosphoglucomutase 2 (PGM2)
15. Adenylate Kinase (AK)
16. Creatine Kinase 1 (CK1)
17. Creatine Kinase 2 (CK2)
18. Acid Phosphatase (ACP)
19. Esterase D (ESTD)
20. Peptidase A (PEP-A)
21. Peptidase B (PEP-B)
22. Adenosine Deaminase (ADA)
23. Fructose-Bisphosphate Aldolase 2 (FBA-2)
24. Mannose-6-Phosphate Isomerase (MPI)
25. Transferrin (TF)
26. Albumin (ALB)
27. Hemoglobin 1 (HB1)
28. Hemoglobin 2 (HB2)
29. Malate Dehydrogenase (NADP+) (MDHP2)
30. m-Superoxide Dismutase (mSOD)
31. s-Aconitate Hydratase (sACOH)

Allozyme data matrix:

Tuptex	A C B B D A D B ? A C C C C A B B A D G I F D F A A B B C B B
Ameame	C A C C C A C B ? D A E B B A B ? B C H C B C E D B C A { B D } B B
Cneare	D B C A E A E D ? E D A C B A A C { C D } B D G ? ? D E ? C B A A A
Cneburs ti	? B C A B A A C B C B A A B A C C C D D B B C { B C } B { E F } A B B B B
Cnecoscos	B D C A B A A { B C } C C B B A B A C C A { A E } B { B E } { B E } C B B E A B B B B
Cnecosgri	? B C A B A A { B C } B { B C } { B C } A A B A C C C D D { B D } B C B A D A B B B B
Cnegul	? B C A B A A B B C B B A B A C C C D D D C C { B C } B F A B B B B
Cneino	C B C A A A A B B C C B A A A C C C D A E A C B C D A B B B B
Cnelac	B B C A A A D D A A C C C B A D C B B C C E C E F E B B B B B
Cnelemlem	D B C A E A E D A E D B C B A A C C B E F { D E } A { D E } E C C B B A B
Cnelemspl	D B C A E A E D ? E D B C B A A C C B E G E ? D E ? C B B A B
Cnesca	? B C A B A A C B C { B C } B A B A C C C D D D C C B B E A B B B B
Cnesep	? B C A B A A C B C B B A B A C C C D D D D C B B E A B B B B
Cnesexvir	C ? C A A A A B B C C B A A A C C C { B E } A G B C B B F A B B B B
Cnetigpun	C ? A A A A ? C B C B A B A A C C C D B A B C A C D A B B B B
Cnetigmar	{A C} ? A A A A A C B C B A B A A C C C C D B D B C A B D A B B B B
KenaltN	D B ? A F ? B D ? ? ? D C ? A B A ? C ? ? ? ? ? ? ? A ? ? B C
Kencal	D B C A F B B D ? B C D C B A B A B C F G D B E E C A B B B B
Kenstr	D B ? A F B ? ? ? ? C D C B A B A ? C ? ? ? ? ? E C A ? ? B C

APPENDIX 4
MORPHOLOGICAL DATA

Taxon abbreviations are given in Appendix 2, except: Cnemur = *Cnemidophorus murinus*, and Cneoce = *Cnemidophorus ocellifer*. The characters, character states, and codes are listed below. All multistate characters are unordered, unless otherwise noted.

1. Tongue sheath (Burt, 1931: 12, fig. 1): (A) present at base of tongue, clearly separating it from the glottis (also visible laterally); (B) absent.
2. Posterior edge of scaly portion of tongue (Burt, 1931: 12, fig. 1): (A) not forked or only slightly so; (B) clearly forked, with free or nearly free lateral posterior extensions.
3. Surface of ventral scutes: (A) smooth; (B) keeled.
4. Typical number of rows of ventral scutes across midbody: (A) 8; (B) 10–12; (C) 14; (D) more than 15.
5. Dorsal scales (noted for dorsolateral scales at midbody): (A) granules; (B) somewhat enlarged, not imbricate; (C) enlarged and imbricate.
6. Number of conspicuously enlarged anal spurs on each side of adult males: (A) 0; (B) 1; (C) 2.
7. Postantebrachial scales (Duellman and Zweifel, 1962: 164, fig. 2): (A) granular; (B) slightly enlarged; (C) enlarged.
8. Mesoptychial scales edging posterior gular fold: (A) somewhat enlarged over size of scales within posterior fold, the more anterior mesoptychials becoming abruptly enlarged (Echternacht, 1971: 43, fig. 18); (B) somewhat enlarged over scales in fold, more anterior ones gradually enlarging, then yet more anterior ones becoming smaller (Burt, 1931: 24, fig. 4); (C) abruptly enlarged over scales in fold, more anterior ones becoming smaller (Burt, 1931: 24, fig. 5).
9. Typical number of parietal scales: (A) 3; (B) 5; (C) 5 across, but lateral-most scales divided into anterior-posterior halves.
10. Typical number of supraocular scales on each side: (A) 4; (B) 3; (C) 2.

Morphological data matrix:

Pholio	B B A A C A C C A C	Cnelemspl	B B A A A B A A B A
Tuptex	A A A D B A A A A A	Cnelon	B B A B A A A B A A
Ameame	A A A B A A A A B A	Cnemur	B B A B A B A {A C} B A
Ameaub	A A A B A A {A B} A B A	Cneoce	B B A A A A A C B A
Amebif	A A A {A B} A A {A B} {A B} B A	Cnesca	B B A A A A C C A A
Amechr	A A A B A A A A B A	Cnesep	B B A A A A C C A A
Amequa	A A A A A A A A {A B} B	Cnesexsex	B B A A A A B C A A
Ameund	A A A A A A {A B} A A B	Cnesexvir	B B A A A A B C A A
Cneare	B B A A A B A A B A	Cnetigaet	B B A A A A A {A B C} A A
Cneburbur	B B A A A A C C A A	Cnetigpun	B B A A A A A {A B} A A
Cnebursti	B B A A A A C C A A	Cnetigmar	B B A A A A A {A B} A A
Cnecoscos	B B A A A A C C A A	Cnetigmax	B B A A A A A C A A
Cnecosgri	B B A A A A C C A A	Cnetigsep	B B A A A A A B A A
Cnedep	B B A A A A A C A B	Cnetigtig	B B A A A A A B A A
Cnegra	B B A A A B A A B A	Dicgut	B B A A A A A B C A
Cnegul	B B A A A A C C A A	KenaltN	A B B C A C A C A {A B}
Cnegut	B B A A A A A C A B	KenaltS	A B B C A C A C A {A B}
Cnehyp	B B A A A A A C A {A B}	Kencal	A B B C A C A C A A
Cneino	B B A A A A B C A A	Kenpel	A B B C A C A C A B
Cnelac	A B A B A A {A B} C {A B} {A B}	Kenstr	A B B C C C A C A A
Cnelemlem	B B A A A B A A B A	Teitey	B B A A A A A C {A B C} {A B}

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