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Review of Teiid Morphology with a Revised Taxonomy and Phylogeny of the Teiidae (Lepidosauria: Squamata)

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Abstract

Despite advances within particular groups, systematics of the Teiidae has long been unsatisfactory, because few morphological characters have been described for this family. Consequently, most species have been assigned to the large, polyphyletic, and poorly defined genera *Ameiva* and *Cnemidophorus*. We describe 137 morphological characters and score them for most species of Neotropical Teiidae. Important, but previously undescribed, character suites include pupil shape; the frontal ridge; longitudinal division of the interparietal; the rostral groove; patterns of supraciliary fusion; the preauricular skin fold; the "toothy" first supralabial; modified apical granules; the pectoral sulcus; expansion of scales at the heel; tibiotarsal shields; scales between the digital lamellae along the postaxial edges of the toes; scale surface microstructure of macrohoneycomb, macroridges, or lamellae; distribution patterns and morphology of lenticular scale organs; types of epidermal generation glands; and several hemipenial structures. We propose a new taxonomy of the Teiidae based on recovered evolutionary history and numerous morphological characters surveyed in this study. We recognize three subfamilies: Callopistinae **new subfamily**, Teiinae Estes *et al.*, and Tupinambinae Estes *et al.* To resolve polyphyly of *Ameiva* and *Cnemidophorus*, we erect four new genera for various groups of Neotropical Teiidae: *Ameivula* **new genus,** *Aurivela* **new genus,** *Contomastix* **new genus,** and *Medopheos* **new genus.** We resurrect *Holcosus* Cope from the synonymy of *Ameiva* and *Salvator* Duméril and Bibron from the synonymy of *Tupinambis*. On the basis of shared derived characters, we propose new species groups of our redefined *Ameiva* and *Cnemidophorus*. We incorporate our new characters into a key to the genera and species groups of Teiidae. A phylogenetic hypothesis of Teiidae based on morphological characters differs substantially from hypotheses based on mitochondrial DNA. The phylogeny based on morphology is consistent with well-established biogeographic patterns of Neotropical vertebrates and explains extreme morphological divergence in such genera as *Kentropyx* and *Aurivela*.

Key words: *Ameivula* new genus, *Aurivela* new genus, Callopistinae new subfamily, *Contomastix* new genus, generation glands, *Holcosus*, *Medopheos* new genus, scale surface morphology, *Salvator*

Introduction

Prior to Boulenger's systematic rearrangement of lizards, the various teiid genera were scattered among several families. In his key to genera, Boulenger (1885b) divided the teiids up into four groups; his Group I was defined by nasals not separated medially by a frontonasal, limbs well developed, and body moderate to large. The group included the various genera of "macroteiids," a term perhaps first used by Ruibal (1952). The remaining groups included various genera of microteiids and are currently assigned to the Gymnophthalmidae. Later, the macroteiids were placed in a separate subfamily containing two clades formally recognized as the tribes Teiini and Tupinambini by Presch (1970, 1974a). Little doubt remains that the Teiidae and Gymnophthalmidae are monophyletic groups (Castoe *et al.* 2004; Pellegrino *et al.* 2001), and Presch's clades are generally regarded as subfamilies (Estes *et al.* 1988). Recognition of these subfamilies has received mostly unambiguous support from separate analyses of chromosomal (Gorman 1970), hemipenial (Böhme 1988), osteological (Presch 1974a), integumental (Vanzolini & Valencia 1965), myological (Rieppel 1980, but see Abdala & Moro 2000), neurological (Northcutt 1978), and mitochondrial DNA (Giugliano *et al.* 2007) character sets. A third subfamily Chamopsiinae accommodates extinct genera from North America and may be the sister group of the extant subfamilies (Denton & O'Neill 1995; but see note added to proof of Sullivan & Estes 1997). The Teiidae is almost certainly the sister group of the Gymnophthalmidae, and teiids likely arose in the middle Cretaceous from a common ancestor shared with the extinct Polyglyphanodontidae (Conrad 2008; this group has been considered an additional subfamily of the Teiidae by some authors, e.g., Estes 1983a; Gao & Norell 2000).

The genus-level taxonomy of the Teiidae has long been unsatisfactory. This problem is particularly acute within the speciose radiation of cnemidophorines in which most tropical species are assigned to the large polyphyletic genera *Ameiva* and *Cnemidophorus*. Polyphyly urgently requires resolution, because teiids are often the most conspicuous elements of many New World herpetofaunas and have been the subject of numerous detailed ecological studies. As researchers make ecological comparisons among teiid species, draw inferences about their biogeography, propose conservation strategies, and conduct other studies of their comparative biology, polyphyly of genera such as *Ameiva*, *Cnemidophorus*, and *Tupinambis* will likely produce what Bortolus (2008) called "error cascades," where seemingly trivial taxonomic problems become magnified in the development of scientific knowledge. However, the problem is not just one of polyphyly. Some genera have never been adequately diagnosed, whereas others are defined by apparent symplesiomorphies. These problems contribute to misidentification in the field and incorrect or uncertain assignment of newly discovered species.

While reviewing several groups of *Cnemidophorus* (Harvey, unpublished data; Ugueto & Harvey 2010; Ugueto *et al.* 2009) and *Ameiva* (Ugueto & Harvey 2011), we discovered numerous unreported morphological characters of the Teiidae. In a phylogenetic analysis, we combine these new characters with traditional characters used in earlier revisions. Based on this large dataset, we propose a revised taxonomy of extant Teiidae and resolve most problems of polyphyly inherent in the current taxonomy. We also provide detailed diagnoses and definitions of each genus. We develop a new key to genera and species groups to aid in the correct identification of teiids.

Material and Methods

We scored 742 specimens (101 species and subspecies) for 137 morphological characters, generating a data matrix of 101,654 cells (matrix available on the Morphobank website, The Morphobank Project 2012). We also examined small samples of 12 additional species and subspecies for selected characters used in the diagnoses (Appendix). Some characters such as contact between the first subocular and supralabials occasionally show bilateral asymmetry, thus creating an obvious problem when coding specimens for the phylogenetic analysis. To avoid this problem, we assessed these characters on one side only (left side except when damaged) or combined counts from both sides.

In the taxonomic accounts, we diagnose taxa by citing specific characters unique to the group or through comparisons. We base the definitions on data collected solely from specimens examined in this study, although we occasionally reference published reports of variation not encountered by us. Although lengthy, the definitions should not be confused with descriptions, in that they include only the traits listed in the synopsis of characters.

We examined partially to fully everted hemipenes attached to the following specimens: *Ameiva a. ameiva* (UTA 15596), *A. praesignis* (UTA 1996, 3466, 3467; MHUA 11536) *A. bridgesii* (MECN 6725), *A. septemlineata* (USNM 152408), *A. sp. F* (*bifrontata* complex; FMNH 242238), *Callopistes maculatus* (UTA 12998), *Cnemidophorus arenivagus* (AMNH 142582), *C. arubensis* (UMMZ 57226–27), *C. lemniscatus espeuti* (UMMZ 127880), *C. l. gaigei* (UMMZ 54893), *C. l. lemniscatus* (YPM 14127), *C. l. splendidus* (FMNH 242236), *Crocodilurus amazonicus* (UTA 7233), *Kentropyx altamazonica* (TCWC 40401), *K. calcarata* (UTA R-50183), *K. pelviceps* (TCWC 39052), *K. striata* (TCWC 59191). For more detailed study, we removed single organs from *Ameiva anomala* (AMNH 109694), *A. chrysolaema* (KU 232025), *A. edracantha* (KU 12149), *A. festiva* (UTA 29347), *A. leptophrys* (MVZ 83221), *A. septemlineata* (USNM 285778), *A. undulata* (UTA 46728), *Aspidoscelis gularis* (UTA 32588), *A. sexlineata* (UTA 17921), *A. tigris* (UTA 51087), *Callopistes flavipunctatus* (FMNH 41588), *Cnemidophorus ocellifer* (FMNH 44156), *C. vanzoi* (KU 44155), *C. vittatus* (UTA 58475), *Crocodilurus amazonicus* (USNM 200689), *Dicrodon heterolepis* (KU 163770), *Kentropyx altamazonica* (UTA 59487–88), *Teius oculatus* (USNM 12320), and *T. teyou* (FMNH 44155). We prepared organs with the methods described in detail by Harvey and Embert (2009), Myers and Cadle (2003), and Zaher and Prudente (2003). Single, partially everted organs were removed from specimens, softened in 1% KOH with Alizarin Red, fully everted with petroleum jelly stained with blue candle wax dye, tied off, and returned to 70% ethanol for permanent storage.

We examined sculpturing of the β-keratin containing layers (i.e., the oberhautchen and β-layer) by mounting “loose scales” onto glass slides with a drop of 70% ethanol and a coverslip. The so-called “loose scales” are not entire scales, but only the outermost layers of the epidermis. Alcohol is thought to leach out lipids from the underlying mesos layer, thereby weakening it and making the outer layers easy to remove from preserved specimens (Harvey 1991; Harvey & Gutberlet 1995). We studied the distribution of lenticular scale organs using high magnification (40X) under a stereoscope. When pigmented, generation glands were clearly visible under a stereoscope. In species without pigmented generation glands, we mounted several scales from ventral surfaces of the proximal tail and thigh and posterior belly on glass slides with alcohol and a coverslip. In these preparations, unpigmented glands were visible in the β-keratin containing layers of some groups such as northern *Cnemidophorus*.

We coded characters for parsimony analysis with generalized frequency coding (GFC), which Smith and Gutberlet (2001) developed to extract maximal phylogenetic information from patterns of polymorphism within terminal taxa. The method is useful not only for polymorphic binary characters (Wiens 1995) but also for polymorphic multistate, meristic, and continuous characters. We used the program FastMorphologyGFC (Chang & Smith 2001) to convert the raw data into a Nexus file for analysis with PAUP* v4.0b10 (Swofford 2002) and used unequal subcharacter weighting, as recommended by Smith and Gutberlet (2001).

In order to assess the effects of different character classes on the phylogenetic results, we conducted several analyses. In most analyses, all characters that could be ordered on the basis of morphological intermediacy or adjacency were treated as ordered. In Analysis 2, we treated these characters as unordered (similar to the approach of Gutberlet 1998, and Gutberlet & Harvey 2002). In other analyses, we excluded meristic characters, color characters, or both. In all analyses, we used *Callopistes maculatus* as the outgroup to root trees and excluded characters 1 (maximum snout-vent length) and 2 (relative tail length). The complete data matrix contains several type species that were not available for study. To code these species, we relied on original descriptions and photographs, however many characters could not be assessed and the entries are incomplete. We considered these species when formulating generic definitions and diagnoses, however we excluded them from phylogenetic analyses, leaving 87 terminal taxa.

We conducted maximum parsimony analyses with PAUP*, using heuristic searching with 200 random-taxon-addition sequences and tree bisection reconnection (TBR) branch swapping. We evaluated support for nodes with nonparametric bootstrapping (Felsenstein 1985), with 1000 full heuristic pseudoreplicates and two random-taxon-addition sequence replicates per pseudoreplicate.

Review of Teiid Morphology and Synopsis of Characters

To avoid repetition when describing characters used in this analysis, we refer to a group of similar species from trans-Andean Colombia and Ecuador (*Ameiva anomala, A. bridgesii,* and *A. septemlineata*) as "western *Ameiva*," to species of the *Ameiva ameiva* and *A. bifrontata* complexes as "eastern *Ameiva*," and to *A. chaitzmani, A. festiva, A. leptophrys, A. niceforoi, A. quadrilineata,* and *A. undulata* as "Central American *Ameiva*." Similarly, we refer to species of *Cnemidophorus* with preanal spurs as "northern *Cnemidophorus*" and the heterogeneous assemblage of species occurring south of the Amazon River as "southern *Cnemidophorus*."

Below, we describe each morphological character used in the phylogenetic analysis. Many of these characters have never been described before, whereas others have never been formally defined and their descriptions have been contradictory among authors.

Morphometrics

1. *Maximum Snout-Vent Length (SVL) in Males*.—We obtained maximum snout-vent lengths from original descriptions and revisions (e.g., Avila-Pires 1995; Echternacht 1971; Henderson & Powell 2009; Ugueto & Harvey 2011) of most species. In some instances, specimens examined in this study have the maximum known snout-vent lengths for the species in question. These include *Ameiva bridgesii* 111 mm (FMNH 165157, female), *A. edracantha* 93.78 mm (MECN 446, male), *A. griswoldi* 134 mm (UF 11361 male), *A. septemlineata* 135 mm (USNM 27680, male), *Cnemidophorus vittatus* 76 mm (MHNC R-197, male), *Crocodilurus amazonicus* 222 mm SVL (UTA R-7233, male), and *Tupinambis teguixin* 400 mm (MHUA 10394, male).

Ameiva niceforoi is known from few specimens (Echternacht 1970), the largest with 82 mm SVL. The specimen is likely a subadult, and we suspect that this species attains a SVL comparable to *A. festiva* (maximum 129 mm), its likely sister species. We coded this species as unknown (?) for maximum SVL.

As currently defined, *Cnemidophorus ocellifer* consists of a complex of species and therefore poses problems for coding this character. Vitt's (1983) sample of 464 specimens from Pernambuco, Brazil, included some specimens reaching 85 mm, whereas the largest specimens we examined were under 75 mm. Older reports of 120 mm (Vanzolini *et al.* 1980) may have been based on larger species of the *C. ocellifer* complex. Most specimens we examined came from southern populations of *C. ocellifer* in the Cerrados of Mato Grosso and Gran Chaco of Paraguay. Nonetheless, one specimen (AMNH 36375) from Bahia comes from a locality in the same morphoclimatic domain (Caatinga) as Vitt's sample and is near the type locality of the species. We assigned 85 mm as the maximum SVL to the specimen from Bahia based on Vitt's study and 75 mm to the southern samples based on our measurements of specimens from southern populations.

2. *Relative Tail Length*.—We express this character as a ratio of tail length to SVL. In Teiinae, the regenerated portion of the tail begins with an annulus about twice as long as the unregenerated annulus preceding it.

Teeth

3. *Posterior Teeth Compression*.—The posterior mandibular and maxillary teeth are longitudinally (0) or transversely (1) compressed.

Presch (1974b) pointed out that the Tupinambinae have mostly conical, recurved teeth adapted for grasping prey, whereas the Teiinae mostly have bicuspid or tricuspid teeth adapted for an insectivorous diet. Nonetheless, posterior maxillary and mandibular teeth are usually tricuspid in both groups. Posterior maxillary teeth of *Tupinambis* become molariform in large adults, whereas they are molariform even in juvenile *Dracaena* (Boulenger 1885a, Dalrymple 1979; Presch 1974b). Pterygoid teeth occur in some teiids such as *Callopistes*, *Ameiva bifrontata*, *A. ameiva*, and some *Kentropyx*, but are absent from others (e.g., other *Ameiva* examined by Presch 1974b).

Presch (1974b) provided detailed descriptions of the transversely oriented, bicuspid teeth of *Dicrodon* and *Teius*. He thought that the distinctive teeth of these genera were designed for crushing insects based on their similarity to tooth structure of insectivorous mammals. Both genera are highly herbivorous (Holmberg 1957; Schmidt 1957) and important seed dispersers (Varela & Bucher 2002). Nonetheless, *Teius* consumes a variety of invertebrates (Alvarez *et al.* 1992). Interestingly, transversely oriented, bicuspid teeth also occur in some extinct teiids, such as *Polyglyphanodon* from the upper Cretaceous of Utah, U.S.A. (Estes 1983a).

Teeth are difficult to study on entire specimens preserved with their mouths closed. Here, we choose only to code compression and number of cusps on posterior maxillary and mandibular teeth, since these are easily examined by gently depressing the lower lip of whole specimens. A more thorough review of dental morphology is deferred until the skull can be studied in detail.

4. *Posterior Teeth Cusps*.—The posterior mandibular and maxillary teeth are tricuspid (0) or bicuspid (1).

Eye

5. *Pupil*.—The pupil (Fig. 1) is round (0) or reniform (1).

FIGURE 1. Pupil (character 5) of *Anadia marmorata* from near El Junquito, Miranda, Venezuela (A, photo by G. N. Ugueto), *Salvator merianae* from São Martinho, Santa Catarina, Brazil (B, photo by A. Kwet), *Crocodilurus amazonicus*, juvenile from Amazonas, Venezuela (C, photo by C. L. Barrio-Amorós), and *Ameiva bifrontata bifrontata* from Playa Guacuco, Isla de Margarita, Nueva Esparta, Venezuela (D, photo by G. N. Ugueto).

Crocodilurus, *Tupinambis teguixin*, and Teiinae have a reniform (i.e., kidney-shaped) pupil, whereas *Callopistes*, *Dracaena*, *T. merianae*, *T. rufescens*, and gymnophthalmids we examined (*Anadia*, *Cercosaura*, and *Leposoma*) have round pupils.

Cephalic Roofing Scales

6. *Rostral-Frontonasal Contact*.—Nasals separate the rostral from the frontonasal (0) or the rostral contacts the frontonasal (1).

In teiids, nasals ordinarily separate the rostral from the frontonasal (Fig. 2). State 0 is actually one of the characters Boulenger (1885b) used to define his Group I of the Teiidae (= Teiidae auctorum). However in a footnote to his key, Boulenger (1885b, p. 331) noted the nasals are "sometimes separated in *Teius*." The rostral broadly contacts the frontonasal in most photographs we've seen of *T. oculatus* and in 60% (*n* = 5) of specimens we examined. We never found this character in *T. teyou*. Among other species, we only encountered this trait in *Ameiva bridgesii*, where the rostral contacts the frontonasal at low frequencies (33%, *n* = 6).

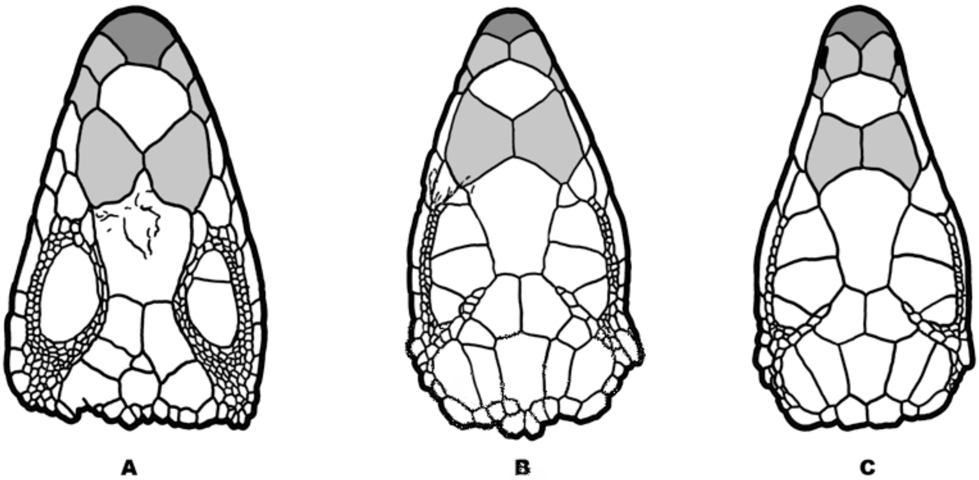

FIGURE 2. Rostral-frontonasal and nasal-prefrontal contact (characters 6 and 7) in *Teius oculatus* (A, USNM 65813), *Cnemidophorus arenivagus* (B, USNM 21709), and *Cnemidophorus lemniscatus splendidus* (C, FMNH 242236).

7. *Contact Between the Nasal and Prefrontal*.—The nasal and prefrontal may be separated (0) or in contact (1).

When the nasal and prefrontal are in contact (7.1) (Fig. 2), the frontonasal is subcircular to hexagonal, whereas the same scale is roughly octagonal when the scales are separate (7.0). Thus, degree of contact between the nasal and prefrontal defines the shape of the frontonasal. Shape of the frontonasal has recently been used to diagnose *Cnemidophorus arenivagus* (Markezich *et al.* 1997). Although occasional specimens of other northern *Cnemidophorus* have these scales in contact, *C. arenivagus* is the only species of the group with the prefrontal and nasal almost always in contact.

Although fixed in some species, this character exhibits considerable polymorphism in others. Recent keys to Central American *Ameiva* (e.g., Echternacht 1971; Savage 2002) characterize *A. quadrilineata* as having state 1 and use this character to separate *A. quadrilineata* from *A. leptophrys*. However, *A. quadrilineata* is polymorphic for this character; 18% (*n* = 11) of specimens in our sample have state 0. We find development of the fifth toe (well-developed in *A. quadrilineata*, reduced in *A. leptophrys;* character 107) to be a more reliable difference between these species.

8. *Contact Between First Supraciliary and Prefrontal*.—The prefrontal and first supraciliary are separated by the loreal and first supraocular (0) or in contact (1) (Fig. 3).

9. *Frontal Division*.—The frontal scale is entire (0), divided transversely into two scales (1), divided transversely into three scales (2), or replaced by three or more small irregular scales (3). Based on morphological intermediacy, we ordered this character as follows: 0 > 1 > 2 > 3.

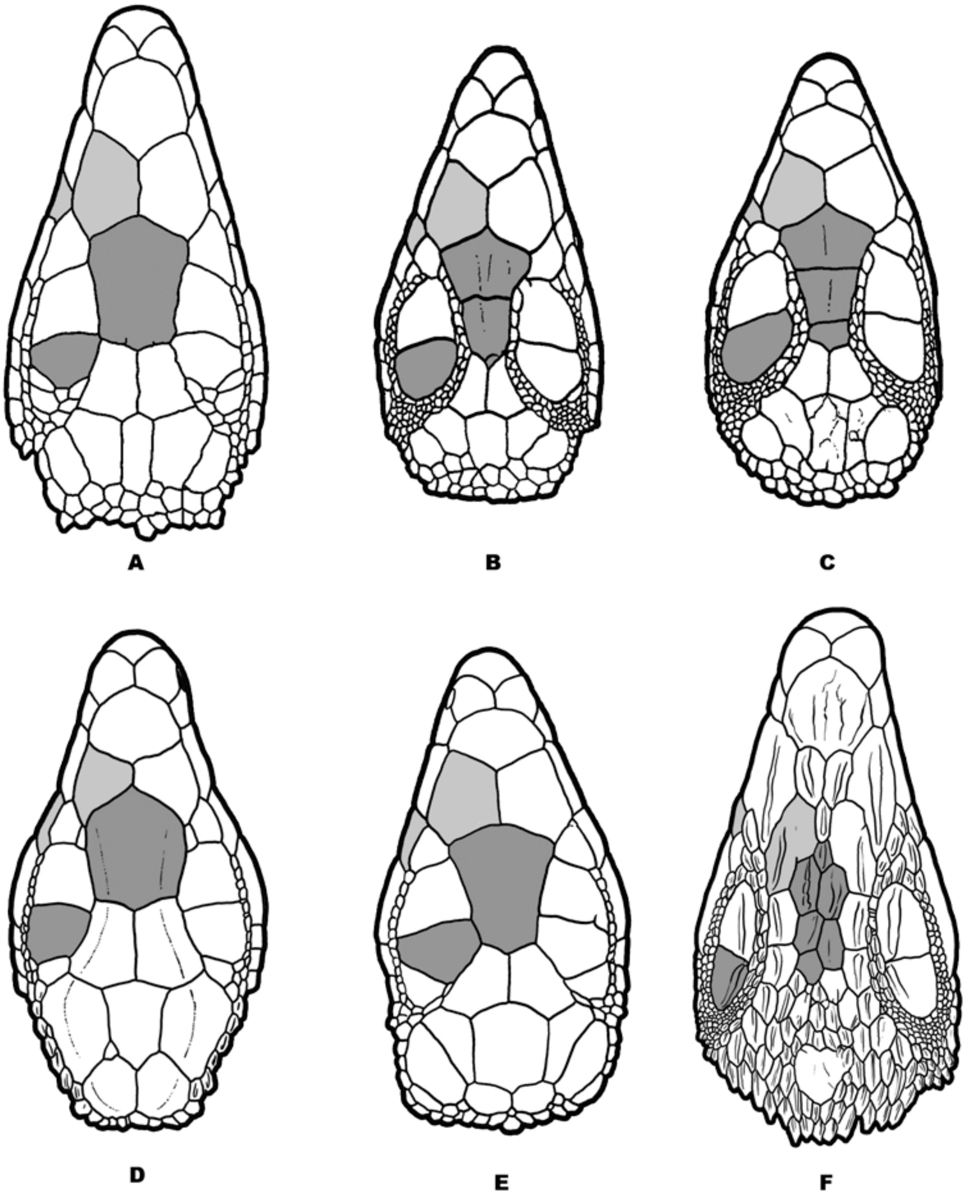

FIGURE 3. Contact between first supraciliary and prefrontal, frontal division, and position of frontal suture relative to third supraocular (characters 8, 9, and 10) in *Ameiva praesignis* (A, USNM 121196), *Ameiva bifrontata* (B, USNM 79219), *A. bifrontata* (C, SDMNH 34945), *Kentropyx altamazonica* (D, UTA 59487), *Cnemidophorus flavissimus* (E, MCZ 50206), and *Holcosus anomalus* (F, AMNH 109693).

Transversely divided frontals characterize taxa of the *Ameiva bifrontata* complex (Fig. 3). This character occurs at low frequencies in some other Teiinae such *A. ameiva* (Ugueto & Harvey 2011) and *Cnemidophorus vittatus*. When transversely divided, the shape of the original frontal scale is evident (9.1–9.2). In contrast, the original shape of the frontal is not evident in the heavily fractured frontal scales of western *Ameiva* and *Callopistes flavipunctatus* (9.3).

10. *Position of Frontal Suture Relative to Third Supraocular*.—The posterior suture of the frontal aligns with the suture between the second and third supraoculars (0), contacts the third supraocular (1), or contacts the second supraocular (2). Based on morphological intermediacy, we ordered this character as follows: 1 > 0 > 2.

Species with state 2 have the frontal suture positioned far anterior, because they have relatively long frontoparietals (Fig. 3).

11. *Frontal Ridge*.—The frontal scale lacks (0) or bears (1) a longitudinal ridge.

Teius, *Dicrodon*, and all taxa of the *Ameiva bifrontata* complex have a prominent, rounded ridge extending longitudinally down the center of their frontal scale (Fig. 4). Some specimens of *A. atrigularis* appear to have a much lower, subtle ridge in the same area (11.0), but other species of the *A. ameiva* complex lack this feature.

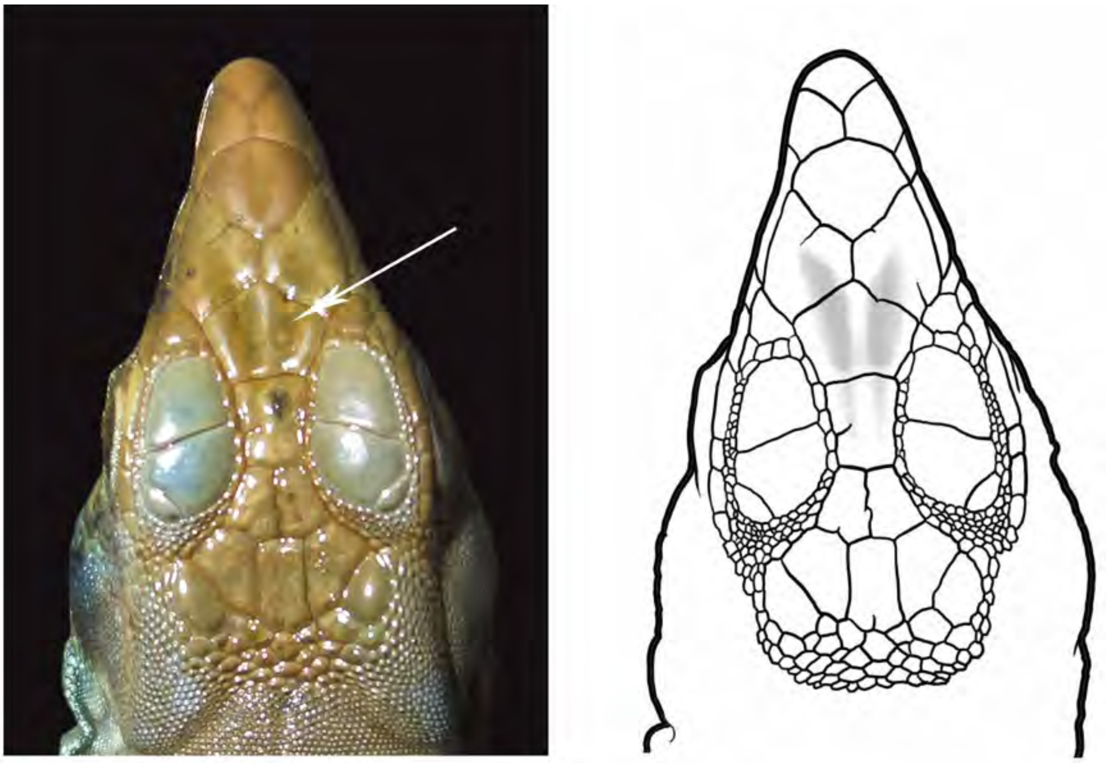

FIGURE 4. Frontal ridge of *Ameiva bifrontata* (FMNH 242238, character 11.1).

12. *Texture of Scales in the Frontoparietal Region*.—Scales of the frontoparietal region (frontal, frontoparietals, and parietals) are mostly smooth (0) or heavily keeled (1).

13. *Frontoparietal Fusion*.—the frontoparietals are paired (0) or fused (1) (Fig. 5).

14. *Key-Hole Shaped Depression of the Frontoparietal Region*.—the frontoparietal region is outwardly convex to flat (0) or bears a keyhole shaped depression (1).

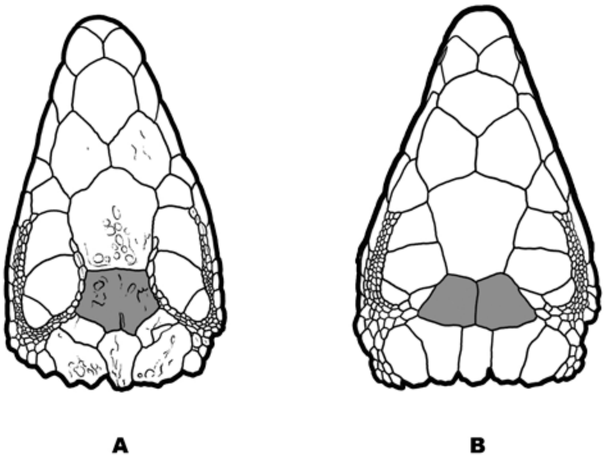

FIGURE 5. Frontoparietal fusion (character 13) of *Dicrodon heterolepis* (A, FMNH 39357) compared to paired frontoparietals of *Cnemidophorus ruthveni* (B, UMMZ 57277).

As noted by Avila-Pires (1995) who illustrated this feature for *Kentropyx pelviceps* (her figure 182), species of *Kentropyx* have a roughly key-hole shaped depression formed by raised lateral edges of the prefrontals (indistinct), frontal, frontoparietals, parietals, and posterior edges of the occipitals (Fig. 6). She noted that this trait is best developed in large specimens.

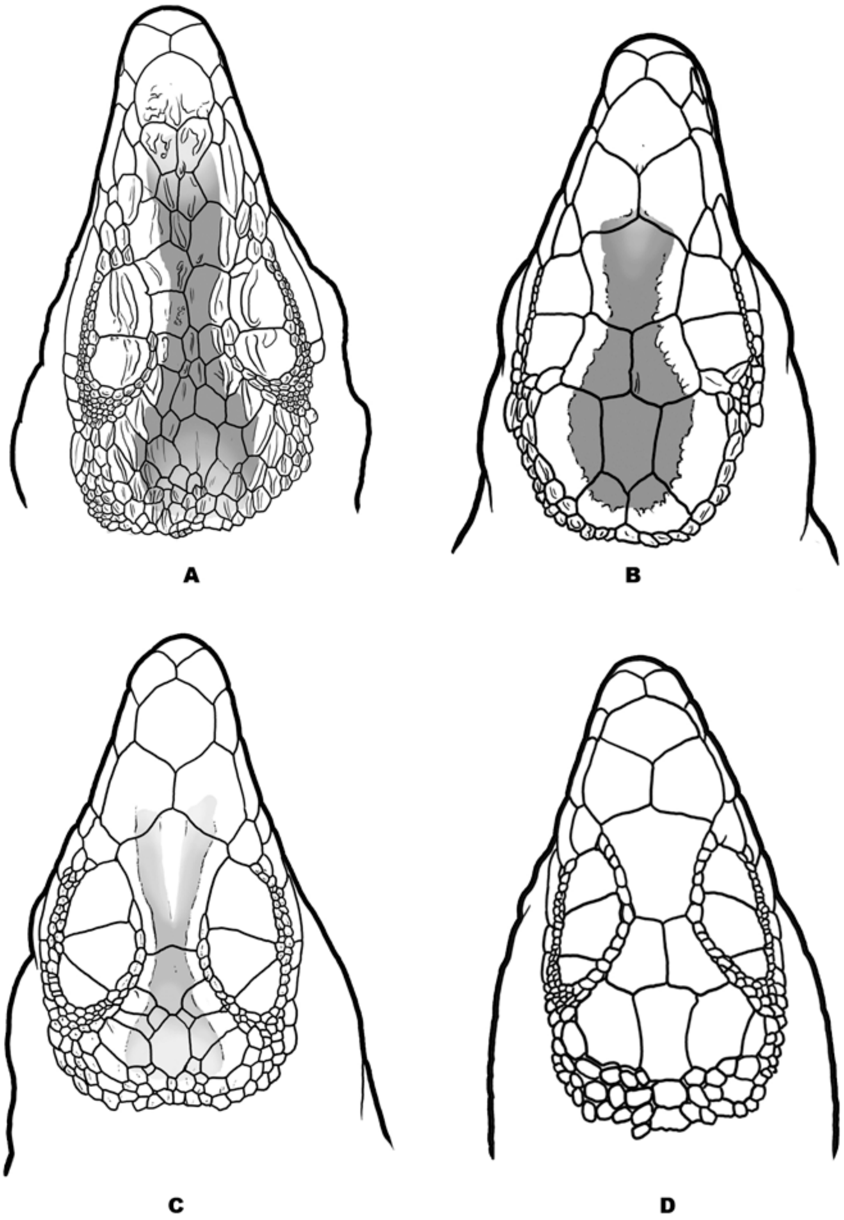

FIGURE 6. Keyhole shaped depression (character 14) of frontoparietal region in *Holcosus septemlineatus* (A, FMNH 27679), *Kentropyx altamazonica* (B, UTA 59488), and *Dicrodon guttulatum* (C, FMNH 53856) compared to convex frontoparietal region of *Ameivula ocellifera* (D, FMNH 44156).

Although these same scales are heavily fractured in western *Ameiva*, aligned, high keels form a similar structure in this group. Cope (1869a, p. 306) noted this fact when describing *A. bridgesii*: "Behind this point they [=*the parietal scales*] are too numerous to homologize, except that a small median occipital is surrounded by a series of tubercular or keeled scales, which are arranged in curved series running behind the occipital." Keels of scales in the central region of the depression are very low. As in *Kentropyx*, the keyhole shaped depression of western *Ameiva* develops during ontogeny. Two small juvenile *A. anomala* (KU 152679–80, SVLs 52 and 47 mm, respectively) have smooth dorsal head scales and the parietal region is outwardly convex. Prominent keels are already present in a slightly larger specimen (KU 152678, SVL 59 mm). In this specimen, high aligned keels on scales just medial to the circumorbitals form the anterior part of the depression walls; a differentiated interparietal is smooth and other scales in the center of the head have much lower keels than the scales forming the key-hole wall. Yet, the parietal region is still outwardly convex in this subadult. In larger specimens, the parietal region has flattened out and the depression is more obvious.

Among other teiids, *Crocodilurus amazonicus* has a well-developed keyhole shaped depression that is identical to the depressions in *Kentropyx*. With some hesitation, we coded *Dicrodon guttulatum* and *Callopistes flavipunctatus* as having state 1. The depression is poorly developed in *D. guttulatum*. As in western *Ameiva*, scales of the frontal and parietal regions of *C. flavipunctatus* are heavily fragmented. Nonetheless, a differentiated and slightly enlarged interparietal scale is usually visible in this species. As in species with obvious keyhole shaped depressions, the interparietal and surrounding scales as well as the center of the head between the eyes is depressed in adult *C. flavipunctatus*.

15. *Longitudinal Division of the Interparietal*.—The interparietal is entire (0) or longitudinally divided into 2–4 scales (1).

Ameiva from the Lesser Antilles have high frequencies of longitudinally divided interparietals (Fig. 7). In this group, the parietals on either side are ordinarily entire and regular. Lesser Antillean *Ameiva* also have noticeably short parietals and interparietals followed by differentiated occipitals. The parietal series in *Ameiva* from the Greater Antilles is comparable in length to that in mainland species (*A. dorsalis, A. exsul, A. taeniura*) or noticeably longer than in mainland species (*A. auberi, A. lineolata, A. maynardi*). We did not develop a separate character for relative length of the parietal series, but suspect that it would be a useful character in future revisions of Caribbean *Ameiva*.

While examining this character in other teiids, we found that *A. undulata* and *A. chaitzami* have a deep longitudinal furrow running almost the entire length of the interparietal. The furrow is continuous with the suture between the frontoparietals. This trait is present in each of the five *A. undulata* we examined and also present in the holotype of *A. chaitzami*. We found a similar furrow in a single specimen of *A. festiva* (UTA R-29347), whereas other *A. festiva* and all other Central American species in our samples lack this character. Stuart (1942) used division of the interparietal to diagnose *Holcosus chaitzami*, however Echternacht (1970, 1971) found division of the interparietal to be a variable character found throughout the genus in Central America. Modern frequency coding methods (Smith & Gutberlet 2001; Wiens 1995), allow high frequencies of longitudinal interparietal division in *H. undulata* and *H. chaitzami* to contribute to analyses of evolutionary relationships of these species.

16. *Arrangement of Parietal Scales*.—The parietals and interparietal comprise three regular scales (0), five regular scales (1), or extensively and irregularly fractured scales (2), or consist of oblique rows of divided parietals (3). This character was unordered in all analyses.

Most teiids have three regular parietals (Fig. 7). Five parietals occur in the *C. ocellifer* complex, northern *Cnemidophorus*, and most *Ameiva*. However, Central American *Ameiva* normally have three parietals. *Ameiva leptophrys* usually has small scales separating the parietals from the frontoparietals and, frequently, small scales separating the posterior portions of the parietals from the interparietal. Three regular parietals (16.0) were present in all of the specimens we examined, although Echternacht (1971, see his figure 7) documented more extensive fracturing of the scales.

In *Teius teyou* and *Dicrodon*, the parietals (Fig. 7) extend obliquely behind the frontoparietals (16.3). The parietals are divided obliquely into 2–3/2–3 scales in most (78%, n = 9) *T. teyou* and 3–4/3–4 scales in *D. guttulatum*. One or two parietals contact the interparietal in *Dicrodon*, whereas a longitudinal row, 1–2 small scales wide, separates the parietals from the interparietal in *T. teyou*. Similarly, small scales separate the last one or two pairs of parietals from the interparietal. Infrequently (20%, n = 10), a small scale may also separate the first pair of parietals from the interparietal in *D. guttulatum*.

In contrast to its congener, *Teius oculatus* ordinarily has three regular parietals (16.0). The frontoparietals are unusually long in this species and constrict the parietals on either side of the interparietal. Moreover, the single parietal on each side contacts the interparietal. Occasional specimens may have five parietals: the left parietal is divided and the right partially so in USNM 65575.

17. *Relative Size of Interparietal*.—The interparietal is smaller than (0), subequal to (1), or larger than each of the flanking interparietals (17.2) (Fig. 8). Based on morphological intermediacy, we ordered this character as follows: 0 > 1 > 2.

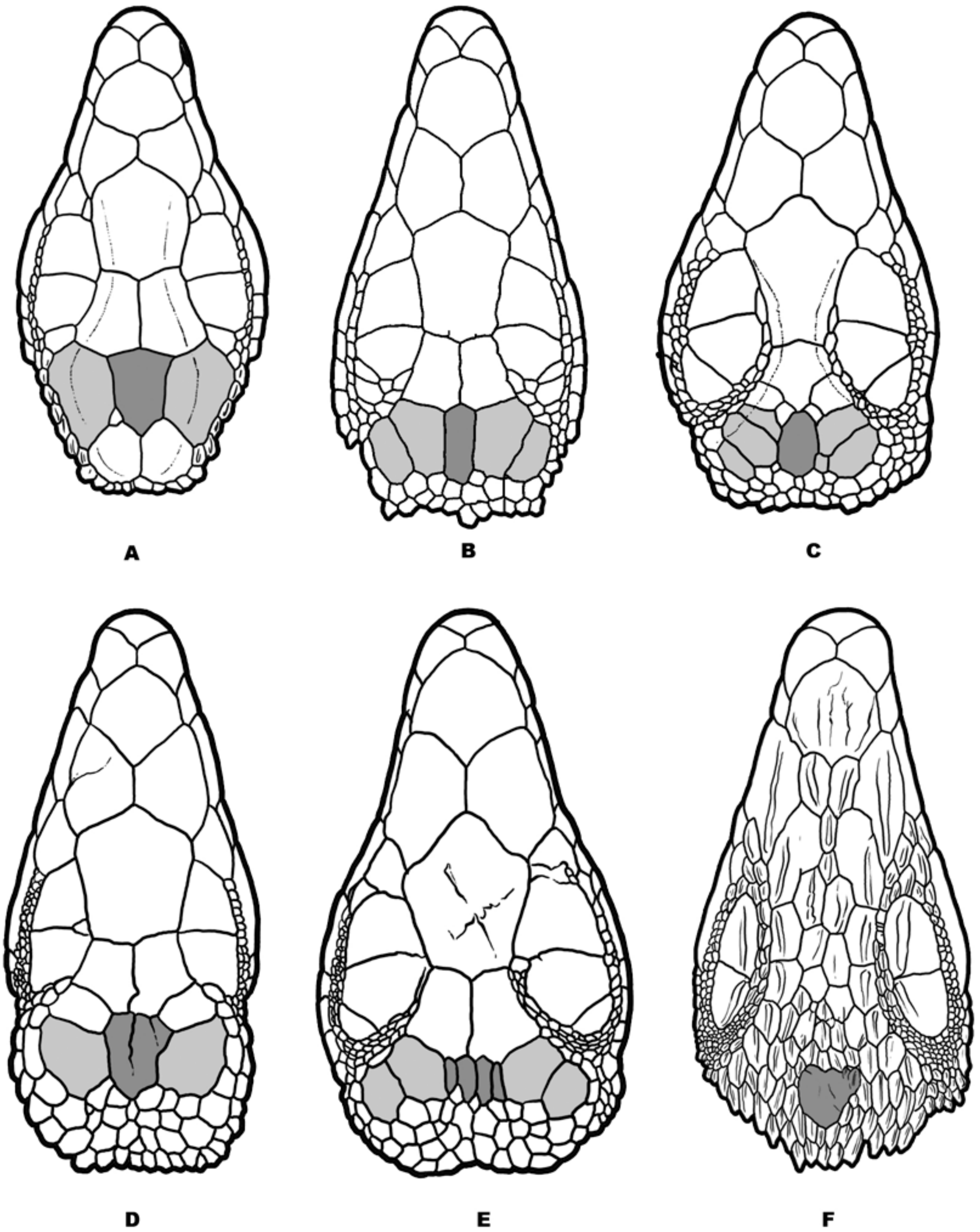

FIGURE 7. Parietals and occipitals (characters 15 and 16) of *Kentropyx altamazonica* (A, UTA 59487), *Ameiva praesignis* (B, USNM 121196), *Dicrodon guttulatum* (C, FMNH 53856), *Holcosus undulatus* (D, UTA 46734), *Ameiva griswoldi* (E, UF 11361, showing longitudinal division of interparietal), and *Holcosus anomalus* (F, AMNH 109694).

This character is not applicable to species with highly fractured parietal scales [character 16.2] such as western *Ameiva* and *Callopistes flavipunctatus*. In most of these species, a discernable interparietal may be visible or completely absent. These same species almost always lack discernable parietals. As mentioned above (16.3), *Dicrodon* and *Teius teyou* have an unusual arrangement of parietal scales and this character is not applicable (17.?) to these species.

18. *Enlarged Pair of Medial Occipitals*.—A pair of noticeably enlarged occipitals in contact with the interparietal is flanked by smaller lateral scales (0), or occipitals form a small to enlarged row of scales bordering the parietals and interparietal (1).

An enlarged pair of occipitals occurs in *Crocodilurus*, *Kentropyx*, and most northern *Cnemidophorus* (Fig. 8).

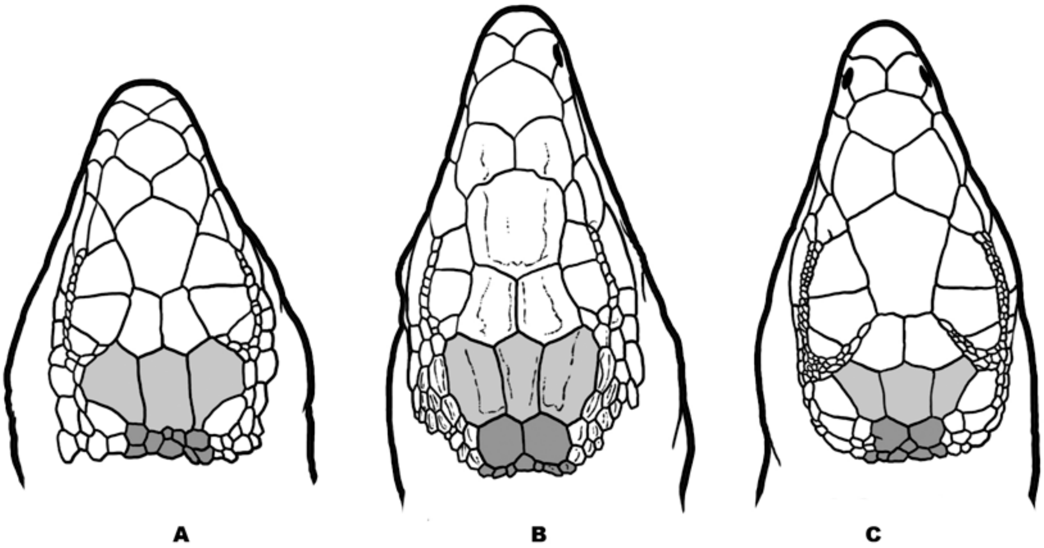

FIGURE 8. Relative size of interparietal, enlarged pair of medial occipitals, and occipitals compared to first row of dorsals (characters 17, 18, and 19) in *Contomastix lacertoides* (A, AMNH 65210), *Kentropyx striata* (B, TCWC 44880), and *Cnemidophorus senectus* (C, MCZ 9916).

19. *Size of Occipitals Compared to First Row of Dorsals*.—The occipitals are larger than (0) or subequal to (1) the scales of the first dorsal row immediately posterior to them.

This character is not applicable to species with heavily fractured parietals, because occipitals cannot be distinguished from fractured scales homologous with the parietal scales of other species.

20. *Number of Occipitals*.—Our counts of occipitals include all scales bordering the parietals and interparietal (Ugueto *et al.* 2009).

This character is not applicable to species with heavily fractured parietals, because the "occipitals" cannot be distinguished from fractured scales homologous with the parietals. In species with one or more supratemporals contacting the parietals (22.1), the supratemporal scale(s) is included in the count of occipitals.

21. *Supratemporals*.—The supratemporal scales are slightly to moderately enlarged (0) or form a distinctive row of large, angulate scales behind the supraciliaries (1).

Large, angulate supratemporals (Fig. 9) occur in *Crocodilurus* and some species of the *Tupinambis teguixin* group.

22. *Supratemporal-Parietal Contact*.—The first supratemporal is separated from the parietals by one or more rows of occipitals (0) or contacts the parietal (1).

In most teiids, one or two small scales separate the supraciliary series from the first of a series of enlarged supratemporal scales (Fig. 9). The first of these scales is usually largest. In Caribbean *Ameiva*, the first supratemporal is positioned in a row of scales bordering the orbit and extends dorsally from the last subocular. Like those scales, the first supratemporal is taller than wide. It contacts the supratemporal in the holotype of *A. wetmorei* and in most *A. lineolata* (67%, *n* = 9) and *A. maynardi* (100%, *n* = 5). However, this condition is rare in other Caribbean species. In our samples, we encountered it on one side only of a single specimen of *A. dorsalis* (UF 18524) and in no other species. *Crocodilurus* has broad contact between the supratemporals and parietals. Otherwise we did not encounter this trait in mainland teiids.

Nasal and Loreal Regions

23. *Rostral Groove*.—A short to moderate rostral groove is absent (0) or extends anteriorly from the anteroventral corner of the nasal (1).

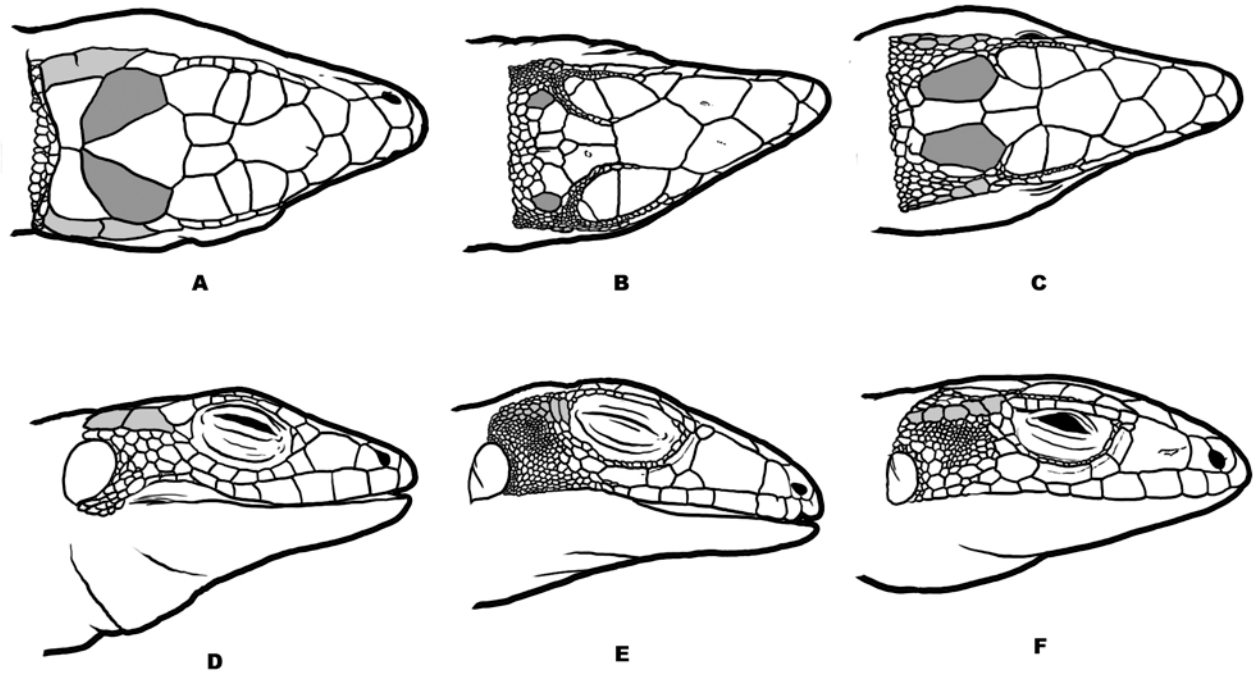

FIGURE 9. Dorsal and lateral views of head showing condition of supratemporals and contact between supratemporals and parietals (characters 21 and 22) in *Crocodilurus amazonicus* (A and D, USNM 200689), *Ameiva plei analifera* (B and E, UF 11404-5), and *Medopheos edracanthus* (C and F, FMNH 9830).

Among the species examined in this study, we found a rostral groove only among certain groups of Teiinae (Fig. 10). The trait is absent from western *Ameiva*, *Kentropyx*, *Teius*, most Central American *Ameiva*, and many northern *Cnemidophorus*.

24. *Position of Nostril Relative to Nasal Suture*.—The nostril is anterior to and not touching the nasal suture (0), mostly anterior to but in contact with the nasal suture (1), or slightly anterior to (2), centered in (3), somewhat posterior to (4), or posterior to the nasal suture (5). Based on morphological intermediacy, we ordered this character as follows: 0 > 1 > 2 > 3 > 4 > 5.

The second, third, and fourth of these states were defined by Markezich *et al*. (1997). We expand their system here to account for variation among other Teiidae (Fig. 10).

25. *Shape of Nostril*.—The nostril is oval (0) or subcircular to subtriangular (1).

Most Teiinae have a narrow, oval nostril oriented dorso-posteriorly. A large, subcircular nostril (Fig. 10) occurs in all Tupinambinae, northern *Cnemidophorus*, *C. lacertoides*, *C. longicauda*, *C. tergolaevigatus*, *Kentropyx lagartija*, *K. viridistriga*, and some Caribbean *Ameiva*.

26. *Count of Loreals*.—Loreals are positioned between the nasal and first subocular (Fig. 11). *Callopistes maculatus* has three loreals; *Dracaena* and species of the *Tupinambis rufescens* group have two loreals; and *Crocodilurus*, species of the *Tupinambis teguixin* group, and the Teiinae have one loreal. This character is not applicable to *Callopistes flavipunctatus*, which has heavily fractured scales in the loreal region. In some Teiinae, a rounded scale is inserted between the loreal and second subocular, separating the first subocular from the supralabials (28.3). As discussed under character 28, we do not consider this scale to be a loreal. Based on morphological intermediacy, we ordered this character as follows: 1 > 2 > 3.

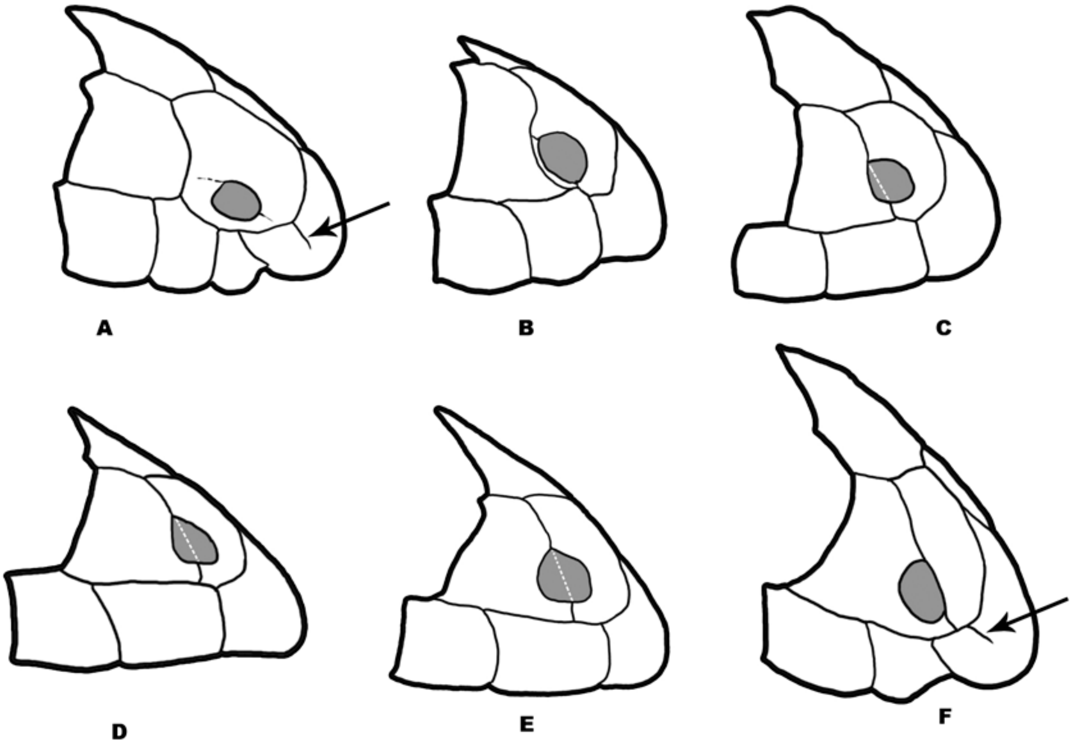

FIGURE 10. Rostral groove (arrow), position of nostril relative to nasal suture, and shape of nostril (characters 23, 24, and 25) in *Aurivela tergolaevigata* (A, AMNH 144520), *Contomastix charrua* (B, AMNH 116321), *Cnemidophorus lemniscatus lemniscatus* (C, USNM 7409), *C. flavissimus* (D, MCZ 50206), *C. arenivagus* (E, AMNH 109992), and *Ameiva bifrontata divisa* (F, UMMZ 55027).

Ocular Series

27. *Number of Supraoculars*.—Counts of supraoculars are a total of both sides and include scales divided by transverse or obliquely transverse sutures (Fig. 12). One or more of the posterior supraoculars are bordered by the supraorbital semicircles, and a row of tiny granular scales may separate the first supraocular from the others in some specimens. Our counts do not include irregularly fractured scales wedged between the supraoculars and frontal or frontoparietal.

28. *First Subocular*.—The first subocular (sensu Ugueto & Harvey 2010, Fig. 13) contacts the supralabials and is entire (0), contacts the supralabials and is longitudinally divided (1), is separated from the supralabials by anterior expansion of the second subocular (2), or is separated from the supralabials by a scale inserted between the suboculars and loreal (3). This character was unordered in all analyses.

We have shown previously (Ugueto & Harvey 2010) that this character suite is relatively conservative, and this fact is borne out by our wider sampling across the Teiidae. Echternacht (1971) and Presch (1973) referred to the scale inserted between the loreal and first subocular (28.3) as a loreal, respectively considering some specimens of Central American *Ameiva* as having two loreals and *Tupinambis* as having 2–3 loreals. We use the term loreal to refer to scales extending between the supralabials and frontonasal and/or prefrontals.

The subocular series of *Kentropyx* can be difficult to interpret. Unlike all other teiids except *Crocodilurus amazonicus*, the subocular keel may be entirely lost or visible only on the first or first and second suboculars in *Kentropyx*. Most species of this genus have a small, elongate first subocular separated from the supralabials by anterior expansion of the second subocular (28.2). This scale is followed by a large second, very long third, and small fourth subocular. *Kentropyx altamazonica* is an exception to this generalization and has state 0. Although these states for character 28 are ordinarily clear-cut, we had to code the character as not applicable (28.?) to *K. pelviceps*. In this species, scales in front of the anterior ocular angle are heavily fractured. Some specimens may have a slightly enlarged scale resembling a subocular, and this scale may or may not be positioned well posterior so that it appears to be part of the series of scales covering the lower eyelid (i.e., an enlarged palpebral rather than a subocular). Like congeners, *K. pelviceps* has four suboculars, but the first is very large, in contact with the supralabials, and widely separated by several scales from the supraciliaries.

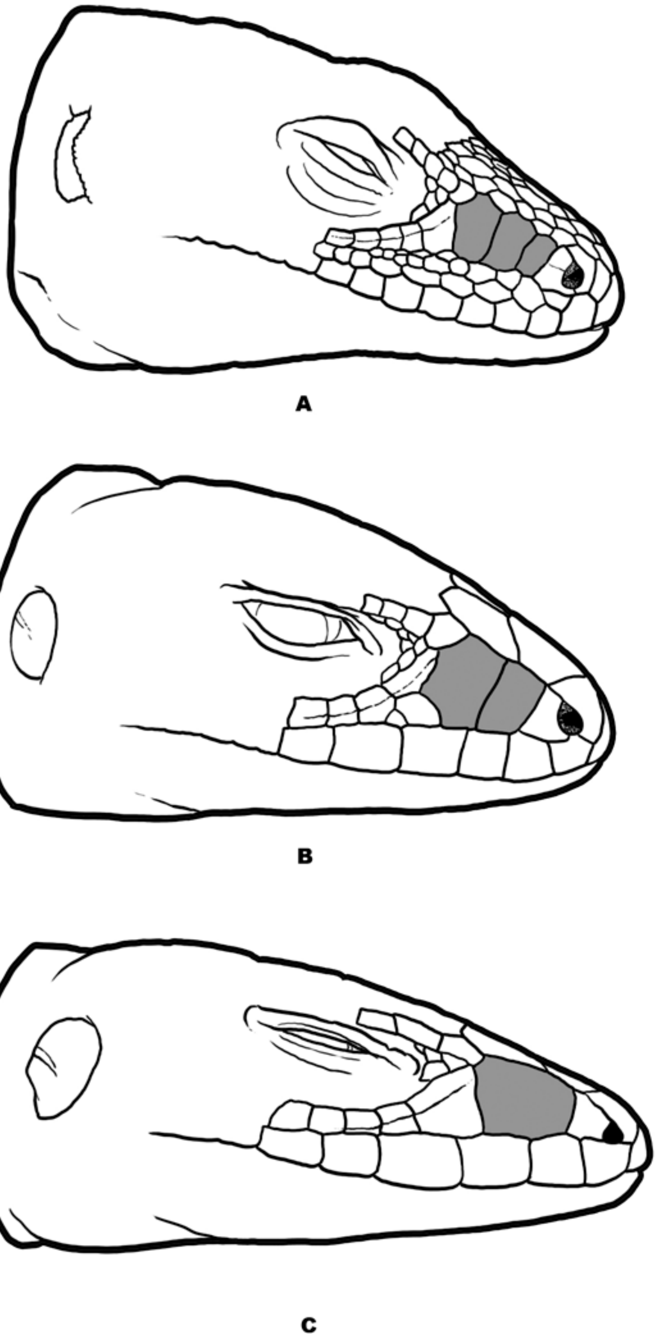

FIGURE 11. Loreals (character 26) of *Callopistes maculatus* (A, FMNH 9934), *Salvator merianae* (B, UTA 59492), and *Tupinambis teguixin* (C, KU 175382).

In *Callopistes maculatus*, 2–3 rows of lorilabials separate the suboculars from the supralabials. We coded this species as having state 0, because the ventral margins of the first and second suboculars are parallel, the first subocular contacts the loreal throughout its length, and there is no anterior expansion of the second subocular. This character is not applicable to *C. flavipunctatus*, which has heavily fractured loreals and suboculars.

Dracaena guianensis has heavily fractured suboculars, nonetheless a large scale abutting the posterior loreal is about the same relative size and in the same position as a similar scale in many Teiinae and species of the *Tupinambis rufescens* group. For this reason, we assigned state 3 to this species.

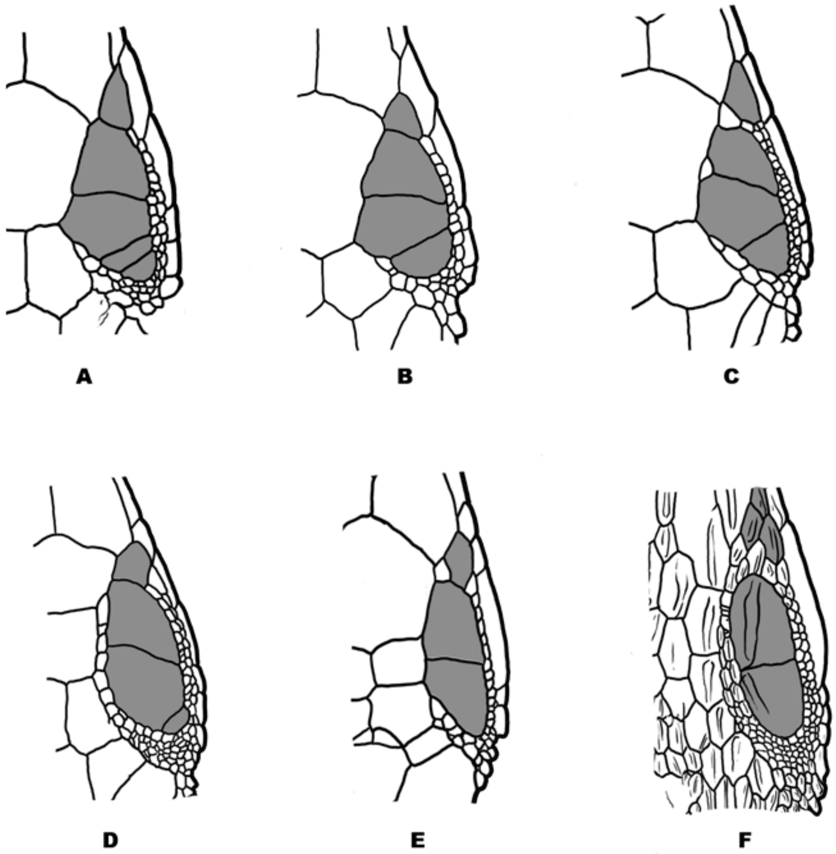

FIGURE 12. Supraoculars, first supraocular division, and contact between second and first supraoculars (characters 27, 29, and 30) in *Cnemidophorus gramivagus* (A, AMNH 97418, characters), *C. gramivagus* (B, AMNH 97411), *C. arubensis* (C, UMMZ 57244), *Ameiva bifrontata bifrontata* (D, SDNHM 34946), *Holcosus leptophrys* (E, FMNH 170102), and *Holcosus anomalus* (F, AMNH 109694).

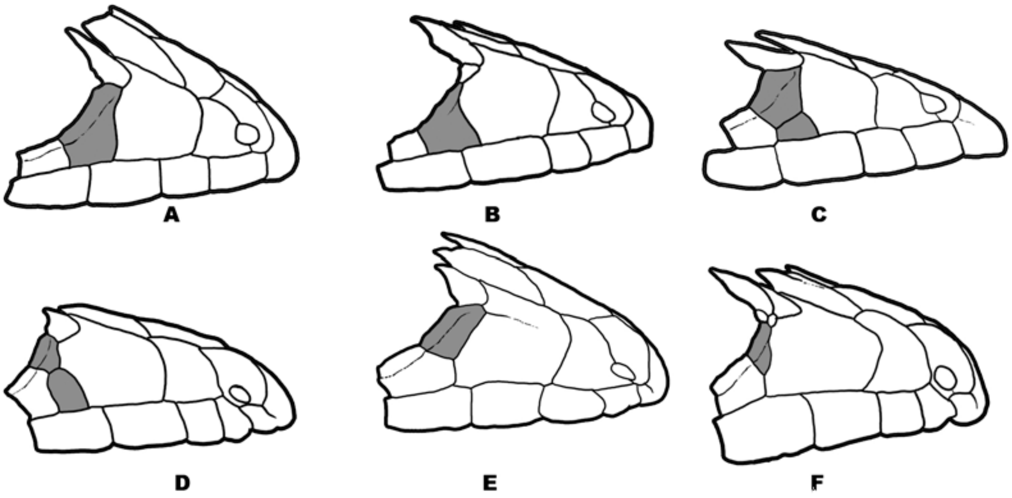

FIGURE 13. Condition of first subocular (character 28) in *Cnemidophorus nigricolor* (A, UCM 45309), *Kentropyx altamazonica* (B, UTA 59487), *C. rostralis* (C, SDNHM 34888), *Dicrodon heterolepis* (D, FMNH 34244), *Ameiva ameiva ameiva* (E, USNM 80615), and *Dicrodon guttulatum* (F, FMNH 53856).

29. *First Supraocular Division*.—The first supraocular is entire (0) or heavily fractured (1).

The first supraocular is positioned dorsal and medial to the first supraciliary. It is ordinarily entire in all teiids except *Callopistes* and western *Ameiva*, which have heavily fractured first supraoculars (Fig. 12).

30. *Contact Between First and Second Supraoculars*.—The first supraocular may be in contact with the second supraocular (0), partially separated from the second supraocular by small scales on either side of the suture (1), or separated from the second supraocular by a complete row of small scales (30.2) (Fig. 12). Based on morphological intermediacy, we ordered this character as follows: 0 > 1 > 2.

When the circumorbital semicircles reach the first supraocular (character 34.1), scales on either side of the suture between the supraoculars partially separate them (character 30.1). Nonetheless, characters 30 and 34 are independent: some species with very short semicircles (characters 34.2.7–3.3) such as *Cnemidophorus vittatus* also usually have a small scale medial to the suture (30.1). At the opposite extreme, a row of scales separates the longitudinally divided scales of the first supraocular (30.2) in *Ameiva bridgesii*, even though the circumorbitals rarely reach the first supraocular in this species (most specimens have 34.2.5-2.7).

31. *Size of Fourth Supraocular Relative to First Supraocular*.—The fourth supraocular is smaller (0), subequal to (1), or larger than (2) the first supraocular.

In teiids with four supraoculars, the first and fourth supraoculars are smaller than the other two. But the size of the fourth supraocular can be rather variable among species. This character is not applicable to specimens with only three supraoculars. Occasional anomalous specimens have transversely or obliquely divided fourth supraoculars on one or both sides. We compared the first supraocular to the combined fourth and fifth in these anomalous specimens.

32. *Number of Rows of Lateral Supraocular Granules*.—Teiids have up to five longitudinal rows of small granular scales between the supraciliaries and supraoculars. Herein, we refer to these scales as “lateral supraocular granules” (Fig. 14). Previously, we assigned discrete states to the number of rows (Ugueto & Harvey 2010; Ugueto *et al.* 2010), however we counted the number of rows in this study. At the suture between the second and third supraocular, the number of rows frequently increases by one (i.e., a “partial row” is added). Partial rows were counted as one-half a row. That is, we scored species with partially doubled rows such as some species of *Cnemidophorus* (Ugueto *et al.* 2010) as having 1.5 rows. *Callopistes flavipunctatus* is unusual in having 4–5 rows of granules, reducing to 2–3 rows lateral to the last supraocular.

33. *Count of Lateral Supraocular Granules*.—Our counts include all scales between the supraciliaries and supraoculars on both sides of the head (Fig. 14).

The lateral supraocular granules do not include scales forming a partial or complete oblique row (30.1–30.2) between the first and second supraoculars of some species.

34. *Anterior Extent of Circumorbital Semicircles*.—Anterior extent of the circumorbital semicircles (Fig. 14) has long been used to diagnose teiids. When coding this character, we used a system of semicontinuous codes similar to the digital webbing formulae commonly used when describing anurans. State “1” was assigned to species with circumorbitals reaching the posterior border of the first supraocular, “2” to species with circumorbitals reaching the second supraocular, etc. Intermediate conditions were assigned thirds: thus, “2.3” for circumorbitals extending beyond the middle of the third supraocular but not reaching the posterior border of the second supraocular, “2.5” for scales reaching the middle of the third supraocular, and “2.7” when the scales pass the posterior border of the third supraocular but do not reach the middle of the scale. This character causes some difficulties in specimens without four supraoculars. In western *Ameiva*, both the first and fourth supraocular are lost through fracturing of the scales. Our system is nonetheless applicable to these species, because the circumorbitals normally extend parallel to the second or third supraocular. On the other hand, the fourth supraocular is frequently divided transversely in some *Cnemidophorus* such as *C. vittatus*. When this condition occurs, we scored this character as though the scale was entire (i.e., we did not assign a number greater than 4).

Callopistes flavipunctatus is unique among teiids in having two complete rows of circumorbitals between the supraoculars and scales of the frontal region. A single row of circumorbitals extends to the posterior border of the first supraocular in *C. maculatus*. Other Tupinambinae usually have only 1–3/1–3 circumorbitals restricted to the posterior border of the fourth supraocular (34.4) or have no supraocular semicircles (34.?).

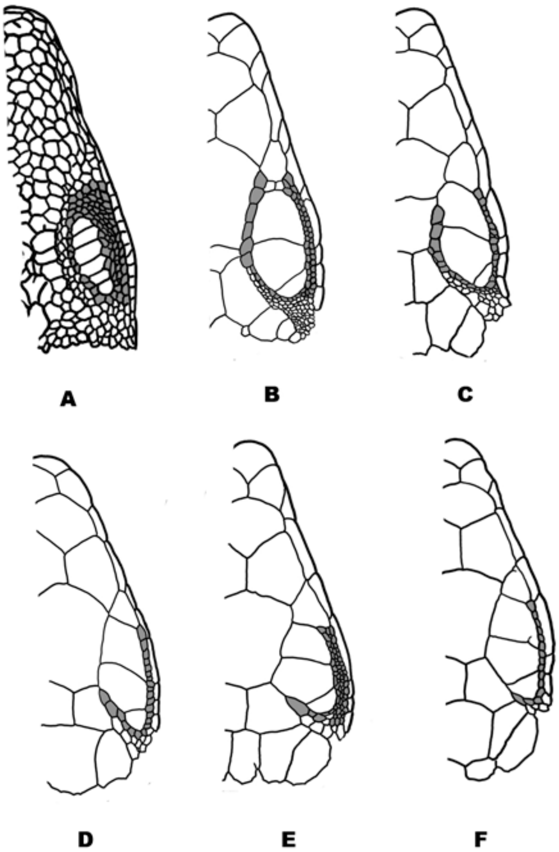

FIGURE 14. Rows of lateral supraocular granules and anterior extent of circumorbital semicircles (characters 32 and 34) in *Callopistes flavipunctatus* (A, FMNH 41584), *Teius teyou* (B, FMNH 195982), *Ameiva bifrontata divisa* (C, UMMZ 55027), *Aspidoscelis burti* (D, UMMZ 105426), *Cnemidophorus ruthveni* (E, UMMZ 57277), and *C. flavissimus* (F, MCZ 50206).

35. *Number of Circumorbital Scales*.—Total number (combined count of both sides) of scales bordering supraoculars medially.

36. *Count of Supraciliaries*.—In most Teiinae, supraciliaries extend from the loreal almost to a large, rounded scale (absent in *Teius*) in the temporal region. Usually, a small, longitudinally divided scale separates the rounded temporal from the last supraciliary.

37. *Contact Between First Subocular and Supraciliary*.—The first subocular and supraciliary are separated by a row of small granular scales (0) or in contact (1) (Fig. 15).

38. *Pattern of Supraciliary Fusion*.—The supraciliaries (Fig. 15) are more or less subequal (0), the second is greatly elongate (1), the first is long (2), the first is small and the second and third are enlarged and subequal (3), or the third is greatly elongate (4). This character was unordered in all analyses.

Among the Tupinambinae, the supraciliaries are numerous and more or less subequal (38.0). This condition persists in some species of Teiinae such as *Cnemidophorus longicauda*. Nonetheless, several patterns of apparent supraciliary fusion have evolved within the Teiinae. In western and some Central American *Ameiva*, the first supraciliary is small and the second greatly elongated. In these species, the second is as long as all the other supraciliaries combined (38.1). In *Cnemidophorus* and *Kentropyx*, the first supraciliary is long, greater than one-half as long as or subequal to the second (38.2). In cis-Andean species of *Ameiva*, the first supraciliary is small, whereas both the second and third are enlarged and roughly subequal in size (38.3). Finally, in some Central American *Ameiva*, the first and second supraciliaries are small and the third is greatly elongated (38.4). These supraciliary patterns seem to be relatively conservative evolutionarily and exhibit little intraspecific variation.

Ameiva festiva has state 1, whereas two species often thought to be closely related to it (*A. leptophrys* and *A. niceforoi*) have greatly elongate third supraciliaries (38.4). This observation suggests that pattern 4 evolved through fracturing of the long second supraciliary (38.1). We coded *Aspidoscelis tigris* as having state 4, even though about one-half of the specimens had elongate fourth rather than third supraciliaries.

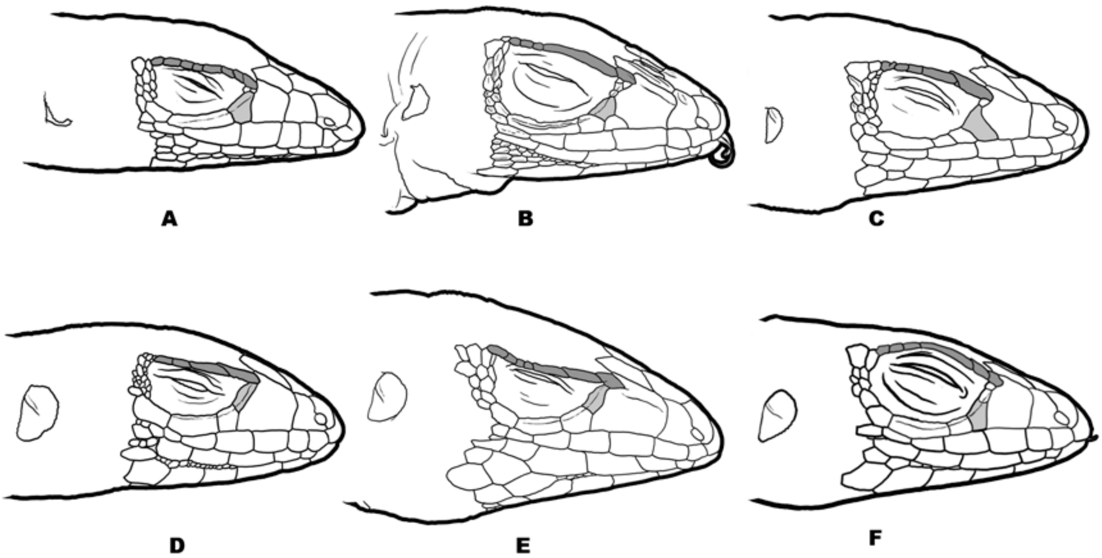

FIGURE 15. Contact between first subocular and supraciliary and pattern of supraciliary fusion (characters 37 and 38) in *Aurivela tergolaevigata* (A, AMNH 144524), *Holcosus anomalus* (B, AMNH 111042), *Kentropyx altamazonica* (C, UTA 59487), *Ameivula ocellifera* (D, FMNH 44156), *Ameiva praesignis* (E, USNM 217029), and *Holcosus niceforoi* (F, KU 210030).

39. *Subocular Keel*.—An angulate, continuous keel extends from the first subocular to the subocular under the eye (0) or is absent (1).

The subocular keel is well developed in all teiids except for *Crocodilurus* and *Kentropyx*. *Kentropyx striata* has a weak keel on the first two suboculars, but not a keel that extends below the eye (39.1).

40. *Subocular Count*.—A scale behind the elongate subocular below the eye is considered to be the last subocular.

Auditory Region

41. *Enlarged Scales in Front of Auditory Meatus*.—A patch of scales in front of the auditory meatus is not enlarged (0), slightly enlarged (1), or distinctly enlarged (2). Based on morphological intermediacy, we ordered this character as follows: 0 > 1 > 2.

42. *Auricular Flap*.—A subtriangular auricular flap is absent (0) or projects posteriorly and ventrally from the anterodorsal edge of the external auditory meatus (1).

The auricular flap of *Cnemidophorus longicauda* and *C. tergolaevigatus* projects over the ear from the dorsal and anterior edge of the auditory meatus (Fig. 16). An analogous structure, the preauricular fold, has evolved in *Callopistes* (character 43.1) and consists of a vertical fold of skin covered in granular scales that partially projects over the anterior margin of the meatus (Fig. 16). The functions of these skin flaps are unknown, however, they may have evolved to prevent sand from getting into the meatus, either during burrowing or during sandstorms. Both flaps occur in species inhabiting sandy desert environments.

43. *Preauricular Fold*.—A vertical fold of skin in front of the external auditory meatus is absent (0) or partially projects posteriorly to cover the meatus (1).

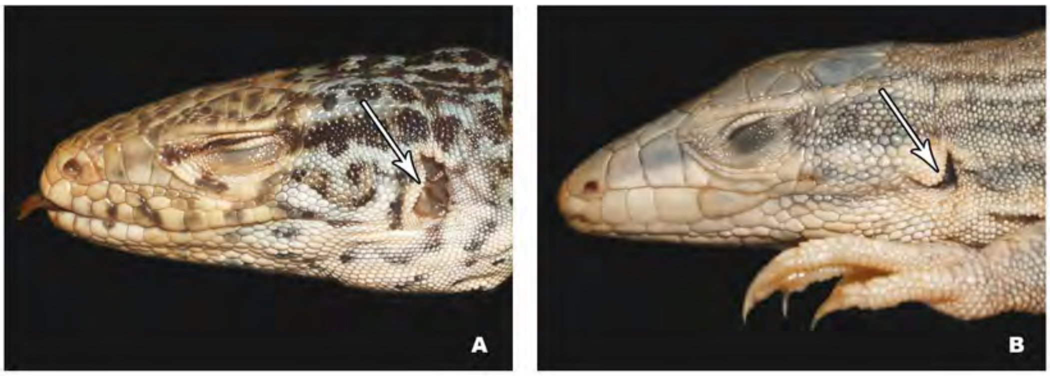

FIGURE 16. Preauricular fold of *Callopistes maculatus* (A, arrows, FMNH 5877, character 43) and auricular flap of *Aurivela tergolaevigata* (B, AMNH 144524, character 42).

Labial Series and Chin

44. *Ventral Margin of First Supralabial*.—The ventral margin of the first supralabial is straight (0), curved (1), or "toothy" (2). Based on morphological intermediacy, we ordered this character as follows: 0 > 1 > 2.

The ventral margin of the first supralabial in the Tupinambinae is straight as in most, if not all, gymnophthalmids. "Toothy" first supralabials are derived structures of many Teiinae. The ventral margin of these short scales slopes posteriorly and bears a tooth-shaped ventral projection just anterior to the posterior scale suture (Fig. 17).

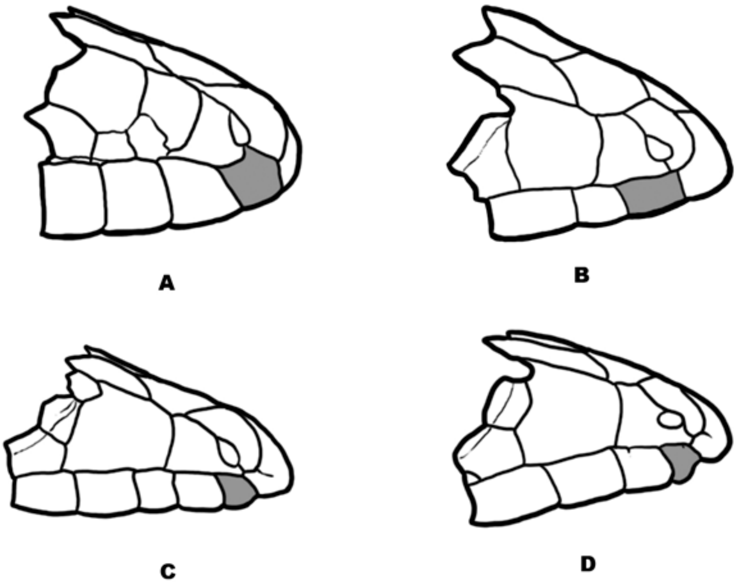

FIGURE 17. Ventral margin and relative size of first supralabial (characters, 44 and 45) in *Salvator rufescens* (A, MVZ 128169), *Cnemidophorus lemniscatus gaigei* (B, AMNH 106218), *Ameiva concolor* (C, UMMZ 59192), and *Ameiva bifrontata* (D, UMMZ 107086).

45. *Relative Size of First Supralabial*.—The first supralabial is smaller than (0), subequal to (1), or longer than (2) the second supralabial. Based on morphological intermediacy, we ordered this character as follows: 0 > 1 > 2.

The first supralabial is usually longer than the second (45.2) in northern *Cnemidophorus*, whereas it is smaller than or subequal to the second in other teiids. Except in *Callopistes*, the first supralabial is longer than tall. In *Callopistes maculatus*, it is about as long as the second (45.1). However, this scale is taller than the other supralabials, extending dorsally to contact the nasal and interrupting the row of lorilabials.

46. *Count of Supralabials*.—The rictus of preserved teiids is usually difficult to locate, and, not surprisingly, methods for counting labials have varied widely. In teiids, the longest subocular is positioned below the center of the eye. We considered the last supralabial to lie below the posterior end of this elongate subocular scale. For this study, we combined counts from both sides of each specimen.

47. *Count of Infralabials*.—The last infralabial is the scale immediately below the last supralabial. For this analysis, we combined counts from both sides of each specimen. Infralabials tend to be subequal among teiids. However, in western *Ameiva*, the third infralabial is usually about as long as the first, second, and fourth combined. Elongation of this scale is most pronounced in *A. bridgesii*.

48. *Condition of First Pair of Chinshields*.—The first pair of chinshields (Fig. 18) are in contact with the infralabials (0), partially separated from the infralabials by a row of granules (1), or completely separated from the infralabials by a row of granules (2). Based on morphological intermediacy, we ordered this character as follows: 0 > 1 > 2.

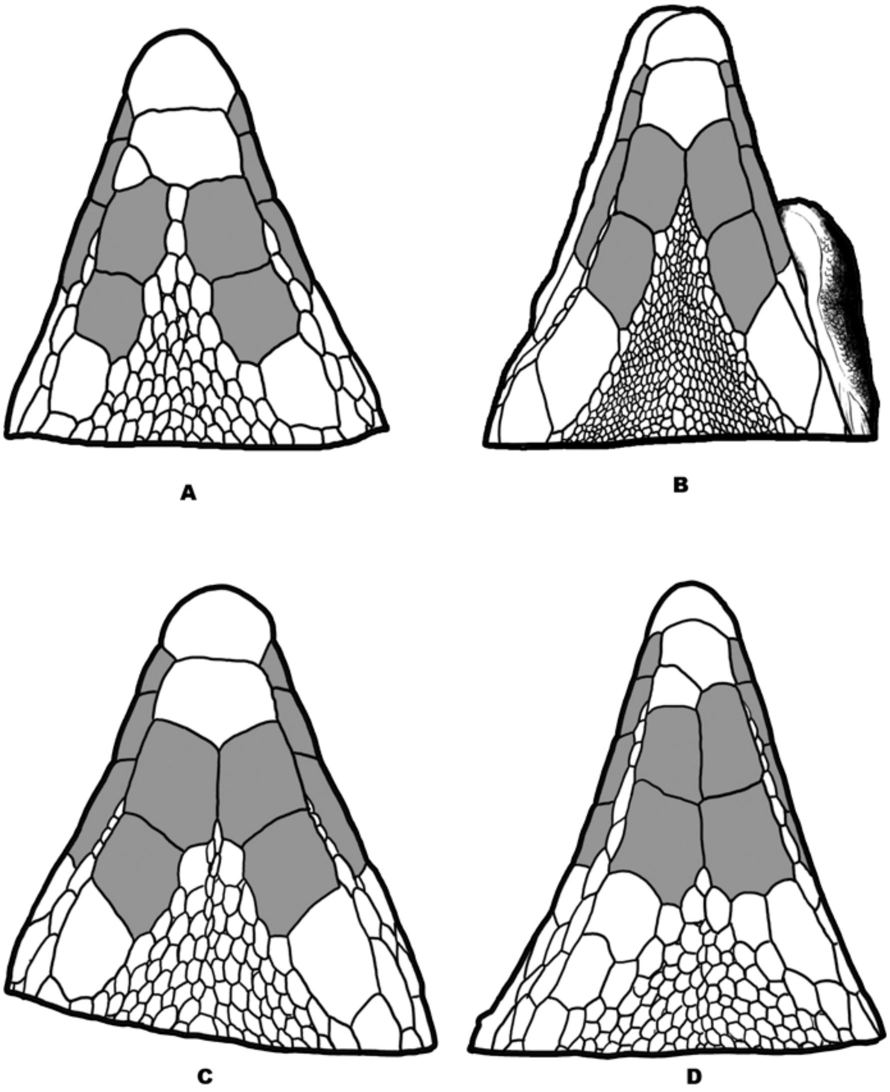

FIGURE 18. Morphology of the chin, showing medial contact between chinshields and contact between the chinshields and infralabials (characters, 48 and 49) in *Contomastix vittata* (A, UTA 58475), *Holcosus festivus* (B, FMNH 43826), *C. charrua* (C, AMNH 116321), and *Aurivela tergolaevigata* (D, AMNH 144525).

49. *Contact Between First Pair of Chinshields*.—The first pair of chinshields do not contact one another medially (0), form a suture shorter than half their length (1), form a suture greater than or equal to half their length (2), or are in complete contact and followed by contact between the second pair of chinshields (3). Based on morphological intermediacy, we ordered this character as follows: 0 > 1 > 2 > 3.

Most teiids have states 1 or 2 with 0 and 3 appearing at low frequencies within a few species. On the other hand, all specimens of *Callopistes, Dracaena, Cnemidophorus longicauda,* and *C. tergolaevigatus* have state 3. Gymnophthalmids also almost always have state 3, and this condition is almost certainly the plesiomorphic state of teiids.

50. *Interangular Sulcus*.—An interangular sulcus is absent (0) or present (1).

Vanzolini and Valencia (1965) described this structure as "similar" to the intertympanic sulcus, but "uniting the angles of the lower jaw." In *Dracaena guianensis*, the interangular sulcus is well defined (Fig. 19) and consists of a complete row of granular scales. One specimen of *T. teguixin* (e.g., KU 175382) has a shallow fold (really just a line) in this region, however no small scales are present in the fold (50.0) and we are not even sure if the fold is natural or some artifact of preservation in this specimen. All other specimens of *Tupinambis* we examined lack these scales and there is no trace of the sulcus (50.0; contra Teixeira 2003, and Vanzolini & Valencia 1965). Since all other teiids lack an interangular sulcus, this character appears to be an autapomorphy of *Dracaena*.

51. *Count of Anterior Gulars*.—We counted these scales in a straight line from the pair of infralabials in medial contact to the interauricular crease or to a straight line adjoining the posterior edges of the auditory meati in species lacking a crease. This character is not applicable to species with a gular patch, because large plate-like scales of the patch overlap the interauricular line.

52. *Gular Patch*.—A medial patch of greatly enlarged scales (Fig. 20) flanked by much smaller granular scales is absent (0) or present (1) in front of the antegular fold.

In most cnemidophorines, medial gulars just anterior to the interauricular crease and antegular fold are at least slightly enlarged and sometimes these scales form patches of enlarged scales (e.g., in some specimens of the *Ameiva ameiva* complex, Ugueto & Harvey 2011). A patch in front of the crease is also particularly well developed in *A. edracantha*. Character 52.1 refers to the greatly enlarged scales in Central American *Ameiva*, which extend both in front of and well behind the posterior margin of the auditory meatus and include both posterior and anterior gulars. These Central American *Ameiva* also have an interauricular crease, so that extension of the patch behind the crease is clearly evident.

A similar patch of enlarged scales is present in *Kentropyx striata* and *K. borkiana*. The gulars of *Kentropyx* including those of the patch are keeled, and the patch is not as obvious. *Kentropyx* also lacks an interauricular crease, but the patch clearly extends well posterior of the auditory meatus.

53. *Count of Posterior Gulars*.—We counted these scales from the interauricular crease to the antegular fold (Ugueto & Harvey 2011).

54. *Intertympanic Sulcus*.—An intertympanic sulcus is absent (0), present and incomplete medially (1), or complete medially (2).

The intertympanic sulcus (sensu Vanzolini & Valencia 1965)[1] is a row of small granular scales within the interauricular crease (Fig. 19). In specimens of *Dracaena guianensis*, the sulcus extends for only a short distance ventrally (54.1). In the middle of the gular region of this species, the anterior and posterior gulars are the same size (no interauricular crease present). Although Vanzolini and Valencia (1965) scored *Tupinambis* as lacking an intertympanic sulcus, they apparently based this report on species of the *T. rufescens* group. A medially complete intertympanic sulcus marked by small granular scales is well developed and obvious in *Callopistes*, *Crocodilurus*, and species of the *T. teguixin* group.

55. *Transition at Intertympanic Crease*.—Larger anterior gular scales may (0) or may not (1) undergo a sharp transition to smaller posterior gular scales along a line (=crease) between the posterior edges of the external auditory meati.

Some species such as *Ameiva septemlineata* have slightly larger anterior gulars positioned medially in the gular region. However, lateral to these scales, the anterior and posterior gulars are subequal, so that there is no

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[1] We prefer to use Vanzolini and Valencia's (1965) original terminology for this structure rather than "supernumerary antegular fold" (Avila-Pires 1995), because the structure is not a skin fold, but a sulcus containing a row of small scales.

sharp transverse line connecting the posterior edges of the auditory meati. The slightly enlarged medial scales may be homologous with the distinct gular patch of some Central American *Ameiva*.

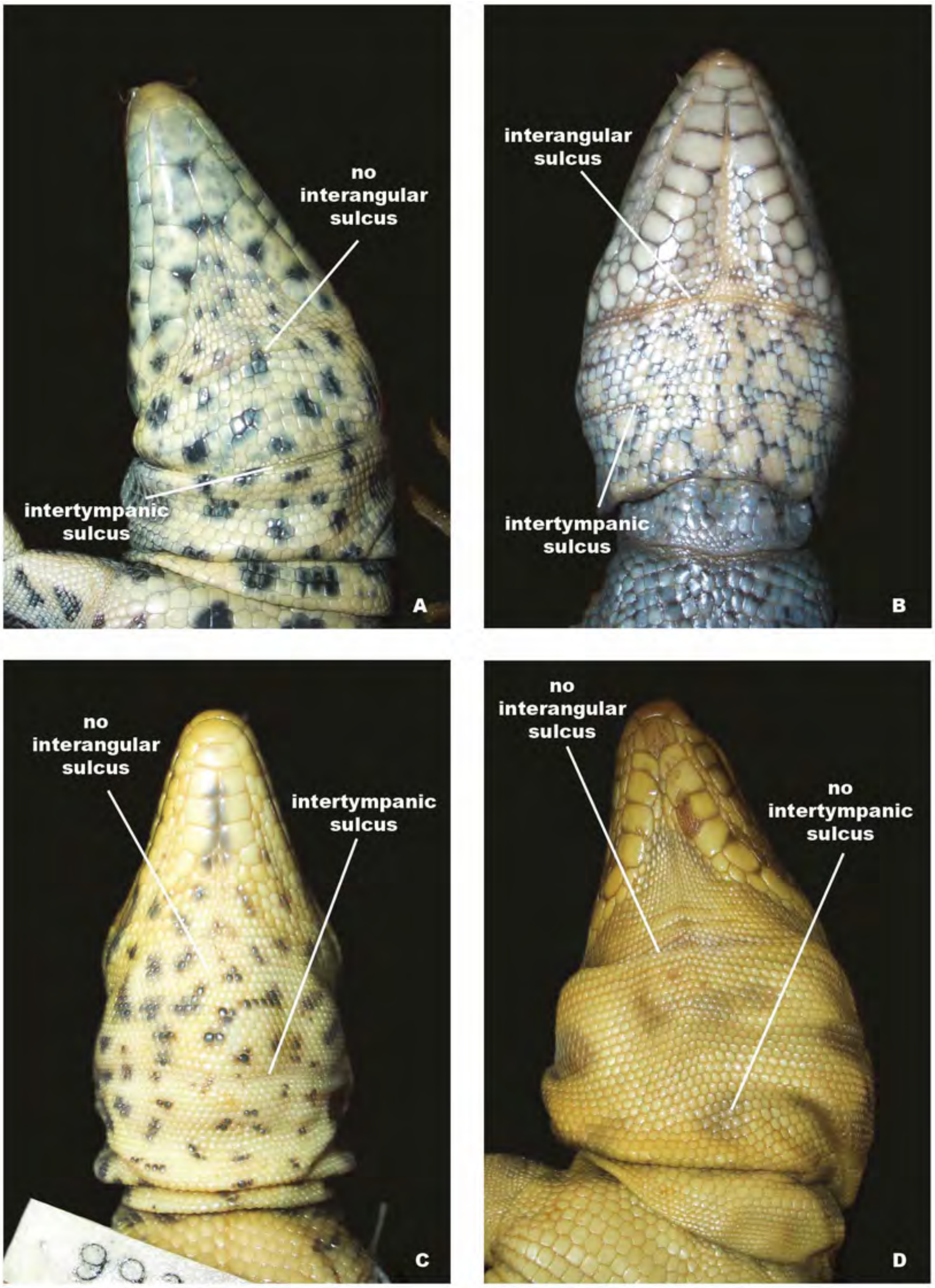

FIGURE 19. Interangular and intertympanic sulci (characters, 50 and 54) of *Tupinambis palustris* (A, UTA 59491), *Dracaena guianensis* (B, TCWC 38121), *Callopistes maculatus* (C, FMNH 9934), and *Salvator rufescens* (D, MVZ 128169).

This character is apparently independent of the intertympanic sulcus (character 54). Species of the *Tupinambis teguixin* group have a clearly defined intertympanic sulcus and a clear transition from larger anterior to smaller posterior gulars. However, scales on either side of the sulcus are subequal in both *Dracaena* and *Crocodilurus*.

56. *Enlargement of Mesoptychials*.—The mesoptychials are not or slightly enlarged (0), moderately enlarged (1), or greatly enlarged (2).

Mesoptychials (Fig. 20) are not enlarged in most Tupinambinae, although they are slightly enlarged in *Crocodilurus*. On the other hand, most Teiinae have at least some moderately enlarged scales in the center of the mesoptychium. As defined here, state 1 encompasses a broad range of sizes; thus, it is the extreme values 0 and 2 that are most likely to contain phylogenetic information. Arrangement and size of mesoptychial scales in the *Ameiva ameiva* complex and several species of Antillean *Ameiva* are surprisingly variable (see also Ugueto & Harvey 2011), whereas many other teiids, notably *Cnemidophorus*, showed relatively little intraspecific variation. Nonetheless, when present, moderately enlarged scales are located medially on the mesoptychium, often interspersed among smaller scales. Among Antillean *Ameiva* we examined, *A. griswoldi* is unique in having a particularly broad transverse row of moderately enlarged mesoptychials, well differentiated from the scales around it. Greatly enlarged mesoptychial scales are relatively rare, occurring in most Central American *Ameiva*, *A. orcesi*, *A. septemlineata*, and *Kentropyx striata*. We assigned state 1 to *A. leptophrys* and *A. quadrilineata*, because their mesoptychials are noticeably smaller than those of other Central American species, however their enlarged mesoptychials form a sharply defined transverse row (57.1) and are noticeably larger than the mesoptychials of cis-Andean and Antillean *Ameiva*.

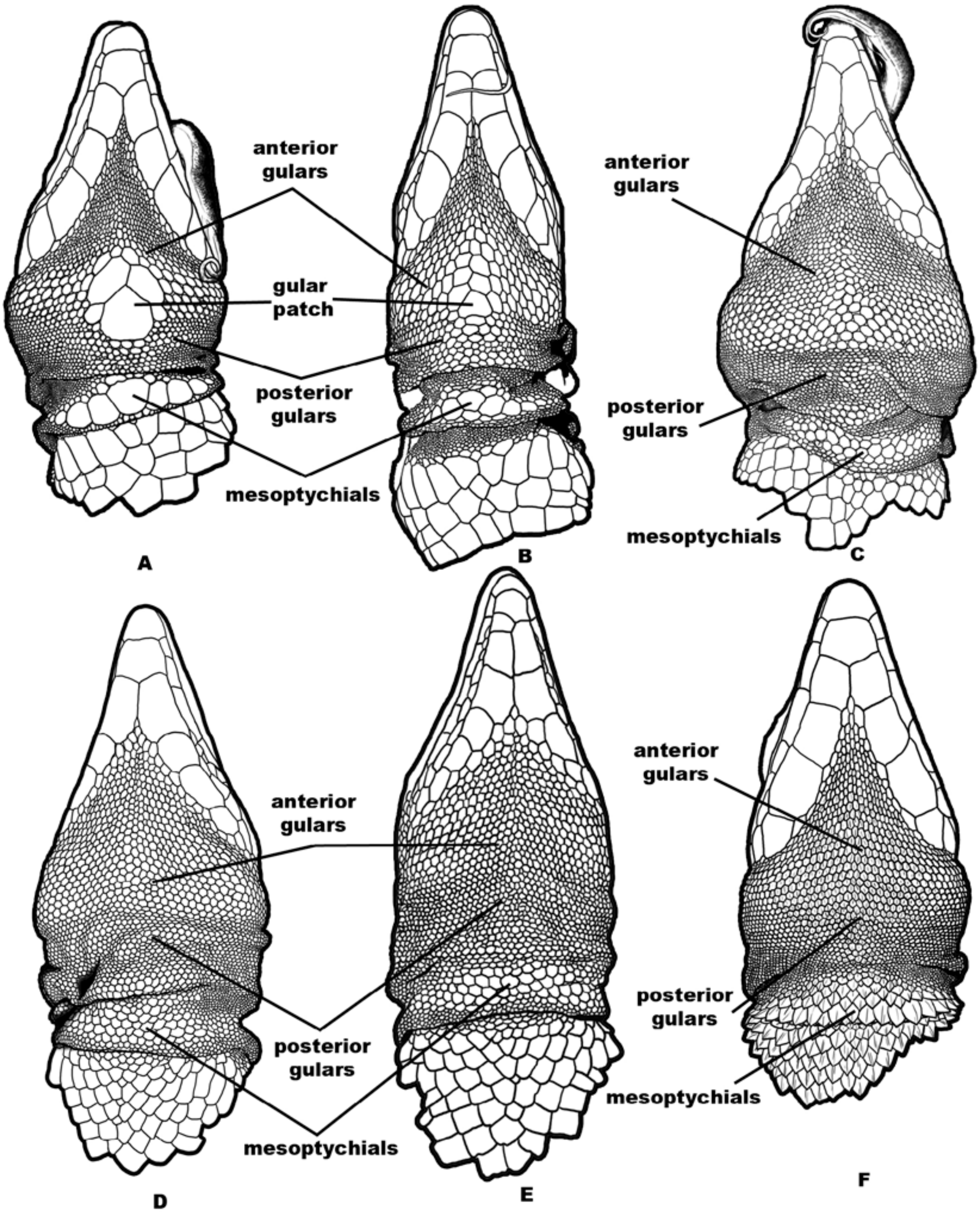

FIGURE 20. Morphology of the gular region and mesoptychium (characters, 51, 52, 53, 56, 57 and 58) of *Holcosus festivus* (A, FMNH 43826), *Holcosus leptophrys* (B, FMNH 170101), *Ameiva atrigularis* (C, USNM 217052), *Cnemidophorus rostralis* (D, SDNHM 34890), *Aurivela tergolaeviagata* (E, AMNH 144520), and *Kentropyx altamazonica* (F, UTA 59487) .

57. *Differentiation of Transverse Row of Mesoptychials*.—A transverse row of mesoptychials (Fig. 20) is not differentiated or bordered by mesoptychial scales that gradually increase approaching the row (0) or differentiated and bordered anteriorly by a sharp transition from very small scales (1).

58. *Serrated Edge of Gular Fold*.—Enlarged scales of the mesoptychium overlap the gular fold, giving the mesoptychium a serrated posterior edge (0) or are separated from the gular fold by granules (1).

Axial Scalation

59. *Dorsal Keeling*.—The dorsals are smooth (0) or keeled (1).

The dorsal scales of teiids are frequently referred to as "granules." However, this terminology masks considerable interspecific diversity. The dorsals are oval (i.e., Tupinambinae, *Ameiva lineolata*, *Cnemidophorus tergolaevigatus*, and *C. longicauda*) to subtriangular (most Teiinae) to phylloid (*Kentropyx*). Distinctly keeled dorsals occur in *Kentropyx*, western *Ameiva*, *Dicrodon heterolepis*, *Crocodilurus*, and *Dracaena*. The area in the center of dorsals is rounded in Central American *Ameiva*, but not keeled. *Tupinambis* is generally thought to have flat, smooth dorsals. Although true for the *T. teguixin* group, dorsals on the posterior body and rump are weakly keeled in species of the *T. rufescens* group. Among the specimens we examined, keeling is best developed in *T. merianae* where keeled scales extend anteriorly to 20 transverse dorsal rows in front of the thigh. In the two adult *T. rufescens* we examined, the keels terminate at the posterior border of the thigh.

60. *Condition of Apical Granule and Bristly Dorsals*.—The apical granule is small (0) or the apical granule is enlarged and both the granule and dorsal project laterally on the flanks (1).

In most teiids, several tiny granules surround the posterior (free) edge of each dorsal scale and one of these is positioned directly under the apex. This apical granule supports the apex so that it projects upward, usually at less than about 15° middorsally and about 30° on the flanks. Rarely, as in *Cnemidophorus vittatus*, the apical granule is represented solely by thickened skin in most instances. At the opposite extreme, dorsals on the flanks of *Callopistes flavipunctatus* and western and Central American *Ameiva* project away from the body at much more than 30° giving the flanks a somewhat "bristly" appearance. Slightly pyramidal, keeled scales produce this "bristly effect" in Western *Ameiva*. The granules of western *Ameiva* are tiny and not positioned under the apex (60.0). On the other hand, modification of the apical granule produces the effect in *C. flavipunctatus* and Central American *Ameiva*: the apical granule (or pair of granules) is much larger than in other teiids, up to about one-third as large as the dorsals. In these species, both the apical granule and the associated dorsal scale project more than 60° to the surface of the skin on the flanks.

Tiny granules are never positioned under the posterior edge of the round, flat dorsals of *Tupinambis*. In *Dracaena guianensis*, a transverse fold of skin covered in tiny granular scales supports each large dorsal posteriorly. Single differentiated apical granules are not present in this species. Perhaps the most unusual modification of apical granules occurs in *Crocodilurus amazonicus*. In this species, the apical granule extends from the posterior edge of the fold of skin behind the dorsal. It is pointed and curves upward and often slightly anteriorly so that its pointed apex touches the apex of the preceding dorsal.

Vanzolini and Valencia (1965) coined the term "cushion scale" for the apical granule. The term is apt, because the apical granules do appear to "cushion" the larger dorsal scales. They assessed presence/absence of cushion scales on the thigh rather than on the dorsum. According to them, these scales are well developed in *Dracaena* and *Tupinambis*, rudimentary in *Callopistes*, *Teius*, and some *Ameiva* and *Kentropyx*, and absent in *Cnemidophorus*, *Dicrodon*, and *Crocodilurus*. The tiny granules are difficult to see, and, we found them to be present on the thighs of all teiids, although they are easily missed in small species. Also, except in *Tupinambis* where granules do not support the dorsals, we found no difference between the trunk and dorsal thighs: granules are present in both places, but are more numerous and prominent on the body.

61. *Transition Between Lateral and Dorsal Scales*.—The middorsal scales are subequal to (0) or much larger than (1) scales on the flanks.

Enlarged dorsal scales (Fig. 21) have long been used to diagnose *Dicrodon heterolepis*, *Kentropyx borkiana*, and *K. striata*. They appear to be unique to these three species among teiids.

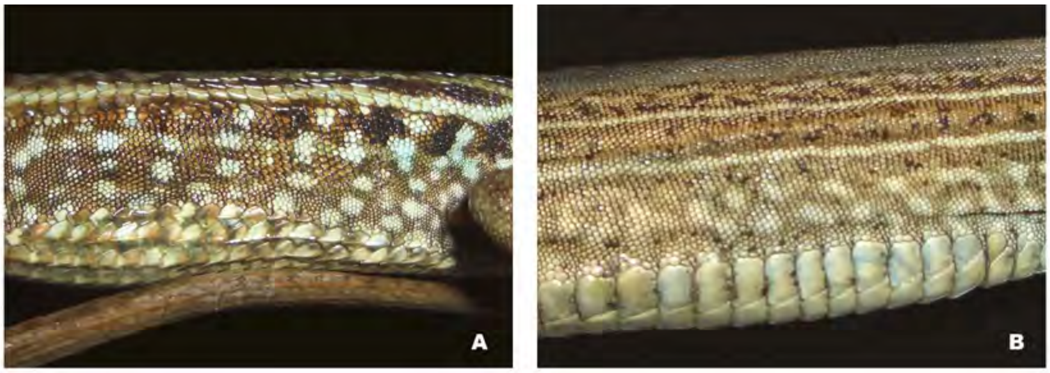

FIGURE 21. Transition between lateral and dorsal scales (character 61) in *Kentropyx striata* (A, TCWC 59191) and *Contomastix charrua* (B, AMNH 116321).

62. *Scales of Rump*.—Scales of the rump (Fig. 22) are much smaller (0) or slightly smaller (1) than proximal caudal scales.

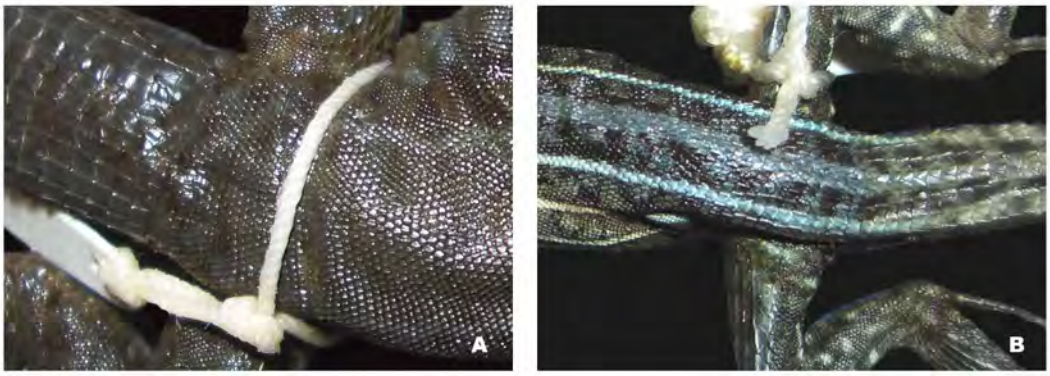

FIGURE 22. Scales of rump (character 62) in *Kentropyx altamazonica* (A, TCWC 39033) and *K. vanzoi* (B, UTA 59490).

In state 1, the transition from scales of the rump to the proximal caudals is slight. Like character 61, this character has recently been used to define species groups of *Kentropyx* (Gallagher & Dixon 1980, 1992).

63. *Condition of Scales on Chest*.—Scales of the chest are large and flat (0) or small, granular, and weakly keeled (1).

Character 63.1 (Fig. 23) is an autapomorphy of *Ameiva anomala* (Echternacht 1977).

64. *Pectoral Sulcus*.—A pectoral sulcus is absent (0) or interrupts the first 2–4 rows of ventrals between the arms (1).

The ventrals of most teiids form transverse rows from the groin to the gular fold. In Lesser Antillean *Ameiva* and some species of the *A. bifrontata* complex, 1–4 longitudinal rows of small granular scales interrupt ventrals medially between the arms (Fig. 23). We refer to this structure as a pectoral sulcus. Usually the pectoral sulcus interrupts three or four transverse rows of ventrals. However, the granules only interrupt two rows in *A. fuscata*.

65. *Condition of the Ventral Scales*.—The ventral scales are smooth (0) or keeled (1) (Fig. 24).

Although authors (e.g., Gallagher & Dixon 1992; Werneck *et al.* 2009) have sometimes stated that species of *Kentropyx* are the only teiids with keeled ventrals, they also occur in *Dracaena*.

66. *Progressive Decrease in Size of Scales Lateral to Ventrals*.—Lateral to the ventrals, scales are small and granular (0) or progressively decrease in size (1).

State 1 (Fig. 25) occurs in all Tupinambinae, in cis-Andean *Ameiva*, and most Caribbean *Ameiva*.

67. *Count of Transverse Rows of Ventrals*.—This count includes transverse rows of ventrals from the gular fold to the preaxial margin of the leg.

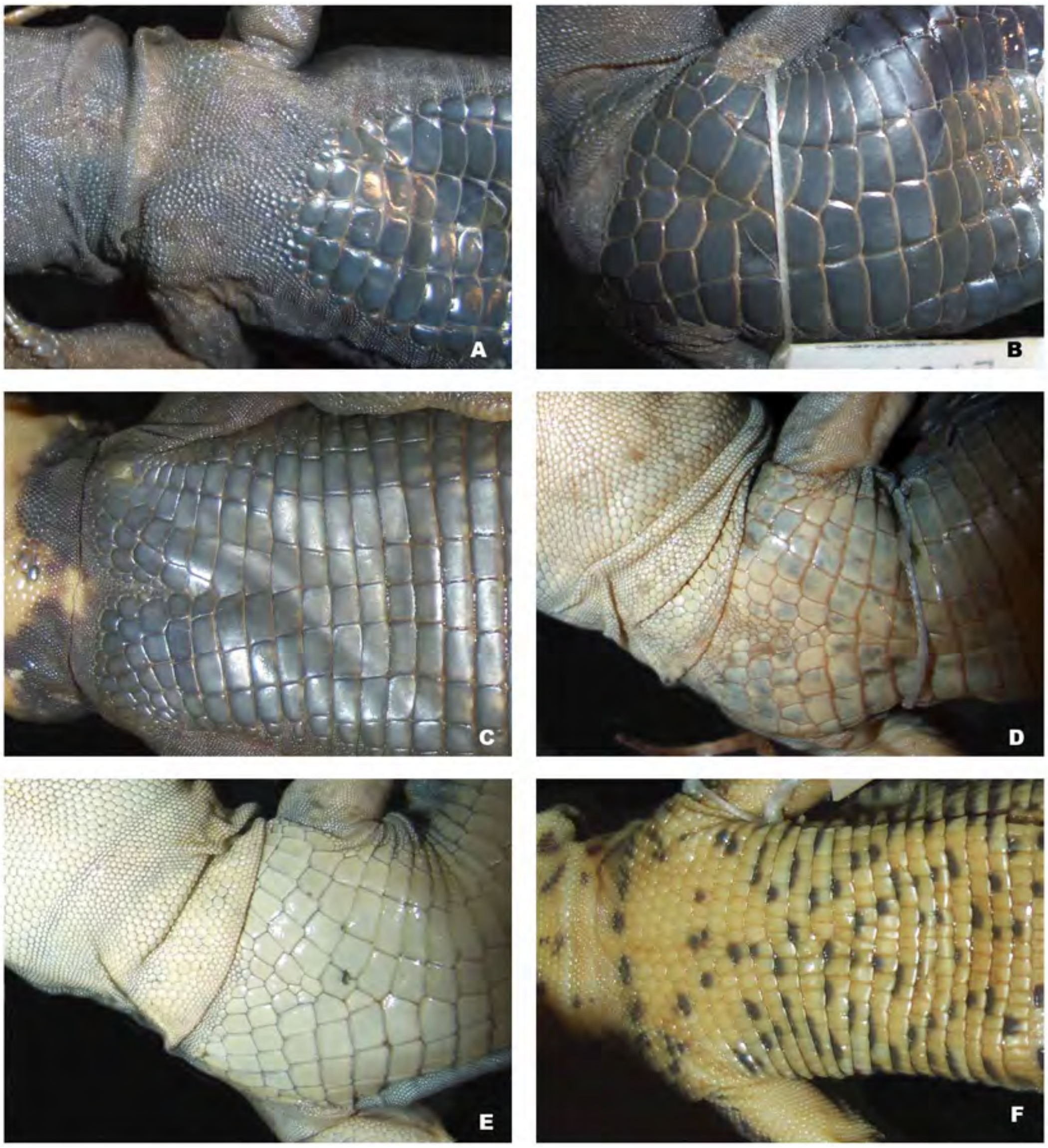

FIGURE 23. Condition of scales on chest and pectoral sulcus (characters 63 and 64) in *Holcosus anomalus* (A, AMNH 109694), *H. septemlineatus* (B, FMNH 27679), *Ameiva erythrocephala* (C, UF 113881), *A. bifrontata* (D, UMMZ 57441), *A. bifrontata* (E, FMNH 242238), and *Callopistes maculatus* (F, FMNH 9934).

68. *Count of Ventrals in Longitudinal Rows*.—Although at first glance this character seems straightforward, it has been a considerable source of confusion and contradictory reports in the literature, especially within the genus *Ameiva*. Our own publications have contributed to some of this confusion. For example, we have used different counting methods in the past (Ugueto & Harvey 2010; Ugueto *et al.* 2009) than those used here. This contradictory information becomes compounded in longer regional treatises (e.g., Schwartz & Henderson 1991), where ranges reflect different counting methods in addition to low levels of intraspecific variation.

In cis-Andean and Caribbean *Ameiva*, 0–3 longitudinal rows of flat, plate-like scales extend lateral to the ventrals (Fig. 26). These scales are separated from one another by one or more rows of granules. They increase in size posterior to the arm and reach their largest size slightly posterior to midbody. At this point, the most medial one is one-half the length of or longer than the adjacent ventral. This medial scale is included in the count of longitudinal rows of ventrals, however, if present, the outer one or two rows are excluded. In other genera of Teiinae, these progressively smaller scales are absent (66.0). Rarely (e.g., in *A. lineolata*, *A. wetmorei*), they may be absent in Caribbean *Ameiva*. Medial to these progressively smaller scales, the ventrals are approximately the same length. The first of these is usually rounded laterally. It may be in broad contact with the scale behind it or separated by one or a few more transverse rows of tiny granules. In an earlier study (Ugueto & Harvey 2010), we excluded this scale from our counts of ventrals in some *Cnemidophorus*. However, as redefined here, we include the scale in our counts.

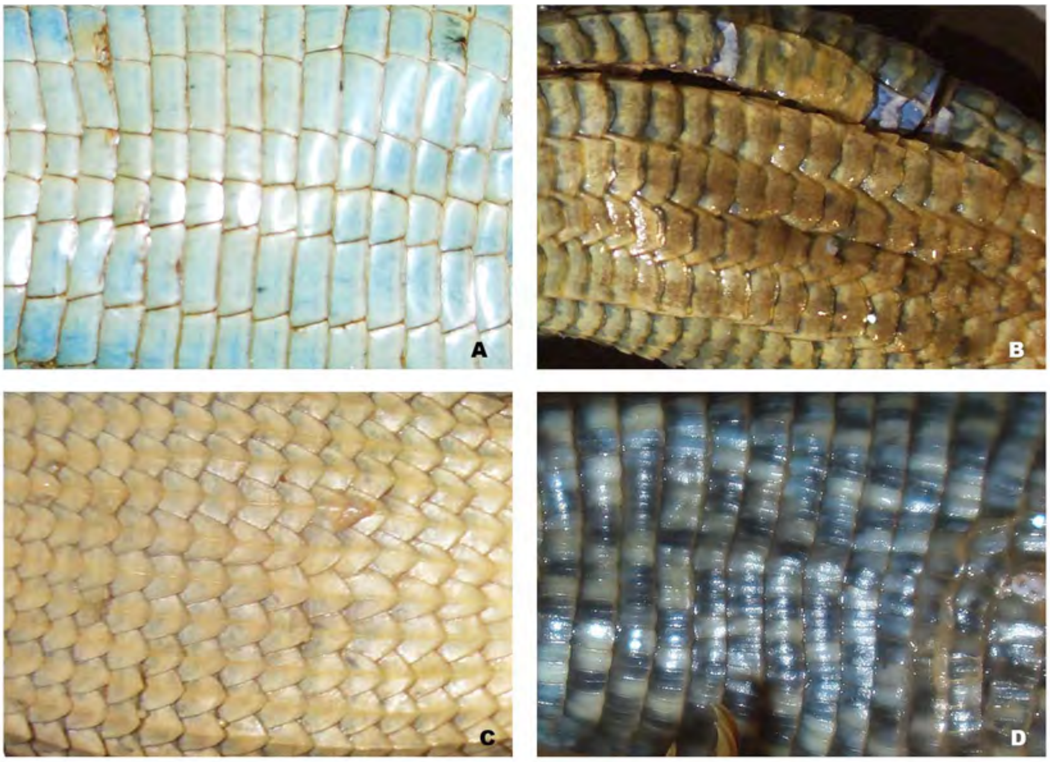

FIGURE 24. Condition of the ventral scales (character 65) in *Cnemidophorus ruthveni* (A, UMMZ 57277), *Dicrodon heterolepis* (B, FMNH 34244), *Kentropyx altamazonica* (C, UTA 59487), and *Dracaena guianensis* (D, TCWC 38121).

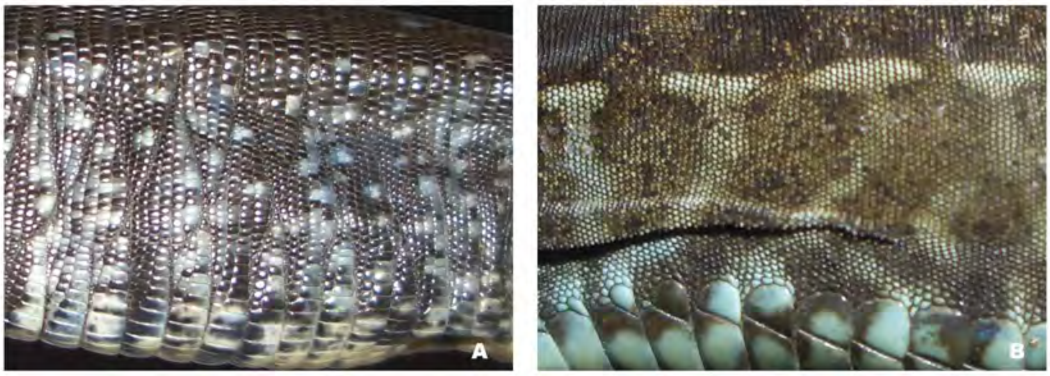

FIGURE 25. Progressive decrease in scales lateral to the ventrals (character 66) in *Tupinambis palustris* (A, UTA 59492) and *Holcosus festivus* (B, UTA 39981).

69. *Preanal Plate*.—A preanal plate (Fig. 27) formed by enlarged preanal scales is absent (0) or present (1).

The preanal region of *Callopistes*, *Dracaena*, and species of the *Tupinambis rufescens* group has uniformly small scales covering the preanal region (69.0). In contrast, the medial preanals are enlarged in *Crocodilurus* and the Teiinae (69.1). Within the *T. teguixin* group, *T. longilineus* and *T. teguixin* have a preanal plate, whereas *T. quadrilineatus* and *T. palustris* lack it.

70. *Count of Preanals*.—We counted the preanal scales in a straight line from a position medial to the femoral pores to (and including) the large posterior scale of the preanal plate. The count does not include small granular scales between the preanal plate and cloaca.

71. *Scales Lateral to Preanal Plate*.—Scales bordering the 2–3 enlarged medial scales of the preanal plate are subtriangular (0) or small and granular (1) (Fig. 28).

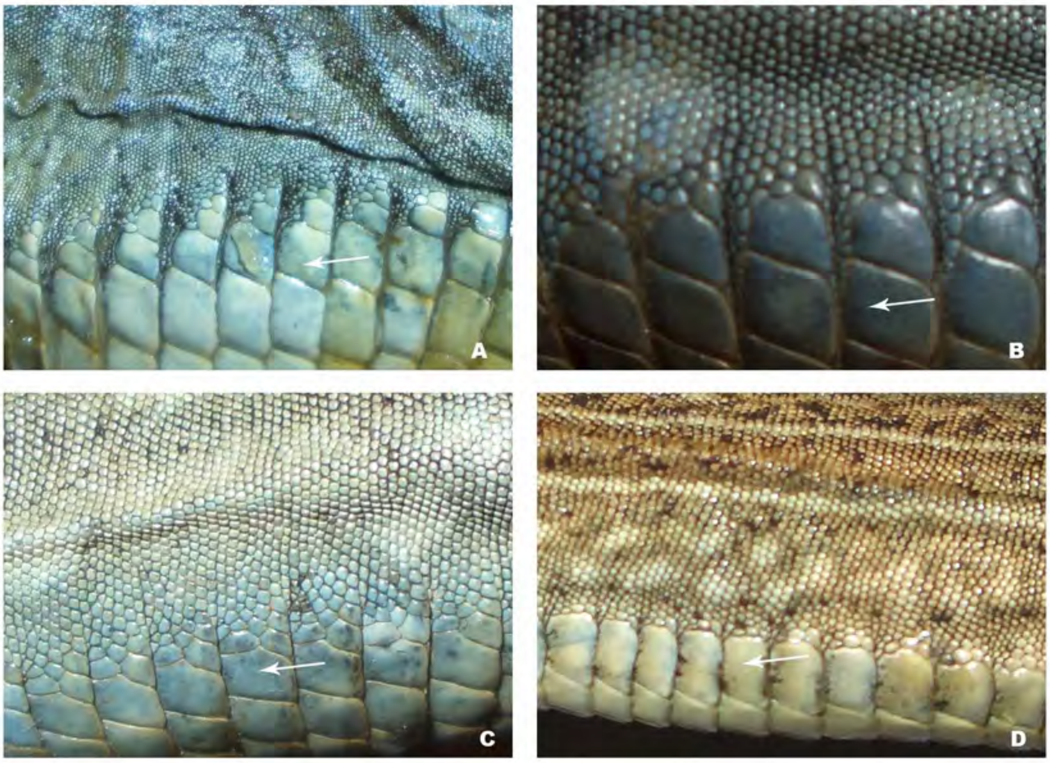

FIGURE 26. Count of ventrals in longitudinal rows (character 68) in *Ameiva bifrontata bifrontata* (A, UMMZ 107086), *Cnemidophorus ruthveni* (B, UMMZ 57275, and C, UMMZ 57277), and *Contomastix charrua* (D, AMNH 116321). Arrow indicates lateralmost ventral in each species.

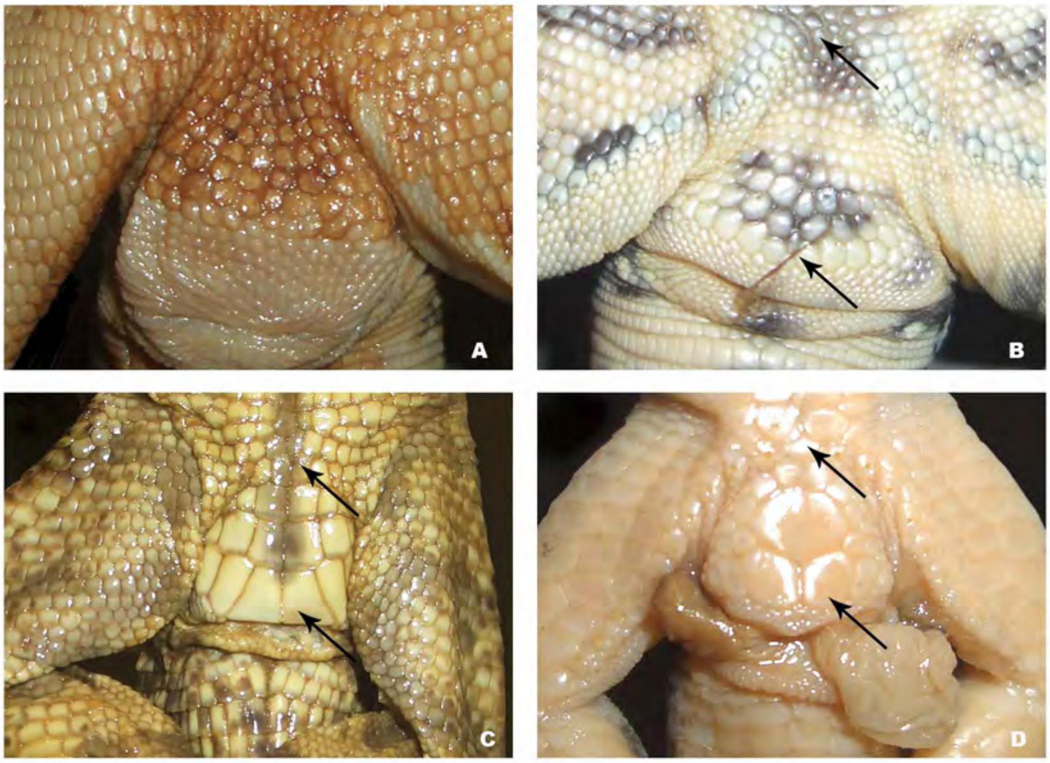

FIGURE 27. Condition and number of scales forming preanal plate (character 69 and 70, arrows indicate anterior and posteriormost preanals) in *Callopistes flavipunctatus* (A, FMNH 41584), *Salvator merianae* (B, UTA 59492), *Crocodilurus amazonicus* (C, USNM 89371), and *Ameivula ocellifera* (D, FMNH 44156).

72. *Relative Size of Preanals*.—The preanals (Fig. 28) are paired and large (i.e., each is one-half as large to larger than the scale anterior to it) (0), are paired and small (less than one-half as large as the scale in front of them) (1), or include a single large median plate, larger than the scale in front of it (2). This character was unordered in all analyses.

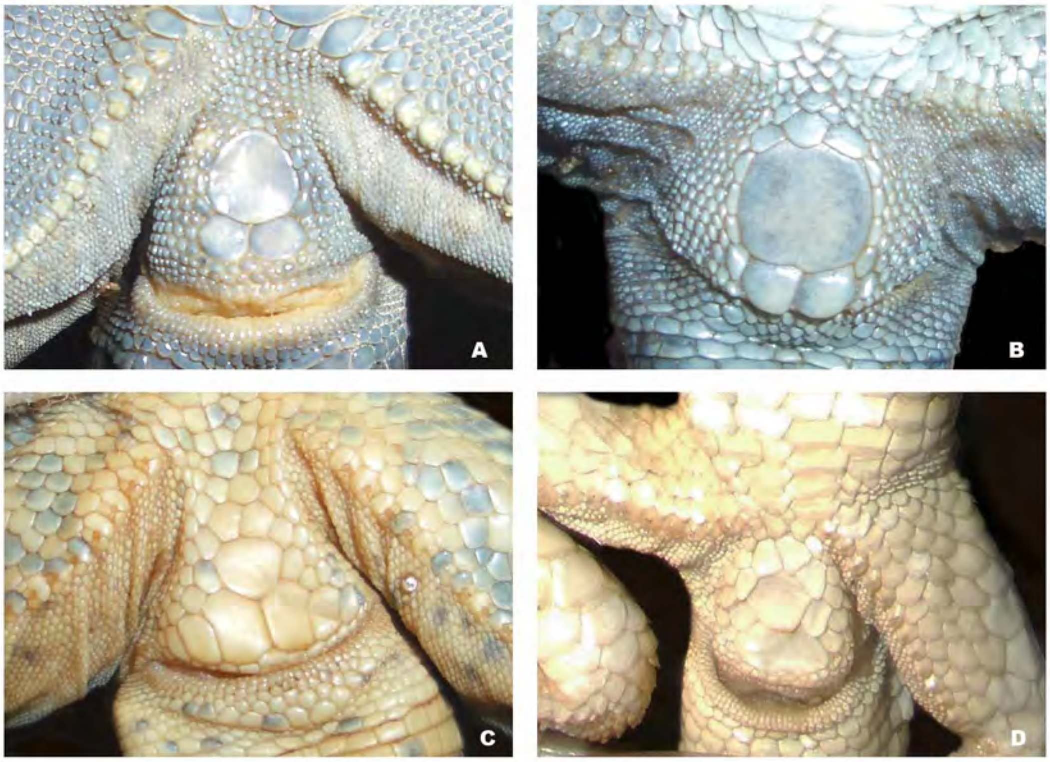

FIGURE 28. Scales lateral to anal plate and relative size of preanals (character 69 and 70) in *Holcosus bridgesii* (A, FMNH 166245), *H. festivus* (B, UTA 39978), *Ameiva atrigularis* (C, CM S-6500), and *Aurivela longicauda* (D, AMNH 17020).

Most Teiinae have relatively large, paired preanals (72.0). These scales are greatly reduced in western and some Central American *Ameiva* (72.1). State 2 is very rare and occurs regularly in only four species. Both sexes of *Ameiva fuscata*, *A. pluvianotata*, *Cnemidophorus longicauda*, and *C. tergolaevigatus* have a single large preanal plate, much larger than the scale in front of it (72.2). In occasional specimens of other cnemidophorines, the normally paired preanal plates may fuse to produce a similar pattern.

Ameiva quadrilineata appears to be unique among congeners in exhibiting marked sexual dimorphism for this trait. In our sample, the large anterior plate projects posteriorly separating two small preanal plates (72.1) in eight males. On the other hand, small granular scales surround a single large preanal plate in three females. Thus, the preanal plate of female *A. quadrilineata* resembles the plate of *C. longicauda* and *C. tergolaevigatus*. However, in the two *Cnemidophorus* species the large shield in front of the vent is subtriangular, whereas it is oval in female *A. quadrilienata*. Since this trait appears to be sexually dimorphic in *A. quadrilineata*, we coded all specimens as having state 1. This species also has postanal plates (79.1). Together, these two traits allow unequivocal sexing of *A. quadrilineata* without recourse to subcaudal incision.

This character is not applicable to *Kentropyx* (88.?). In all species of this genus, a differentiated preanal plate is not evident. Instead, large, imbricate, keeled scales, similar in size to the ventrals cover the preanal region.

73. *Number of Preanal Spurs*.—Males have zero (0), one (1), two (2), or 5–6 (3) preanal spurs on each side (Fig. 29). Based on morphological intermediacy, we ordered this character as follows: 0 > 1 > 2 > 3.

Just anterior to and on either side of the vent, all northern *Cnemidophorus* have a single spur (73.1), all *Kentropyx* have two large spurs (73.2), and *Ameiva edracantha* has a cluster of 5–6 large spurs (73.3). In *Kentropyx*, one small vestigial spur is usually present just dorsal and posterior to the pair of large spurs.

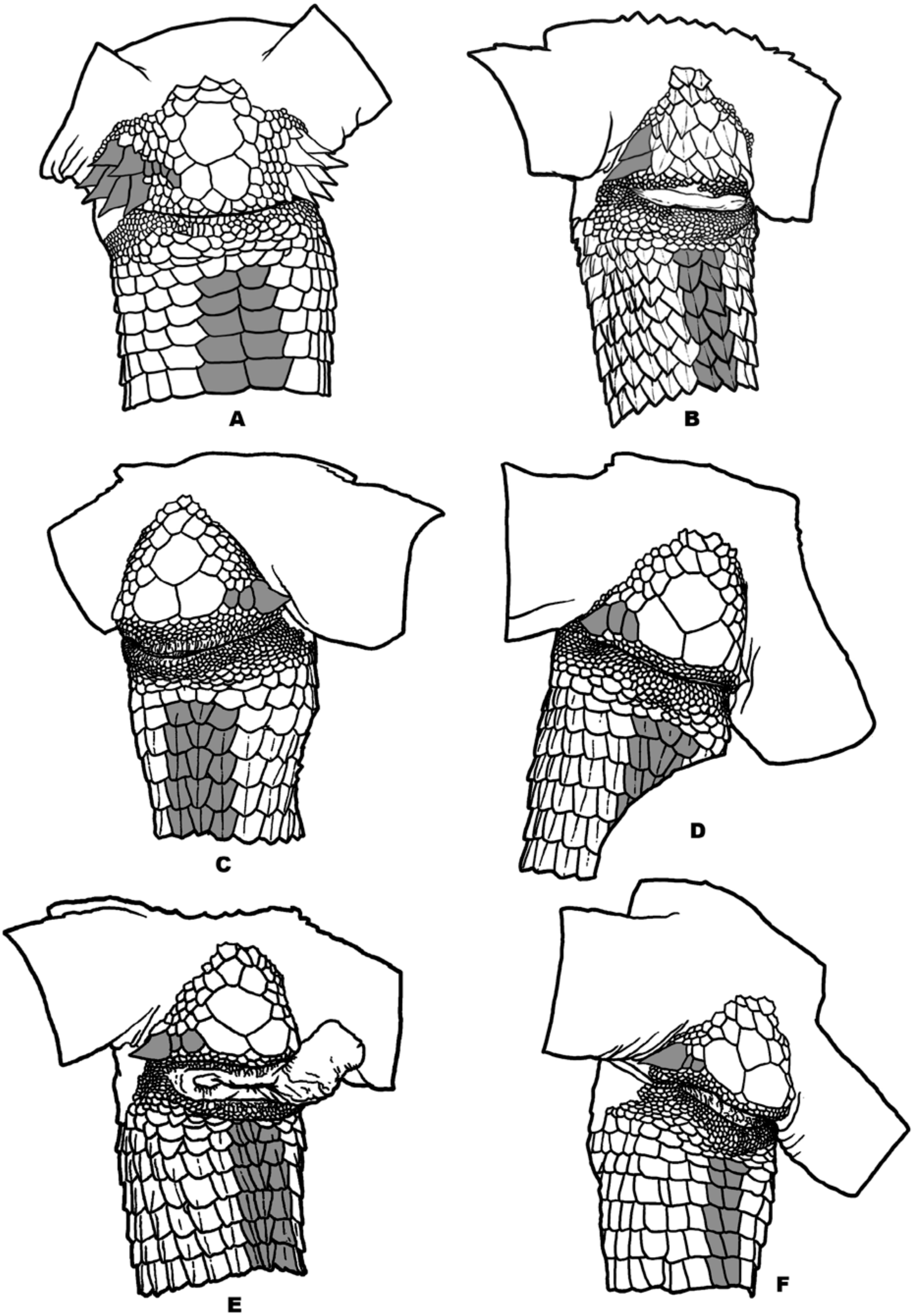

FIGURE 29. Number, shape and orientation of preanal spurs of males, number and size of scales between preanal shield and spur, and condition of proximal subcaudals (characters 73–77, and 83) in *Medopheos edracanthus* (A, FMNH 197961, A), *Kentropyx vanzoi* (B, UTA 59487), *Cnemidophorus lemniscatus lemniscatus* (C, CM 7409), and *C. arubensis* (D, UMMZ 57230), *C. l. gaigei* (E, UMMZ 54895), and *C. rostralis* (F, SDNHM 34890).

Perhaps surprisingly, spurs have never been reported in *Cnemidophorus vanzoi* until now. This species has remained poorly known since Baskin and Williams (1966) described it as an *Ameiva* from the Maria Islands off the southeastern coast of St. Lucia. Baskin and Williams thought *C. vanzoi* was closely related to *A. fuscata*, however Presch (1971) later transferred *A. vanzoi* to *Cnemidophorus* based on tongue morphology. Neither publication mentioned the spurs, which provide evidence that this species is related to other Caribbean *Cnemidophorus*.

74. *Shape of Preanal Spurs*.—The preanal spurs are distinctly broad at the base and short (0), somewhat broad and moderately elongated (1), or narrow and attenuate (2). Based on morphological intermediacy, we ordered this character as follows: 0 > 1 > 2.

We (Ugueto & Harvey 2010; Ugueto *et al.* 2009) recognize the same three character states as Markezich *et al.* (1997), who defined these states with reference to figure 7 of Cole and Dessauer (1993). Characters 74–77 are not applicable to species lacking preanal spurs.

75. *Orientation of Preanal Spurs*.—The preanal spurs project away from (0) or extend next to the body (1).

Cole and Dessauer (1993) noted differences in orientation of the preanal spurs when comparing *Cnemidophorus gramivagus* to *C. lemniscatus*. We (Ugueto & Harvey 2010; Ugueto *et al.* 2009) found this character to be useful in distinguishing among other species in the genus.

76. *Number of Scales Between Preanal Shield and Spur.*—We counted the minimum number of longitudinal rows of scales separating the spur from the preanal plate (Ugueto & Harvey 2010; Ugueto *et al.* 2009).

77. *Size of Scales Between Preanal Shield and Spur.*—Scales between the preanal spur are small (much smaller than the preanal spur base width, Ugueto *et al.* 2010) (0), medium-size (approximately half the width of the preanal spur base) (1), or large (as wide as the preanal spur base width) (2). Based on morphological intermediacy, we ordered this character as follows: 0 > 1 > 2.

78. *Postcloacal Buttons*.—Males lack (0) or have (1) postcloacal buttons.

Postcloacal buttons are a sexually dimorphic trait of the Tupinambinae. They consist of a small cluster of 2—3 slightly raised and enlarged rounded scales just behind the vent of males (Fig. 30).

79. *Postanal Plates*.—A pair of postanal plates (sensu Pietruszka 1981) is absent (0) or present (1) in males.

When present, postanal plates lie immediately posterior to the postanal ridge and are separated from one another medially by 2–4 granular scales (Pietruszka 1981; Fig. 31). They were first reported from *Aspidoscelis* where they apparently occur in all or most species (Ashton 2003; Pietruszka 1981). Postanal plates are unequivocally absent in most South American Teiidae. They are entirely lacking from *Ameiva ameiva* and other eastern congeners. Nonetheless, these structures are present in western and Central American *Ameiva*.

Usually, postanal plates can be used to sex specimens. Occasional male *Aspidoscelis* (Ashton 2003; Pietruszka 1981) and western *Ameiva* (e.g., FMNH 165156, a male *Ameiva bridgesii*) lack them. Our male specimen of *A. orcesi* has a divided plate on the right side and a partially divided scale on the left.

A similar, though apparently nonhomologous structure occurs in *Cnemidophorus rostralis*. This species sometimes has a pair of slightly enlarged scales located in about the same position as the postanal plates, but in the second rather than the first complete row of subcaudals. In our sample, three out of six males and no females (out of five) have these structures. Relatively few specimens of *C. rostralis* have been collected (Ugueto & Harvey 2010), and additional study is required to determine if these enlarged scales are sexually dimorphic in this species. Nonetheless, they are unlikely to be reliable for determining sex since only half of the males in our sample have them. All other *Cnemidophorus* lack postanal plates as well as the enlarged scales of some male *C. rostralis*.

80. *Dorsolateral Row of Serrated Caudals*.—Scales on the dorsolateral edge of the tail are like those on the top and sides (0), or a row of denticulate caudals forms a serrated edge on either side of the tail (1).

In western and Central American *Ameiva*, one row of scales on either side of the tail has laterally projecting mucrons and very heavy keels (Fig. 32).

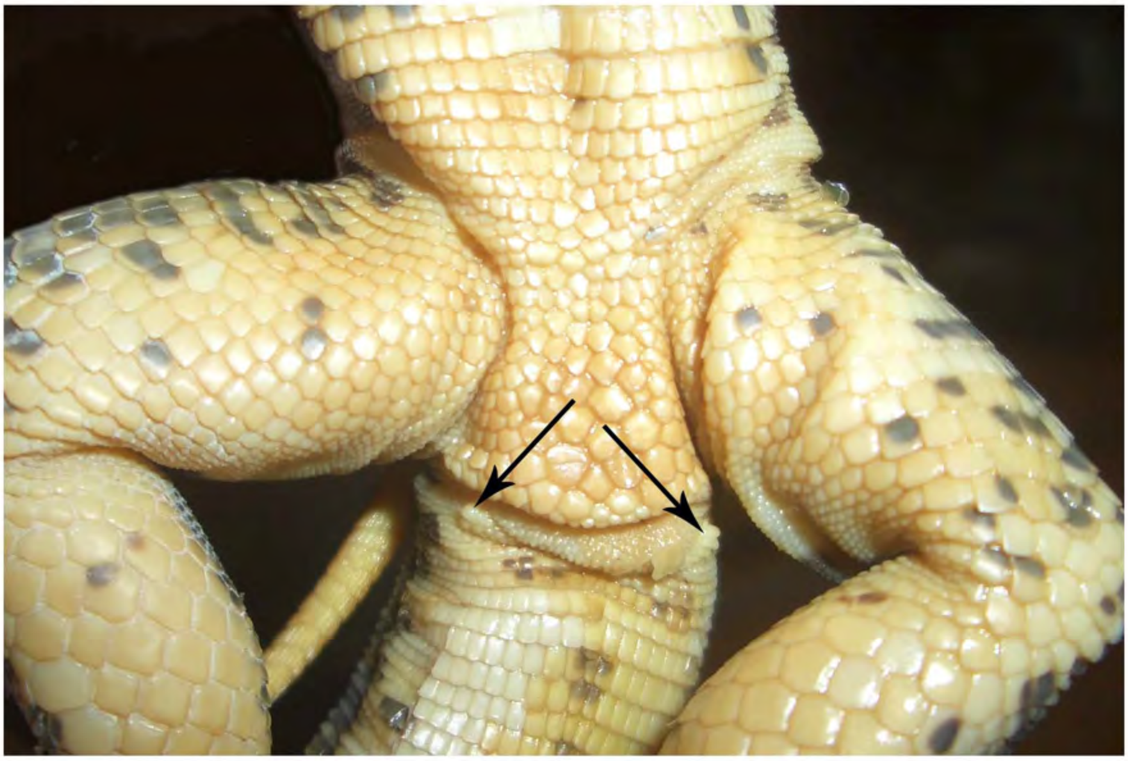

FIGURE 30. Postcloacal buttons (character 78) of a male *Callopistes maculatus* (FMNH 9934).

81. *Dorsolateral Crests on Tail*.—The tail is cylindrical and scales on the dorsolateral edges are unmodified (0), or the tail is flattened and scales on the dorsolateral edge form a prominent crest (1) (Fig. 33).

The aquatic Tupinambinae have similar tail morphologies that likely evolved to facilitate swimming. Flattened tails with dorsolateral crests have evolved in unrelated aquatic lizards such as the gymnophthalmid genus *Neusticurus*, shinisaurid genus *Shinisaurus*, and scincid genus *Tropidophorus*. The crests of *Dracaena* and *Crocodilurus* consist of enlarged, heavily keeled scales that project away from the tail at about 45°.

At the base of the tail, eight rows of enlarged scales are present in *Crocodilurus*: four rows between the dorsolateral crest and another pair positioned lateral to each crest. Each of the crests is separated by 1–2 rows of flat, elongate, and keeled scales, except for the medial rows, which are separated by 9–10 scales. The lateral rows begin on the body, above the preaxial edge of the thigh and extend to the level of supracaudal rows 27–30. The other six crests begin at the base of the tail. The medial row extends 11–16 supracaudals and the row between the medial row and dorsolateral crest extends for 18–25 supracaudals.

Dracaena guianensis has a similar though less regular arrangement of enlarged scales at the base of the tail. In TCWC 42022, for example, the enlarged convex scales on the dorsum become arrayed in 3/3 irregular rows at the base of the tail. The medial 2/2 rows merge to form the dorsolateral crest at the level of the 15th subcaudal, whereas the lateral-most row diminishes in height as it extends to the level of the 22nd subcaudal. Other specimens of *Dracaena* had been returned to the loaning institutions before we noticed the accessory crests, and we do not know how variable this arrangement of scales is.

82. *Division of Caudal Annuli*.—The caudal annuli are complete (0), consist of complete rows alternating with divided rows (1), or consist of two or more complete rows alternating with rows that are mostly complete but irregularly divided dorsally (2). Based on morphological intermediacy, we ordered this character as follows: 0 > 1 > 2.

All Teiinae have complete caudal annuli (Fig. 34). That is, a single row of scales on the sides of the tail corresponds to one subcaudal (82.0). In *Crocodilurus*, *Dracaena*, and *Tupinambis*, complete annuli alternate with annuli that are complete ventrally but divided on the sides and dorsum of the tail (82.1). In both species of

Callopistes some of the annuli divide, but the pattern is irregular and not the same as in other Tupinambinae. When annuli divide in *Callopistes*, they are always separated by at least two rows of complete annuli; the divisions are short, and usually restricted to the dorsum of the tail (82.2).

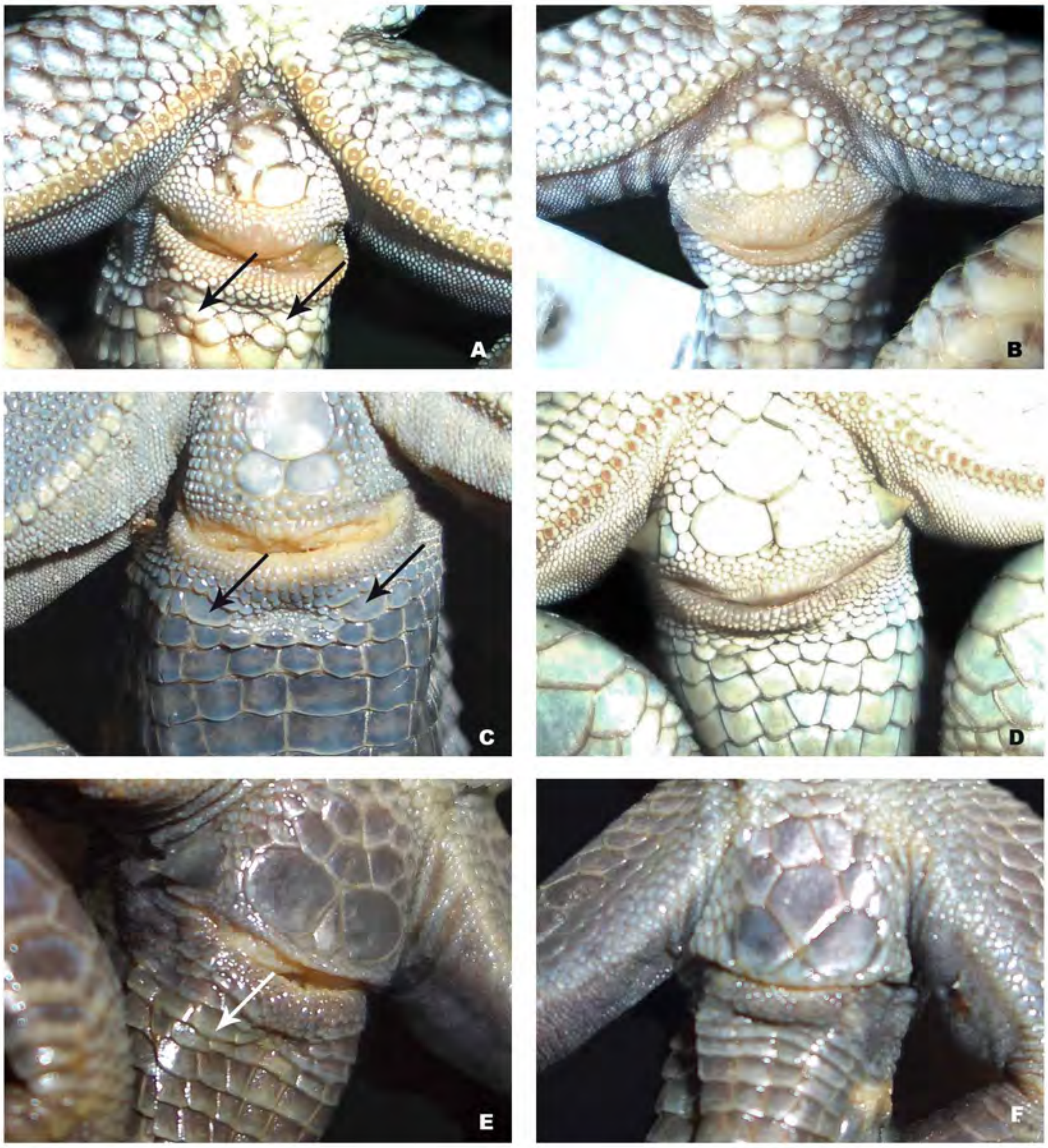

FIGURE 31. Postanal plates (character 79, indicated with arrows when present) in male *Aspidoscelis marmorata* (UTA 44102, A) contrasted with female (UTA 44089, B). Postanal plates in *Holcosus bridgesii* (FMNH 166245, C) contrasted with unmodified subcaudals of *Cnemidophorus lemniscatus lemniscatus* (CM 7409, D). Pair of slightly enlarged subcaudals (arrow) in male *C. rostralis* (SDNHM 34885, E) contrasted with unmodified subcaudals of female (SDNHM 34892, F).

83. *Proximal Subcaudals*.—The proximal subcaudals are smooth (0) or keeled (1).

Keeled proximal subcaudals occur in *Dracaena*, the *Tupinambis rufescens* group, *Kentropyx*, some western *Ameiva*, *C. lacertoides*, *Teius teyou*, and most species of the *Cnemidophorus lemniscatus* complex. We assigned state 1 to species when keels appear on one or more of the proximal five subcaudal rows. As in other teiids, the dorsal caudals of *Callopistes maculatus* are keeled, however the subcaudals have three keels rather than one. A faint trace of the middle keel appears about 7 subcaudals from the vent in this species.

In most species with state 1, keeling extends uninterrupted from the dorsal surface of the tail to the midventral caudals. However, scales on the sides of the tail are smooth and only the medial 2–4 longitudinal rows of proximal subcaudals bear keels in *Teius*. In young *Teius*, keels are evident on proximal subcaudals, whereas generation glands (110.1) obscure the keels in mature specimens. Thus, keels appear to be lost during ontogeny. For example, in FMNH 195991 (an adult male in breeding coloration), the glands densely cover the entire surface of four longitudinal rows of subcaudals until the 17th row, where the first appearance of keels is marked by a thin cream line running down the center of each scale through the glands. Distally, the number and size of glands slowly decrease until glands disappear and low keels replace them on the outer rows, 30 subcaudals from the vent. In this region of the tail, few glands extend on either side of the keel down the center of each subcaudal. By the 32nd subcaudal, glands are no longer evident. Neither keels nor glands are present on the first pair of subcaudals behind the vent in adult male *Teius*. In other species with subcaudal keels and generation glands (*Cnemidophorus lemniscatus* complex species; *Tupinambis rufescens* group species), keeling does not appear to change during ontogeny.

Appendicular Scalation

84. *Scales on Dorsal Surface of Brachium*.—The preaxial and postaxial brachial scales (Fig. 35) are separated by granular scales (0), separated by a continuous band of enlarged subtriangular plates (1), or separated by small triangular scales (2).

Peters (1964) illustrated the preaxial patch of large differentiated scales of *Ameiva septemlineata* and used this character to distinguish this species from *A. bridgesii*. We also found patches on the preaxial and postaxial surfaces of the arm to be useful taxonomic characters in the *Cnemidophorus lemniscatus* complex (Ugueto & Harvey 2010; Ugueto *et al*. 2009). In this paper, we define additional characters of the arm and assess them for a broader sample of Teiidae. *Crocodilurus* is the only genus of Tupinambinae with differentiated preaxial and postaxial brachial scales. Characters 84, 86, and 88 are not applicable to other Tupinambinae, which lack these differentiated scales.

85. *Size of Preaxial Brachial Scales*.—The largest scales on the preaxial surface (Fig. 36) of the brachium are 1.5–2+ times wider (measured from preaxial to postaxial) than long (0), 1–1.5 times as wide as long (1), or longer than wide (2). Based on morphological intermediacy, we ordered this character as follows: 0 > 1 > 2.

86. *Proximal Extent of Preaxial Brachial Scales*.—The preaxial brachial scales extend to or beyond the center of the arm (0) or form a small patch near the distal end of the brachium (1) (Ugueto & Harvey 2010).

87. *Size of Postaxial Brachial Scales*.—The largest scales on the postaxial surface of the brachium are 1.5–2+ times wider (measured from preaxial to postaxial, Fig. 37) than long (0), 1–1.5 times as wide as long (1), or slightly to not enlarged (2). Based on morphological intermediacy, we ordered this character as follows: 0 > 1 > 2.

88. *Proximal Extent of Postbrachial Scales*.—The postaxial brachial scales (Fig. 37) extend to or beyond the center of the arm (0) or form a small patch near the elbow (1).

This character is only applicable to species with differentiated (i.e., at least slightly enlarged) postaxial brachial scales.

89. *Continuation of Enlarged Scales Between Brachium and Antebrachium*.—-Enlarged antebrachial scales are narrowly separated from or in a continuous row with the enlarged preaxial brachial scales (0) or separated from the brachial scales by a large gap on the proximal antebrachium (1).

Four to nine rows of small, square to granular scales separate the plate-like brachials and antebrachials in very few species of Teiinae (89.1). As defined here, this character commonly occurs only in *Ameiva* from the Lesser Antilles and some species of *Cnemidophorus*. In *Ameiva* from the Greater Antilles, the antebrachials gradually decrease in size proximally (89.0). The last plate-like scale is 1.5–2 X as wide as long; and 1–2 scales, each about as wide as long, separate it from preaxial brachial scales.

90. *Condition of Antebrachials*.—The antebrachials are enlarged and smooth (0) or relatively small (1).

The antebrachials form large plate-like scales in all Teiinae except *Kentropyx* where they are relatively small and keeled. Similarly sized, though smooth scales cover the antebrachium of all Tupinambinae.

FIGURE 32. Count of enlarged prefemoral scales (characters 95) and undifferentiated supracaudals of *Ameivula ocellifera* (FMNH 44156, A, B) contrasted with dorsolateral row of serrate caudals (character 80) of *Holcosus anomalus* (AMNH 109694, C, D).

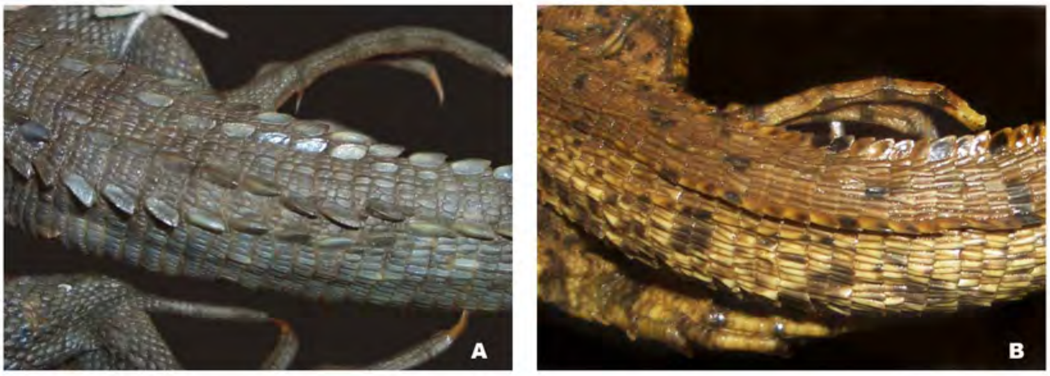

FIGURE 33. Dorsolateral crests on tail (character 81) of *Dracaena guianensis* (TCWC 38121, A) and *Crocodilurus amazonicus* (USNM 89371, B).

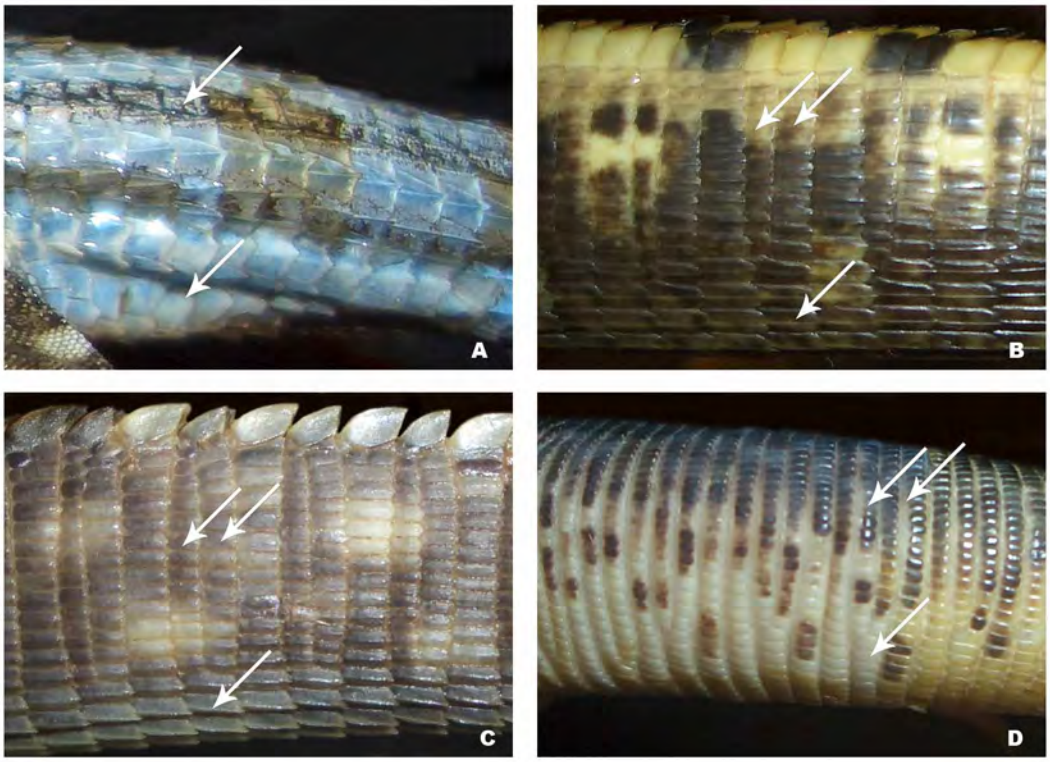

FIGURE 34. Caudal annuli (character 82) in *Cnemidophorus lemniscatus gaigei* (UMMZ 54895, A) contrasted with divided annuli of *Crocodilurus amazonicus* (USNM 200698, B), *Dracaena guianensis* (TCWC 38121, C), and *Callopistes maculatus* (FMNH 9934, D).

91. *Size of Postaxial Antebrachial Scales*.—Scales on the proximal, ventral surface of the antebrachium (Fig. 38) are distinctly enlarged (0), slightly enlarged (1), or granular (2). Based on morphological intermediacy, we ordered this character as follows: 0 > 1 > 2.

Among the Teiinae, enlarged scales may be present near the elbow or near the wrist. Many species of *Aspidoscelis* have distinctly enlarged scales on the ventral surface of the antebrachium, located near the elbow. Among other Teiinae, we found this trait regularly only in *Ameiva undulata*. In *Kentropyx*, slightly enlarged scales are present, however they form a band about four scales wide, proximal to Fingers IV–V. The scales in *Kentropyx* are largest near the wrist and decrease in size proximally. They are present in all species of this genus, but are noticeably larger in *K. pelviceps*. However, in other Teiinae, there is a tendency for scales to enlarge slightly at this position. The condition in *K. pelviceps* is a clear autapomorphy of this species.

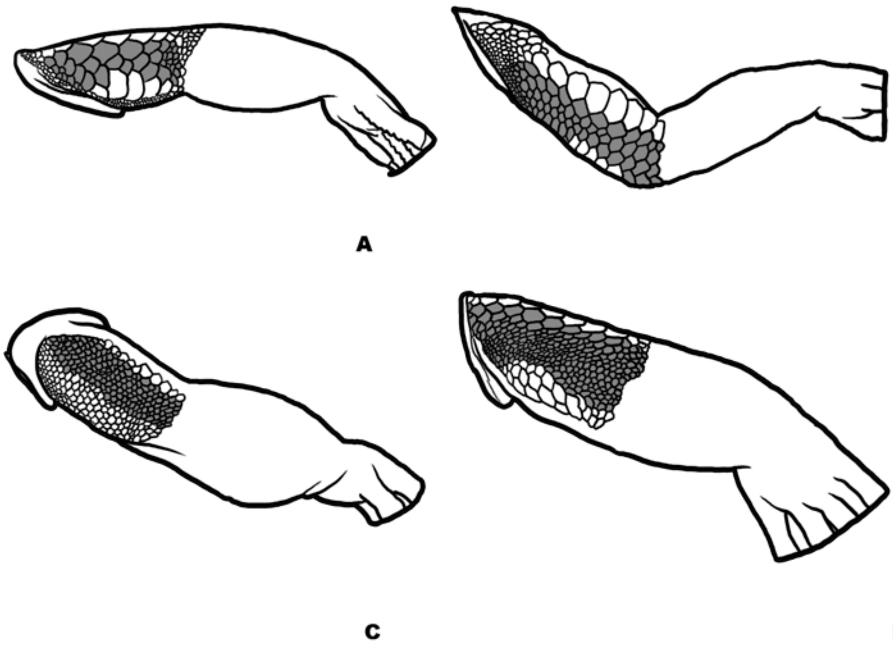

FIGURE 35. Scales on dorsal surface of brachium (character 84) in *Cnemidophorus lemniscatus splendidus* (FMNH 252723, A), *C. senectus* (MBUCV 1018, B), *C. murinus* (FMNH 57246, C), and *Ameiva ameiva* (NMNH 80623, D).

92. *Count of Digital Lamellae Below Fourth Finger*.—We routinely counted subdigital lamellae on a specimen's left side, unless damaged.

93. *Subarticular Lamellae of Fingers*.—The subarticular lamellae of Fingers III and IV (Fig. 39) are homogeneous in size (or have subarticular lamellae slightly enlarged) (0) or heterogeneous in size (noticeably enlarged and projecting or swollen) (1).

In her key to lizards of Brazilian Amazonia, Avila-Pires (1995, p. 20–21) used differences in the subdigital lamellae of the hand to separate *Kentropyx altamazonica* from *K. pelviceps* and *K. calcarata*. She described the lamellae of *K. altamazonica* as "homogeneously swollen" and those of the other species as "heterogeneous, with some interspaced lamellae under each finger distinctly more swollen than the others." The distinctly swollen lamellae referred to by Avila-Pires are located below the phalangeal articulations. In *K. borkiana*, *K. calcarata*, and *K. pelviceps*, the articular subdigital lamellae are noticeably swollen, enlarged, and, with rare exceptions, entire. They are only slightly enlarged, slightly swollen, and entire in *K. altamazonica* and *K. striata*.

Among other teiids, manual lamellae are most often homogeneous. In some species such as *Ameiva ameiva* and *A. chrysolaema*, the lamellae are so uniform in size that subarticular lamellae can only be located by flexing the digits. As in some *Kentropyx altamazonica* the subarticular lamellae may be slightly enlarged (e.g., in *Dicrodon guttulatum*, 93.0). Distinctly heterogeneous lamellae (93.1) characterize western and Central American *Ameiva*. In these species, the subarticular lamellae are up to two times as large as lamellae between articulations and subarticular lamellae project more than adjacent lamellae when viewed from the side.

94. *Division of Subarticular Lamellae of Fingers*.—The lamellae of the fingers are divided (0) or entire with divided subarticular lamellae (1) or all entire (2). We ordered this character as follows: 0 > 1 > 2.

Species of Tupinambinae have mostly divided subdigital lamellae (94.0), whereas most Teiinae have entire subdigital lamellae (94.2). In Teiinae with divided subarticular lamellae (94.1), entire lamellae separate single divided subarticular lamellae. Divided subarticular lamellae occur regularly only in some *Kentropyx* and in all species of northern *Cnemidophorus*. *Ameiva lineolata* frequently has scattered divided subdigital lamellae on the hands. When present, the divided scales are most frequently located under phalangeal articulations and under the proximal phalanges of longer fingers (i.e., Fingers III–IV). Nonetheless, division of the scales is not regular and we code this species as having state 2.

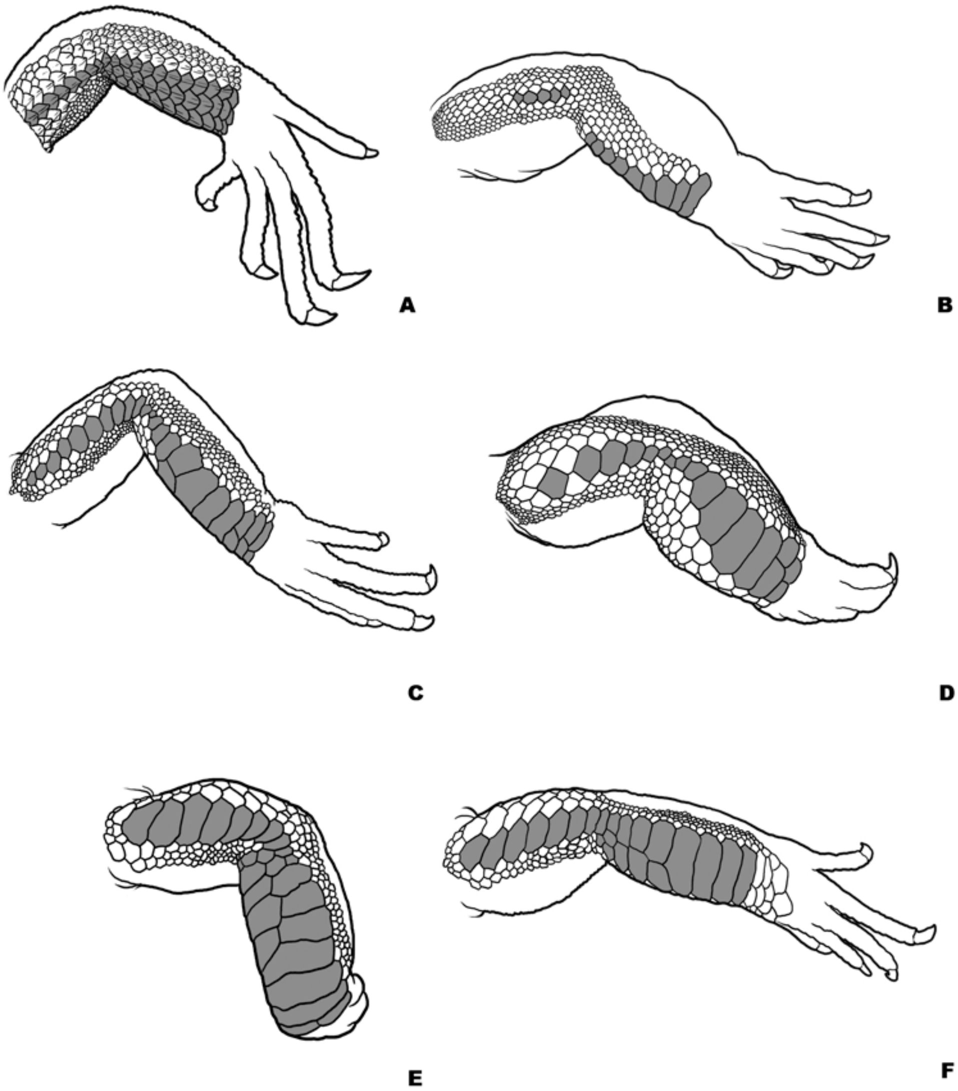

FIGURE 36. Size and proximal extent of preaxial brachial scales, continuation of enlarged scales between brachium and antebrachium, and condition of antebrachials (characters 85, 86, 89, and 90) in *Kentropyx altamazonica* (UTA 59487, A), *Cnemidophorus ruthveni* (UMMZ 57285, B), *C. rostralis* (SDNHM 34885, C), *Ameiva ameiva* (NMNH 561202, D), *C. senectus* (SDNHM 34910, E), and *C. lemniscatus* (CM 7270, F).

Dracaena guianensis has the most highly modified subdigital lamellae of species examined in this study. Lamellae under its most distal phalanges are entire and sharply keeled. Under the penultimate phalanges, the lamellae are divided, and under more proximal phalanges, one or more small scales separate the two sides of the divided lamellae. The number of these small scales increases proximally. At the base of the fingers, the lamellae are completely fractured into numerous (i.e., 7 or 8) small rounded scales arrayed in regular transverse rows.

The most basal lamellae frequently divide evenly in specimens of many other teiids. Many specimens of *Dicrodon heterolepis* approach the heavily fractured condition of Tupinambinae in having up to 2–4 scales under the proximal two phalanges. Nonetheless, their distal lamellae are like those of other Teiinae in being entire (94.2).

95. *Count of Enlarged Prefemoral Scales*.—We counted the number of enlarged prefemoral scales at mid-thigh, perpendicular to the femur and between granules on the dorsal surface of the thigh and the pore-bearing scales.

Ameiva anomala, *A. bridgesii*, *A. septemlineata* (to a lesser degree), some Lesser Antillean *Ameiva* (most conspicuous in *A. erythrocephala* and *A. pluvianotata*), and some *Kentropyx* (most noticeable in *K. altamazonica* and *K. pelviceps*) have numerous rows of small or tiny granular scales between the femoral pores and flat, plate-like prefemoral scales. Consequently, counts are unusually high in these species.

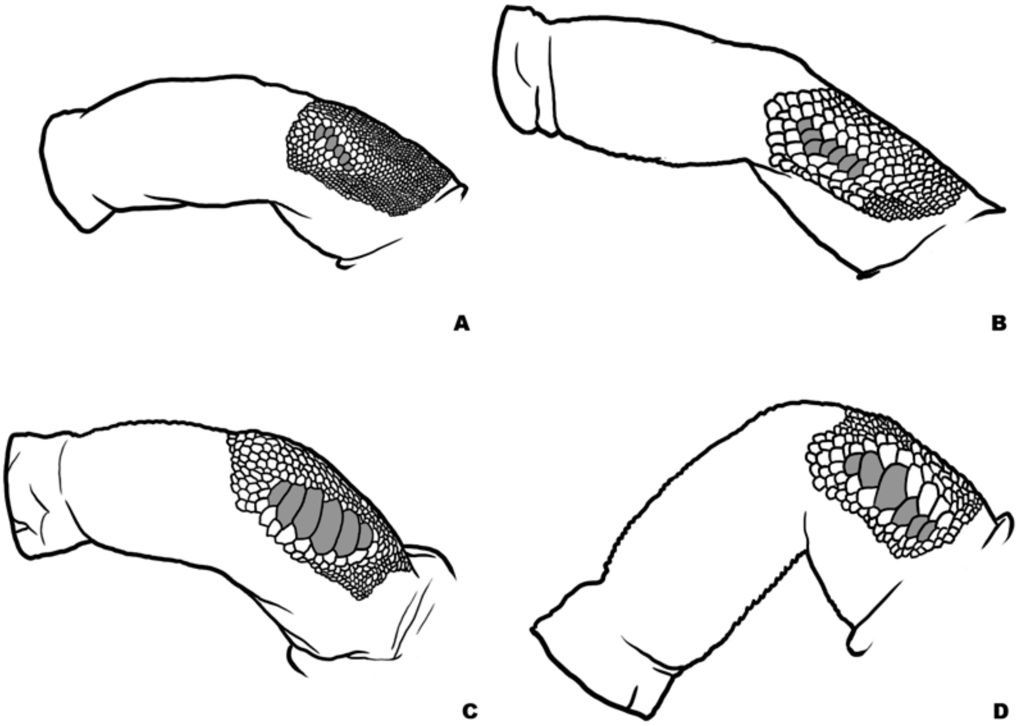

FIGURE 37. Size and proximal extent of preaxial brachial scales (character 87 and 88) in *Ameiva erythrocephala* (UF 11388-1, A), *Cnemidophorus arubensis* (UMMZ 57244, B), *A. bifrontata divisa* (UMMZ 55026, C), and *Holcosus septemlineatus* (FMNH 27679, D).

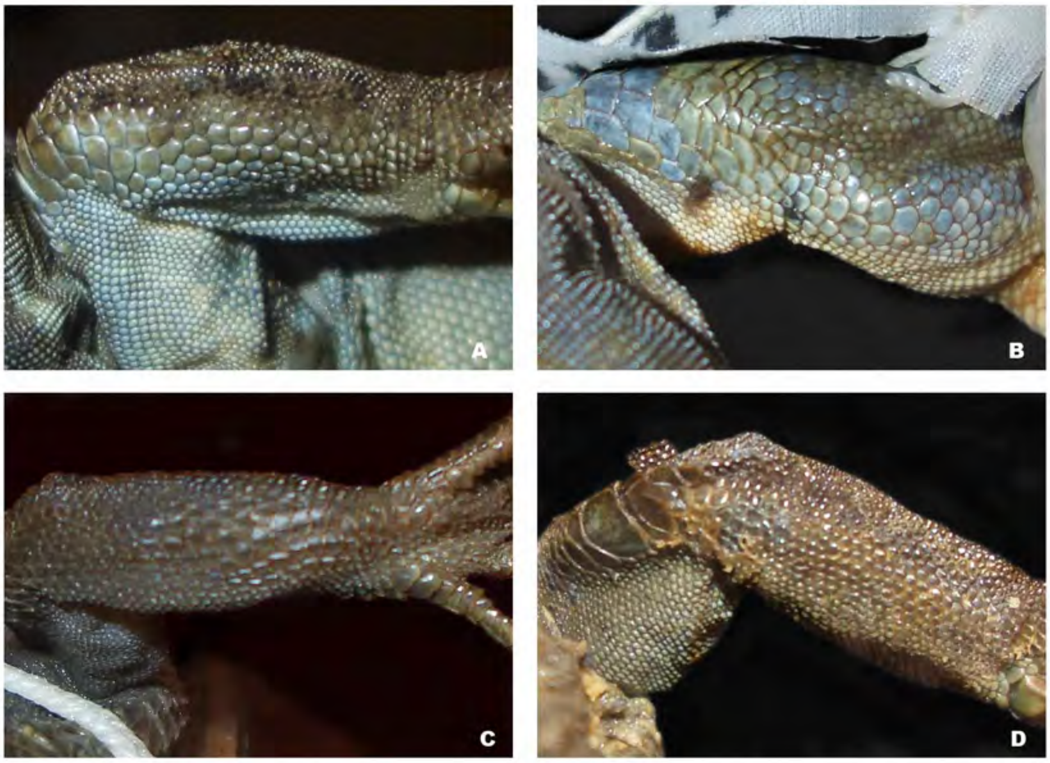

FIGURE 38. Size of postaxial antebrachial scales (character 91) of *Holcosus undulatus* (UTA 46890, A), *Aspidoscelis mexicana* (FMNH 223659, B), *Kentropyx pelviceps* (TCWC 38132, C), and *Holcosus festivus* (FMNH 43816, D).

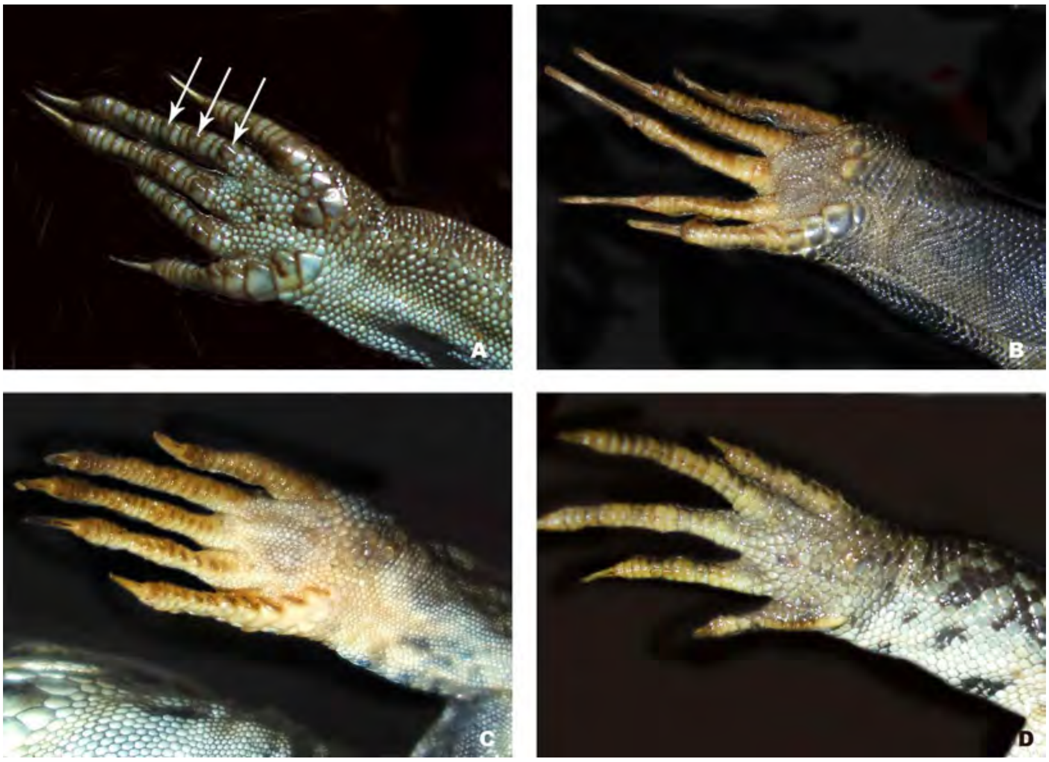

FIGURE 39. Condition of subarticular lamellae of fingers (characters 93 and 94) in *Holcosus festivus* (UTA 39979, A), *Ameiva praesignis* (USNM 127335, B), *Cnemidophorus vanzoi* (KU 234074, C), and *Tupinambis teguixin* (KU 175382, D).

96. *Combined Count of Femoral and Abdominal Pores*.—We counted total number of femoral and abdominal pores, combining counts from left and right sides.

Widespread among lizards (Cole 1966), femoral pores are thought to passively deposit pore secretions as lizards move through their environment (Jared *et al.* 1999). Not surprisingly, the secretions function in chemical communication (Cooper & Vitt 1984; Martin & Lopez 2000). In teiids, pores usually open through partially fused scales at the line of transition between the flat subtriangular prefemoral scales and the oval to rounded granular scales covering the postaxial surface of the thigh. The compound pore-bearing scale usually consists of one of the prefemoral or abdominal scales and 2–6 granular scales forming a rosette. In contrast, pores of *Dracaena* open in the center of single, oval scales.

Counts vary widely among teiids and show weak or no sexual dimorphism, even in morphometric studies of the pores themselves (Imparato *et al.* 2007). *Dracaena* has 1–2 pores on each thigh separated by about five scales from 2–4 pores on each side of the abdomen (8–11 pores total in our sample). The highest counts occur in large *Cnemidophorus* of the Dutch Antilles (up to 86 pores) and *Ameiva erythrocephala* (69–78). *Callopistes* is unique among teiid genera for lacking pores in both sexes.

97. *Gap Between Femoral and Abdominal Pores*.—A gap of 2–6 scales (Fig. 40) separates the femoral from abdominal pores (0) or the femoral and abdominal pores are continuous (1).

A gap of 2–6 scales separates the femoral from the abdominal pores in *Crocodilurus*, *Dracaena*, and *Tupinambis*. A similar gap of 1–3 scales usually separates the distal-most 1–2 femoral pore-bearing scales from other scales in the series in *Tupinambis merianae*. This distal gap is not ordinarily present in other Tupinambinae examined in this study, however these species have fewer femoral pores than *T. merianae*. One *T. teguixin* (UF 87920) has a two-scale distal gap on one side only. The Teiinae lacks distal a distal gap.

98. *Count of Scales Between Femoral Pores*.—Species of Teiinae are thought to lack abdominal (often referred to as “preanal”) pores (e.g., Vanzolini & Valencia 1965). However, the row of prefemoral pores extends onto the abdomen in many species. Most Teiinae, have a single pore on the abdomen on each side, whereas some such as *Cnemidophorus* from the Dutch Antilles have 3–4 abdominal pores on each side. In contrast, the pores fail to reach

the proximal edge of the leg in *Ameiva anomala* and *A. bridgesii* even though both species have relatively high counts. In most Teiinae, the pores extend to the distal end of the thigh. However, they only extend about halfway in *Kentropyx striata*. As in gymnophthalmids (Kizirian 1996), the point at which femoral pores become abdominal pores is often difficult to locate. To quantify proximal extent of the pores, we counted the number of scales separating the proximal-most pores.

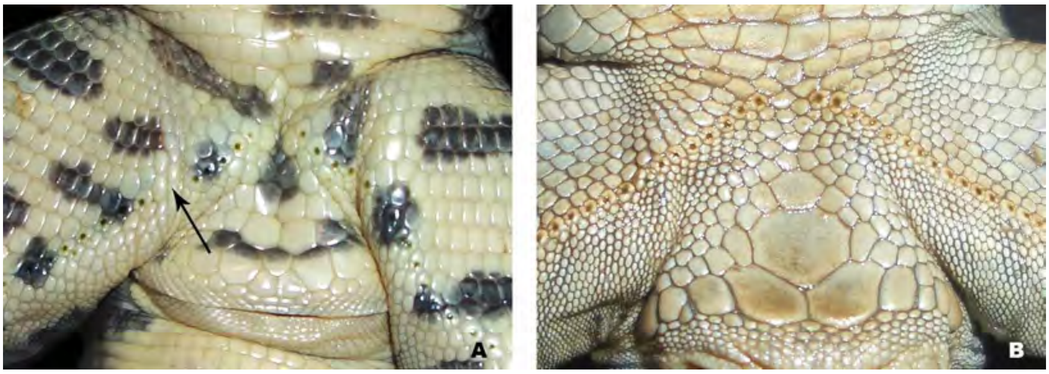

FIGURE 40. Gap between femoral and abdominal pores (character 97) in *Tupinambis palustris* (UTA 59492, A) and *Cnemidophorus ruthveni* (UMMZ 57275, B).

99. *Expansion of Scales at Heel*.—Scales at the heel are numerous and relatively small (0), consist of three relatively large, but subequal scales (1), or consist of one very wide ventral and one wide postaxial shield (2). Based on morphological intermediacy, we ordered this character as follows: 0 > 1 > 2.

In teiids, the subdigital lamellae of the first toe continue as a single row of robust, triangular scales to the heel. In *Aspidoscelis* and Central American and western *Ameiva* two widened plates lie postaxial to the most proximal of these triangular scales (99.2), roughly marking the posterior border of the plantar surface (Fig. 41). The ventral plate is about 3X as wide as long, whereas the postaxial plate is about 2X as wide as long. One or two small granular scales separate the enlarged ventral plate from the robust triangular scales. In most other teiids, 4–10 more or less subequal rectangular plates occupy the same space spanned by these two widened scales. Two *Ameiva* (*A. orcesi* and *A. edracantha*) and some southern *Cnemidophorus* have an intermediate condition of three relatively large, subrectangular scales at the heel (99.1).

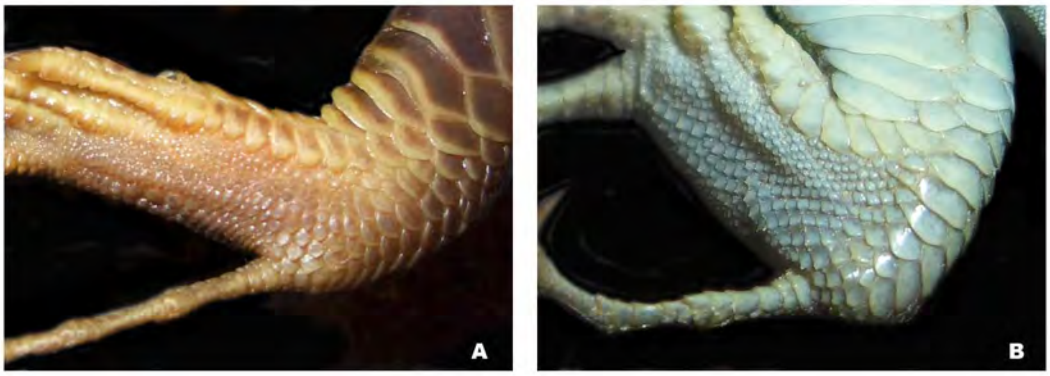

FIGURE 41. Numerous scales at heel of *Cnemidophorus nigricolor* (AMNH 111057, A) contrasted with greatly expanded scales at heel (character 99) of *Holcosus festivus* (UTA 39975, B).

100. *Tibiotarsal Shields*.—Tibiotarsal shields are absent (0) or present (1).

Most teiids have relatively small, subrectangular scales along the postaxial edge of the leg at the tibiotarsal articulation (100.0). In most species of northern *Cnemidophorus*, a row of 5–8 greatly widened scales (3–5 times as wide as long, Fig. 42) extends from the heel onto the distal one-third of the shank (100.1). *Cnemidophorus leucopsammus, C. nigricolor, C. rostralis*, and *C. vanzoi* exhibit a somewhat intermediate condition: the tibiotarsal scales are large but not as greatly widened in these species (100.1). Also, in these species, individual shields in the series are frequently divided.

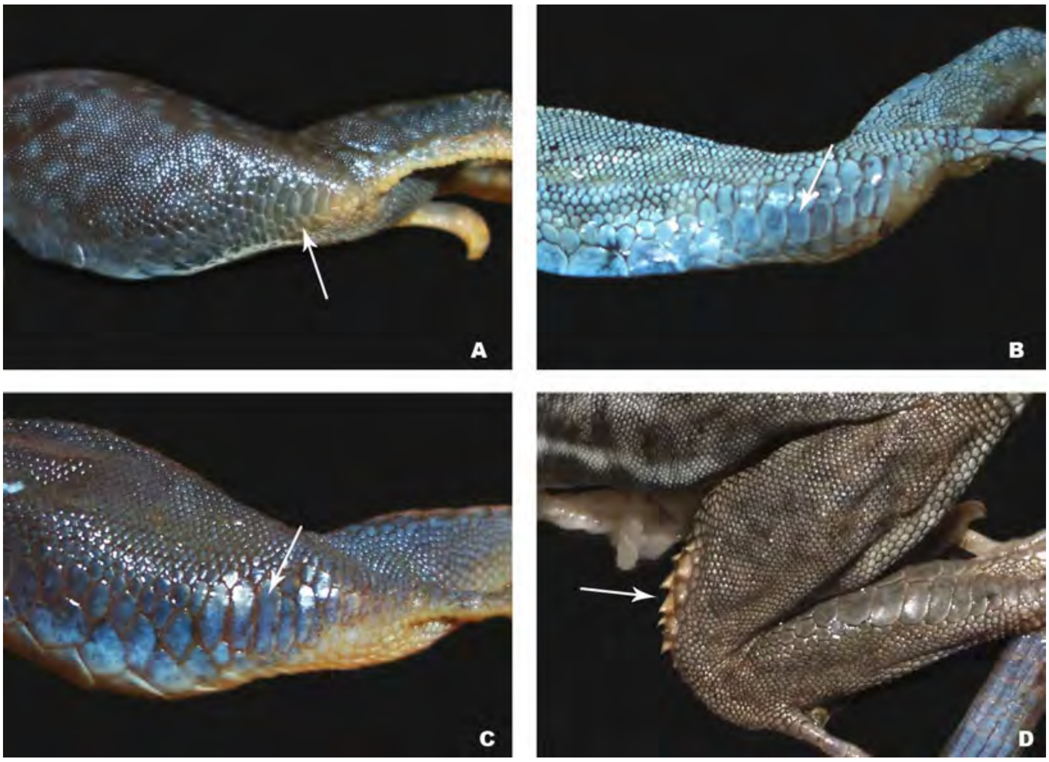

FIGURE 42. Undifferentiated scales at distal end of tibia in *Ameiva griswoldi* (UF 11361, A) contrasted with tibiotarsal shields (character 100) of *Cnemidophorus nigricolor* (UCM 45300, B) and *C. gramivagus* (TCWC 46125, C) and tibiotarsal spurs (character 101) of *A. auberi* (USNM 306540, D).

101. *Tibiotarsal Spurs*.—Tibiotarsal spurs are absent (0), form a cluster of scales with elongate mucrons (1), or consist of a single row of scales with thickened, elevated, and pointed distal edges (2). This character was unordered in all analyses.

In some Caribbean *Ameiva*, two rows of about four (eight total) sharply mucronate scales are positioned along the postaxial edge of the distal end of the shank (101.1) (Fig. 42). These tibiotarsal spurs separate small granular scales on the dorsal side of the shank from large, flat scales on the ventral side. Tibiotarsal spurs are well developed in *Ameiva auberi* from Cuba and *A. dorsalis*. On the other hand, specimens of *A. auberi* from the Bahamas usually lack these structures. USNM 49461 is the only specimen from the Bahamas with moderately developed spurs. In our samples, the structures do not appear to change dramatically during ontogeny and do not appear to be sexually dimorphic. Intraspecific variation in *A. auberi* appears to have a geographic basis, but this character should be examined in larger samples to assess this hypothesis.

In the same postaxial position as in some Caribbean *Ameiva*, *Cnemidophorus longicauda* and *C. tergolaevigatus* have a row of three or four large triangular scales bordering the dorsal granules (101.2). The distal ends of these scales are greatly thickened, elevated, and pointed dorso-distally. These structures are not as distinctive as the spurs of Caribbean *Ameiva* and almost certainly evolved independently.

Finally, we found well-developed tibiotarsal spurs in all *Cnemidophorus ocellifer* from Bahia (*n* = 1) and Paraguay (*n* = 4). As in other species, there is no apparent sexual dimorphism in this species. The spurs of *C. ocellifer* more closely resemble those of *C. longicauda* and *C. tergolaevigatus* than those of northern Antillean *Ameiva* (101.2), but they are arrayed in two rows and number about 12–15 scales. On the other hand, none of the *C. ocellifer* from Mato Grosso (*n* = 5) had tibiotarsal spurs. The postaxial scales on the distal end of the tibia in this population are subtriangular, but lack long pointed mucrons.

Although rarely mentioned in recent literature (but see Arias *et al*. 2011a,b), the importance of tibiotarsal spurs has been appreciated since the 1800s. For example, in his review of *Ameiva*, Cope (1862) followed Gray (1845) in dividing the genus into sections and referred *A. auberi* and *A. dorsalis* to his section D defined by "inner aspect of heel with spinous tubercles" (p. 61, Cope 1862). The function of the spurs is unknown. During what Noble and Bradley (1933) called the third phase of courtship, male *Ameiva chrysolaema*, *A. exsul*, and *Aspidoscelis sexlineata* use their foot to push while vigorously rubbing their leg against their partner's leg. Presumably, tibiotarsal spurs would give purchase during this behavior or perhaps enhance stimulation. Observation of courtship in species with tibiotarsal spurs would test these hypotheses.

102. *Count of Digital Lamellae Below Fourth Toe*.

103. *Texture of Subdigital Lamellae of Fourth Toe*.—The distal subdigital lamellae of the fourth toe are smooth to tuberculate (0) or sharply keeled (1).

104. *Scales Separating Supradigital from Subdigital Lamellae of Toes*.—Scales between the subdigital and supradigital lamellae of the toes are small and mostly restricted to phalangeal articulations (0), form a continuous row along the postaxial edges of all the toes (1), form a low serrate row of keeled scales along the postaxial edges of toes 2–4 (2), or are reduced to 0–1 small scales at the phalangeal articulations of the fourth toe (3). Based on morphological intermediacy, we ordered this character as follows: 3 > 0 > 2 > 1.

Pedal supradigital and subdigital lamellae contact one another between phalangeal articulations in southern *Cnemidophorus*, *Aspidoscelis*, *Ameiva edracantha*, and Central American, western, and most Antillean *Ameiva* (Fig. 43). Nonetheless, small granular or keeled scales separate the lamellae at the phalangeal articulations along the postaxial edges of the toes in these species (104.0). *Ameiva lineolata* and *A. maynardi* lack even these scales or have a single small granule positioned between the lamellae at the distal end of the articulation (104.5).

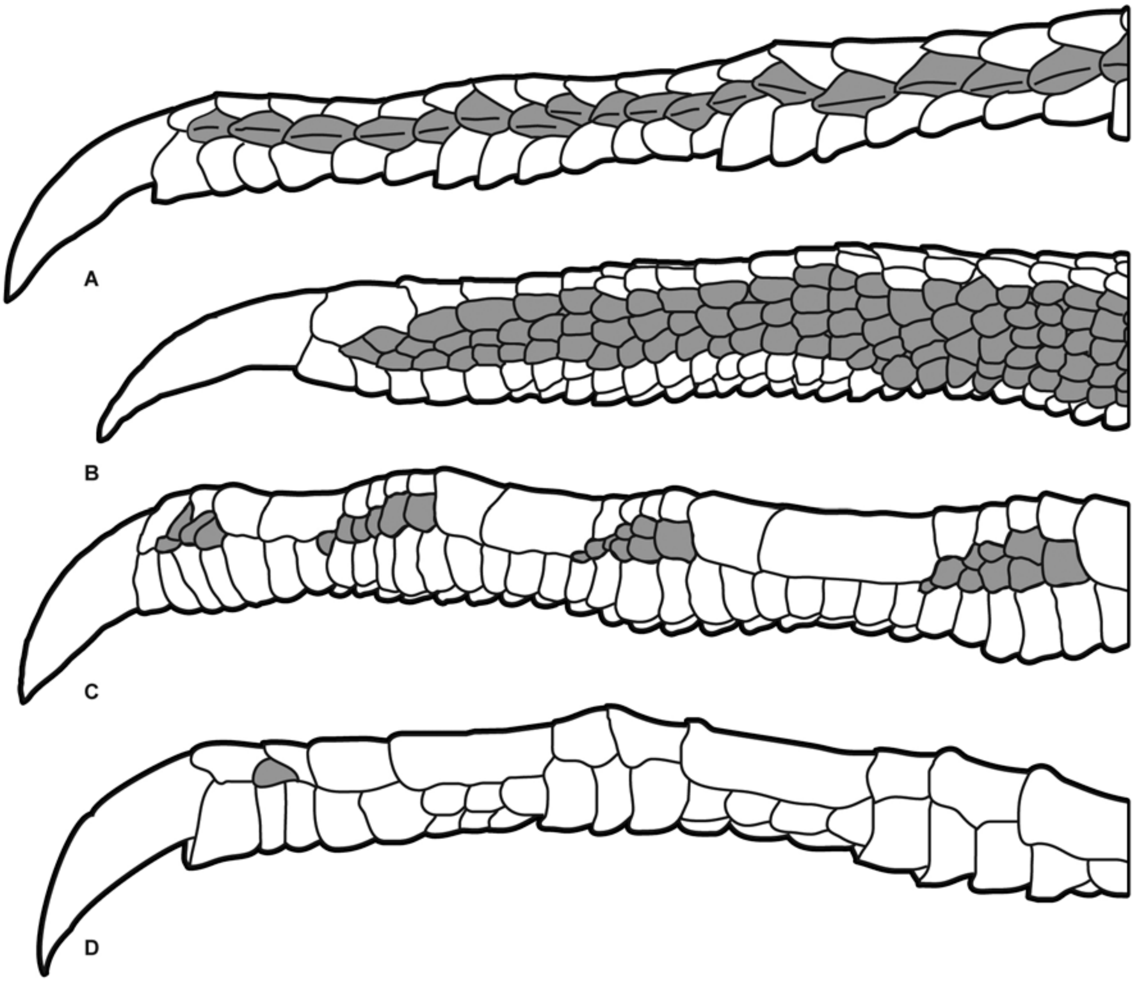

FIGURE 43. Postaxial scales separating supradigital from subdigital lamellae of Toe IV (character 104) in *Cnemidophorus gaigei* (UMMZ 54893, A), *Salvator merianae* (UTA 59492, B), *Ameiva griswoldi* (UF 11361, C), and *Ameiva lineolata* (UF 90810, D).

Complete separation of supradigital and subdigital lamellae takes several forms. In most specimens of *Cnemidophorus lacertoides*, the granular scales completely separate the lamellae of Toes II–III, but lamellae still contact one another on the fourth and fifth toes (104.0). Small granular or keeled scales separate the digital lamellae of all toes in Cis-Andean *Ameiva*, northern *Cnemidophorus*, *Kentropyx*, and Tupinambinae (104.1). In *Teius teyou*, a continuous row of scales separates the lamellae along the postaxial edges of Digits II–IV (104.2). In this species, the scales are smooth proximally and keeled distally, whereas they are all keeled in *Dicrodon guttulatum*, *Cnemidophorus longicauda*, and *C. tergolaevigatus* (104.2). In each of these species, the fifth toe resembles most other Teiinae in having these scales only present at the phalangeal articulations.

This character suite rarely shows polymorphism. Among specimens of *Ameiva chrysolaema*, 40% (n = 10) have state 1 and 60% have state 0. However, the lamellae do not contact one another on the first phalanx in this species. Moreover, contact between lamellae on the distal phalanges of *A. chrysolaema* is somewhat irregular: granules extend further from the articulations than in other species with state 0. Some Lesser Antillean *Ameiva* exhibit an intermediate condition similar to *A. chrysolaema*. In *A. corvina, A. erythrocephala,* and *A. pluvianotata,* granules on the fourth toe mostly separate the lamellae, although distal lamellae of the penultimate and last phalanges are usually in point contact with one another. However, lamellae of the fourth toe are completely separated in UF 11364-6 (*A. pluvianotata*) and only the longest supradigital lamella contacts a subdigital lamella of the last phalanx in UF 11387-1 (*A. erythrocephala*). Nonetheless, the lamellae broadly contact one another on the fifth toes of all specimens in these species (104.0). Of the Caribbean species examined in this study, complete separation of lamellae on all toes occurs only in *A. fuscata* (104.1).

105. *Denticulate Fringe Along Postaxial Edge of Outer Toes*.—Scales separating the supradigital from subdigital lamellae along the postaxial edge of the outer toes are keeled or granular (0) or widened laterally to form a denticulate fringe (1).

Development of a denticulate fringe (Fig. 44) along the postaxial edge of the outer toes has been used as a diagnostic feature of some species of *Kentropyx* (e.g., key of Avila-Pires 1995), where this structure is best developed in *K. altamazonica*. In *K. altamazonica*, *K. borkiana*, *K. calcarata*, *K. pelviceps*, and *K. striata*, the scales are greatly enlarged and form a distinctive denticulate fringe along the digits (105.1). The fringe is not as well developed in the southern species *K. lagartija, K. viridistriga,* and *K. vanzoi* (105.0).

In all *Kentropyx*, a serrated fringe is also present along the most proximal phalanx of the fifth digit. Usually this short preaxial fringe consists of four scales, the last extending beyond the phalangeal articulation and the second greatly enlarged and projecting. These same preaxial scales are present in *Dicrodon* and some *Cnemidophorus*, but they do not project as far from the digit as in *Kentropyx*.

106. *Enlarged Scales Between the Fourth and Fifth Toes*.—A row of noticeably enlarged scales, continuous with the row of scales separating the digital lamellae is absent (0) or present (1).

These scales (Fig. 44) appear to be unique to *Kentropyx*. They form a continuation of the postaxial fringe in *K. altamazonica* and *K. calcarata*, but are also well-developed in all other species of the genus where they are keeled and about as large as the keeled scales separating the digital lamellae. As discussed above (104.1), northern *Cnemidophorus* also have a well-defined, continuous row of large keeled scales between the lamellae, however these scales do not continue onto the postaxial edge of the foot.

While examining the sole of the foot, we noticed that some species have a well-defined row of noticeably enlarged scales proximal to the fourth toe. These scales are particularly developed in some *Ameiva* (e.g., *A. festiva*, *A. leptophrys*) and *Cnemidophorus* (e.g., *C. nigricolor*). Most species have slightly enlarged scales covering the postaxial edge of the foot and plantar surface proximal to the fourth toe. However, the same area is covered in tiny granular scales in some species such as *Teius teyou* and *A. bifrontata*. Although condition of scales in this region may be another potential source of characters, it requires further study.

107. *Reduction of Fifth Toe*.—When adpressed, the fifth toe is long, the base of the claw extending beyond the level of skin between the third and fourth toes (0), shortened, the base of the claw not surpassing the skin between the third and fourth toes (1), or vestigial (2) (Fig. 45). Based on morphological intermediacy, we ordered this character as follows: 0 > 1 > 2.

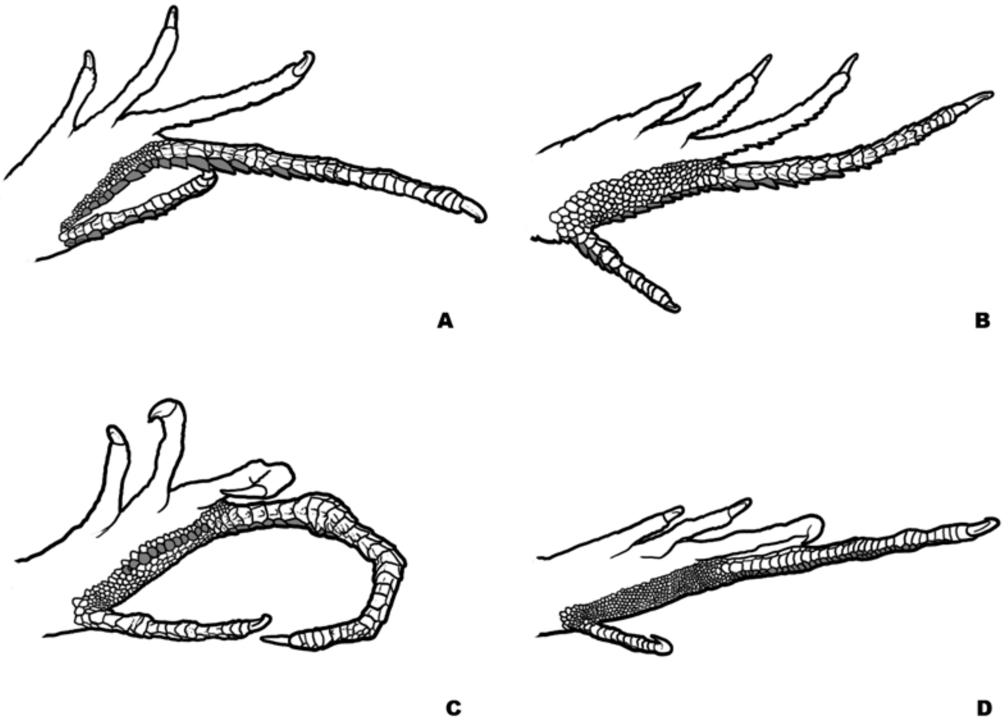

FIGURE 44. Denticulate fringes along postaxial edge of outer toes and enlarged scales between the fourth and fifth toes (character 105 and 106) in *Kentropyx altamazonica* (TCWC 40403, A) and *K. vanzoi* (UTA59489, B) contrasted with unmodified scales of *Cnemidophorus lemniscatus ssp.* (CM 7271, C) and *Ameiva bifrontata divisa* (UMMZ 55027, D).

All teiids have five toes. However, as Vanzolini and Valencia (1965) noted, there is a tendency for the fifth toe to be shortened. They compared length of the fifth toe to the hallux, and noted that the fifth toe is shorter and "very weak" in *Dicrodon* and *Ameiva*. However, this description only applies to some species of *Ameiva* (e.g., species of the *A. ameiva* and *A. bifrontata* complexes, *A. leptophrys*, and *A. undulata*). Both species of *Dicrodon* have shortened fifth toes (107.1), but the fifth toe of *D. heterolepis* is substantially longer than the very short fifth toe of *D. guttulatum*. The fifth toe is shortened in *Aspidoscelis angusticeps, A. burti, A. exsanguis, A. laredoensis,* and *A. montaguae* and long in the other species we examined. Finally, *Cnemidophorus ocellifer* also has a shortened fifth toe. We suspect that the fifth toe is reduced in other species of the *C. ocellifer* Complex, but the character has not been mentioned in recent descriptions of these species. A photo of *C. venetacaudus* (Arias *et al.* 2011a, their figure 4) clearly reveals that this species has a shortened fifth toe.

Reduction of the toe is apparently due to shortening rather than loss of phalanges: all teiids except *Teius* have four phalanges in the fifth toe. The vestigial fifth toe of *Teius* consists of a small nub and lacks phalanges (Greer 1991). The nub is supported ventrally by a thick, keeled, cup-shaped scale, presumably (based on its appearance and position) homologous with a subdigital lamella. Two to three keeled scales cover the nub dorsally, and 4–5 small scales cap the nub distally.

The fifth toe of most teiids extends beyond skin between the third and fourth toe, but not beyond the first free interphalangeal articulation. The fifth toe of *Crocodilurus* is unusually long and extends beyond this articulation.

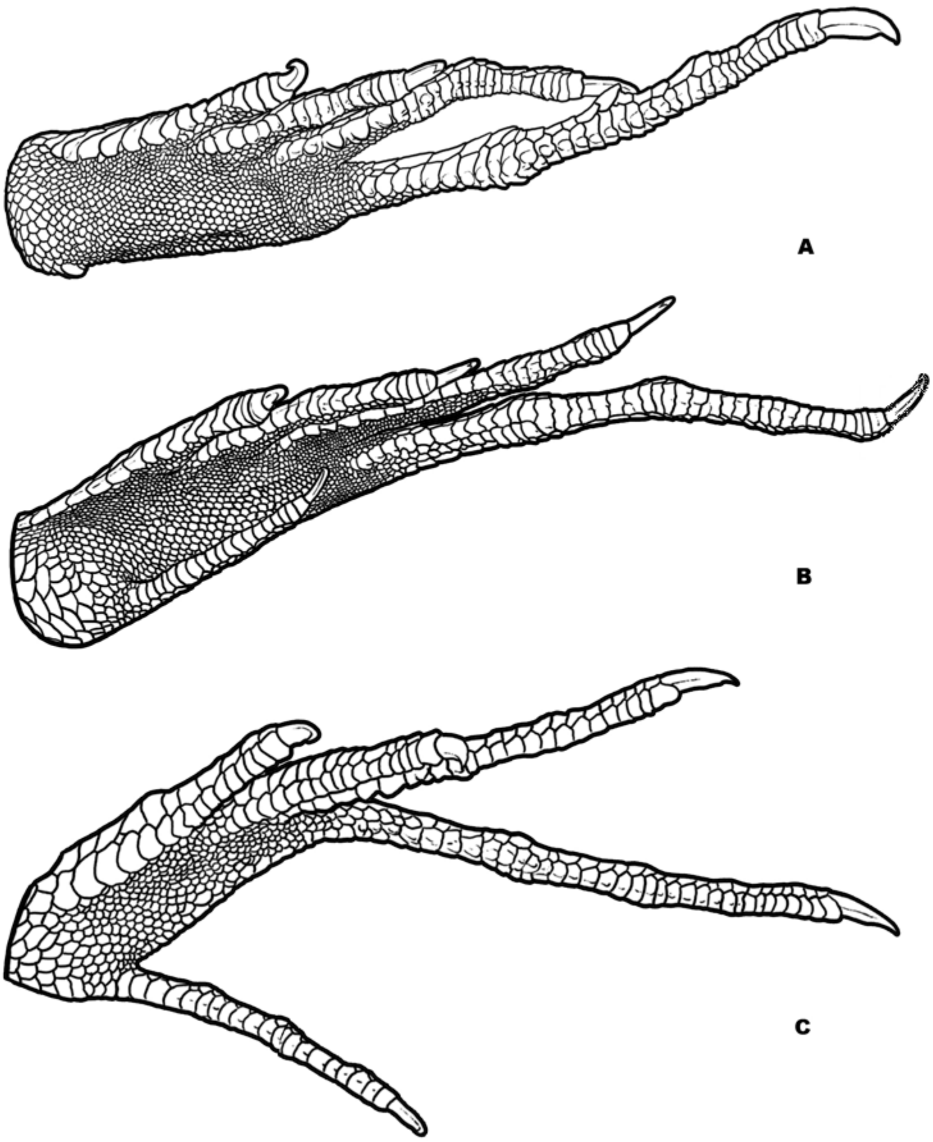

FIGURE 45. Vestigial fifth toe (character 107) on foot of *Teius teyou* (FMNH 44155, A) contrasted with shortened fifth toe of *Ameiva ameiva* (NMNH 80616, B) and long fifth toe of *Cnemidophorus rostralis* (SDNHM 34890).

Scale Surface Morphology and Generation Glands

108. *Dorsal Scale Surface Morphology.*—The dorsal scale surfaces are covered in macrohoneycomb (0), short aligned macroridges (1), or long aligned macroridges (2). This character was unordered in all analyses.

The dorsal scales of teiids exhibit variation in microscopic sculpturing of the β-keratin containing layers (Gasc *et al.* 1982). These types of characters generally fall into two categories (Harvey & Gutberlet 1995, 2000). Subcellular features such as spinules and pits are best studied with scanning electron microscopy, whereas larger structures such as macrohoneycomb and lamellae can be observed with light microcopy. Macrohoneycomb (Fig. 46) form through folding of both the alpha and β-keratin containing layers of the epidermis (Harvey 1991; Harvey & Gutberlet 1995, 2000). They are widespread among lizards, occurring in cordylids, xenosaurids, shinisaurids, varanids, and iguanians. Macrohoneycomb covers the dorsal scales of most teiids, although *Kentropyx* and western *Ameiva* have macroridges covering areas on either side of the keel.

As in other lizards (Harvey & Gutberlet 1995, 2000), ventrals of teiids tend to be smooth or to have low relief microstructure best developed in the hinge region of scales. Nonetheless, high relief macrohoneycomb and microridges appear with keels on the ventral surfaces of the tail. Moreover, species with keeled proximal subcaudals such as *Ameiva anomala* and *Cnemidophorus lacertoides* also have high relief scale surface features located proximally on the tail. The heavily keeled ventrals of *Kentropyx* are uniformly covered in high relief macroridges indistinguishable from those on the dorsum.

Macrohoneycomb also covers scales of most Tupinambinae, although some noteworthy modifications to this morphology occur in this subfamily. The scales of *Callopistes* and *Dracaena* have typical macrohoneycomb, indistinguishable from that of most Teiinae. The larger dorsal scales of *Tupinambis* lack high relief sculpturing and are uniformly covered in simple (i.e., lacking dentate margins like those of scincids and dibamids) lamellae. The lamellae in Tupinambinae resemble those of gerrhosaurids, described in detail by Harvey and Gutberlet (1995). Nonetheless, macrohoneycomb is well developed on the small granular scales surrounding the flat dorsals in *T. merianae* and *T. rufescens*. We found no trace of macrohoneycomb on scales taken from adult and subadult *T. palustris* (n = 1) and *T. teguixin* (n = 5). In these two species, simple lamellae cover all scale surfaces, including the small dorsal granules between larger scales. However, a single hatchling *T. teguixin* (UF 87920, SVL 101 mm) has high relief, aligned macroridges (108.2) on its supracaudal scales. Lamellae also uniformly cover these scales and overlap the macroridges. Dorsal body and thigh scales of *Crocodilurus amazonicus* resemble those of the *T. teguixin* group in being uniformly covered in lamellae and high relief sculpturing; however, long, narrow, closely spaced ridges cover the supracaudals.

The rare types of high relief sculpturing described above for western *Ameiva*, *Kentropyx*, hatchling *T. teguixin*, and *Crocodilurus* likely evolved through modifications to macrohoneycomb. The macroridges of western *Ameiva* and *Kentropyx* are sufficiently similar that we assign them the same character state (108.1). They cover all scales of the body in these species. The ridges in hatchling *T. teguixin* and adult *Crocodilurus* only occur on the tail. We do not assign these species the same character state as the Teiinae, because the ridges are much more elongate (108.2). We may be mistaken about the homology of the ridges of these two species of Tupinambinae, but their apparent absence from dorsal scales other than those of the tail appears to be unique among teiids.

109. *Scale Organs on Dorsal Body.*—Dorsals have one subterminal scale organ positioned in the middle of the scale (0), up to three organs with two positioned laterally on the posterior one-fourth of the scale and the third at the posterior edge (1), or no apparent organs on the dorsal surfaces of the scales (2). Based on morphological intermediacy, we ordered this character as follows: 2 > 0 > 1.

Knowledge about the morphology and distribution of lenticular scale organs has advanced substantially in recent years (Harvey 1991; Harvey & Gutberlet 1995, 2000; Irish *et al.* 1988; Matveyeva & Ananjeva 1995), although few reports of these structures in teiids have been published (Vanzolini & Valencia 1965). In teiids, each dorsal scale on the body, limbs, and tail bears a single, lenticular scale organ located subterminally (Fig. 47). The area surrounding the scale organ is usually darkened by deposition of melanin, so that the organs are quite easy to see at low magnification (5–10X).

Vanzolini and Valencia (1965) reported that *Dracaena* was the only teiid with lenticular scale organs on the trunk. However, with the notable exception of *Kentropyx*, we found scale organs on the dorsals of all teiids. In *Dracaena*, *Crocodilurus*, *Callopistes*, and the Teiinae, the organs are single and positioned subterminally at the highest point of scales (109.0). On keeled dorsals, the organ is positioned atop the keel. This pattern generally holds for both the body and tail, including sides of the tail. An exception to this rule occurs distally on the tail of *Crocodilurus*. There, the keels of supracaudal scales between the dorsolateral crests shift to the edges of the scales (i.e., the keel is located far to the right edge of the scale right of the midline, whereas it is located far to the left on scales positioned left of the midline, Fig. 47). However, the scale organ remains centered, subterminal and, consequently, no longer positioned atop the keel.

The distribution of these structures is complex on the body and tail of *Tupinambis* where dorsals may have 1–3 organs. Moreover, the two groups of *Tupinambis* differ in scale organ distribution. In species of the *T. teguixin* group, 2–3 organs are usually present on middorsal scales (109.1) (Fig. 47). On the flanks and sides of the tail, only one organ is usually present and located medial to the axis of the body. Thus, on the right side of the body, the organ is positioned on the left side of the scale. This pattern of scale organ positioning is widespread among lizards and has been noted previously in *Tropidurus* (Harvey & Gutberlet 2000). In contrast to the *T. teguixin* group, dorsals of the *T. rufescens* group rarely had visible organs on the anterior body or had a single organ positioned subterminally (109.0). On the weakly keeled scales of the posterior body and rump, the organ is positioned atop the keel as in *Dracaena*.

Kentropyx has heavily keeled, mucronate dorsals. Scale organs are not readily apparent on the bodies of any species in this genus (109.2); certainly, they are not positioned atop the keels as in *Dracaena* and *Crocodilurus*. On scales of the neck, the organs are visible and are located at the posterior end of the keel. Careful inspection of several dorsals, with and without removal of the upper β-keratin containing layers leads us to believe that the organs are positioned just below the mucron and, possibly, somehow incorporated into the keel. A better understanding of dorsal scale organ morphology in *Kentropyx* will require advanced histological techniques and is beyond the scope of this study.

110. *Scale Organs on Dorsal Caudal Scales*.—On the supracaudal scales, scale organs are subterminal and centrally located on the keel (0) or paired on either side of the keel (1).

All *Tupinambis* share a similar distribution of scale organs on the tail. The caudal scale organs are paired and located on either side of the keel (110.1). Whereas organs on the body and limbs are round, organs on the keeled scales of the tail are usually elongate ovals in this genus (Fig. 47). On some supracaudals a round organ located further posteriorly than the oval organs may also be present. The organs are single in all other Teiidae (110.0).

111. *Scale Organs on Ventrals*.—The ventral body scales lack (0) or have (1) single, subterminal scale organs.

Ventrally on the trunk, scale organs are generally absent in teiids. In *Tupinambis*, they are present on the small scales forming an incomplete row just posterior to the vent. In *Dracaena*, scale organs are present on scales of the gular region and in the same subterminal position on the keel of ventrals. Under the tail, the organs are present atop the keels of the first two rows of subcaudals, but are absent distally.

112. *Generation Glands*.—Generation glands (Fig. 46) are absent (0) or present (1).

Maderson and Chiu (1970) suggested the term "generation glands" for holocrine secretions that form within the epidermis and are exposed to the external environment with periodic shedding. The glands form as hyperplasia of one or more cell types in the six distinct strata of the lepidosaurian epidermal generation. In geckos, Maderson (1972) distinguished two types of generation glands: "β-glands" in the outermost β-keratin containing layers (β-layer and oberhautchen) and "escutcheon scale-type" glands in the innermost layers (lacunar and clear layers). These structures have been best studied in iguanids (Alexander & Maderson 1972; Dujsebayeva *et al.* 2009), agamids (Boulenger 1885a; Dujsebayeva *et al.* 2007), gekkonids (Kluge 1983; Maderson 1972; Maderson & Chiu 1981), and cordylids (van Wyk & Mouton 1992) where considerable variation exists in their structure, anatomical distribution, and development.

Among teiids, generation glands form on ventral scales of the posterior abdomen, shank, foot, and proximal tail (Fig. 46). They are present in adults of both sexes, although the glands appear more developed in males. At least two types of glands occur. In *Callopistes*, scales in these areas appear collapsed and have calloused distal surfaces. Without more extensive histological study, we cannot assign the glands of *Callopistes* to either of Maderson's (1972) two categories, although we suspect they are the escutcheon scale-type glands. The glands of other teiids apparently are β-glands, because they are embedded within the β-keratin containing layers and are entirely contained in β-layers removed by pressing on the edge of intact scales. In contrast to the glandular scales of *Callopistes*, glandular scales of other teiids appear smooth and convex at low magnification rather than collapsed and calloused. In teiids, the glandular material is pigmented and forms an "arabesque" or spotted pattern (Fig. 46) across the scale. These pigmented scales are easily seen with a stereoscope in adult *Dicrodon*, *Teius*, most Caribbean *Ameiva*, and *Tupinambis merianae* (112.1).

β-glands occur in the *Ameiva bifrontata* complex and many northern *Cnemidophorus*, however they are pigmented and clearly visible with a stereoscope only in *C. murinus* and *C. ruthveni*. In other members of these groups, we removed "loose scales" from the posterior abdominal and proximal tail scales and examined the scales with a compound microscope. Unpigmented β-glands similar in size and distribution to the pigmented glands of *C. murinus* are unequivocally present in the *A. bifrontata* complex and in *C. arenivagus*, *C. arubensis*, *C. gramivagus*, *C. lemniscatus splendidus*, *C. vanzoi*, and two undescribed northern *Cnemidophorus* (112.1). Under a stereoscope the glands are not visible, and the ventral scales of these species appear uniformly black (in the case of *C. nigricolor*) or white.

Absence of generation glands must be interpreted with caution. With a compound microscope, we also examined the β-keratin containing layers of ventral abdominal and tail scales of most species examined in this study. We can unequivocally state that glands are absent in most other cnemidophorines. They are clearly absent from the *Ameiva ameiva*, *A. atrigularis*, *A. pantherina*, *A. praesignis*, *A. edracantha*, Central American *Ameiva*, western *Ameiva*, *A. fuscata*, *A. pluvianotata*, and southern *Cnemidophorus*. Several species of northern *Cnemidophorus* were returned to the loaning institutions before we developed this technique for observing the glands (112.?); all other species of this group have generation glands. We found no trace of generation glands on specimens of *Crocodilurus*, *Kentropyx*, or species of the *Tupinambis teguixin* group. Although most of our specimens of *T. teguixin* were young adults, our sample included a large Colombian male (MHUA 10394, SVL 400 mm) that clearly lacked these glands.

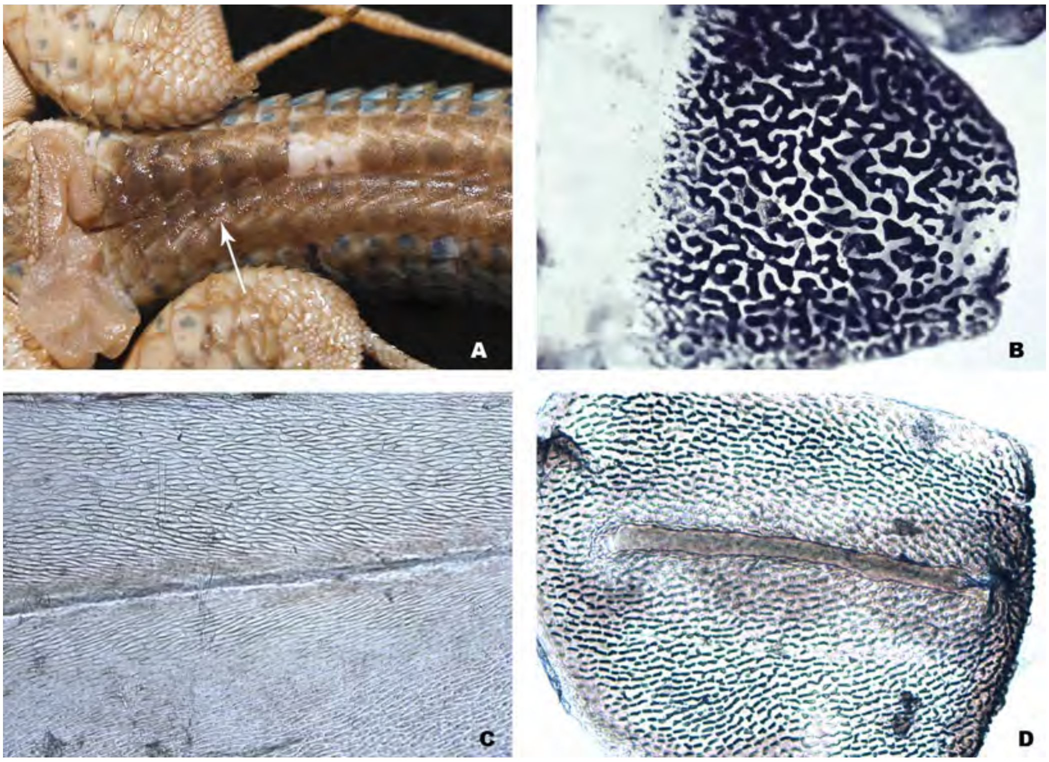

FIGURE 46. Generation glands (character 112) on ventral body and tail of *Dicrodon heterolepis* (KU 163770, A) and ventral aspect of β-keratin containing layers showing black-pigmented generation glands (B) removed from specimen in A. Macrohoneycomb (character 108) covering dorsal caudal scale of *Ameiva chrysolaema* (KU 232040, C) and macroridges covering dorsal body scale of *Holcosus anomalus* (AMNH 109685, D).

We noted some interspecific variation in the distribution of generation glands, although when present in a species, the glands were evident in all adult specimens examined. Nonetheless, one study (Maderson 1972) found well-developed generation glands in only 10% of *Coleonyx brevis.* As Maderson (1972, p.568) remarked, "whether this represents regular individual variation, or a condition that varies from one shed to the next is unknown."

Coloration

113. *Snout Coloration*.—In life, the tip of the snout (and sometimes the area peripheral to the eye) is not red (0) or reddish to brick red (1) (Fig. 48).

Reddish, brick red, or blood red snouts occur only in the *Ameiva bifrontata* complex and in most *Ameiva* from the West Indies (113.1). *Ameiva dorsalis*, *A. lineolata*, *A. polops*, and *A. wetmorei* lack red snouts (113.0). The most extensive red coloration occurs in *A. erythrocephala*. In this species, all sexes and ages have the snout, sides of the head, area around the eye, part of the temporal region, and sometimes even the anterolateral portion of the neck reddish to bright red. This color tends to be most conspicuous on the snout and does not extend onto the throat, which is of a contrasting white color. In contrast, adult *A. polops* have reddish tones on the sides of the head, chin, and throat, but not on the snout or around the eye. Thus, we do not consider the reddish tones of *A. polops* to be homologous with the red snouts of other species. We were unable to observe photographs of live *A. corax, A. corvina, A. maynardi,* or *A. pluvianotata* and do not know if these species have red snouts. In published accounts (e.g., Schwartz & Henderson 1991), the red coloration has been briefly mentioned for some species, but has most frequently gone unreported.

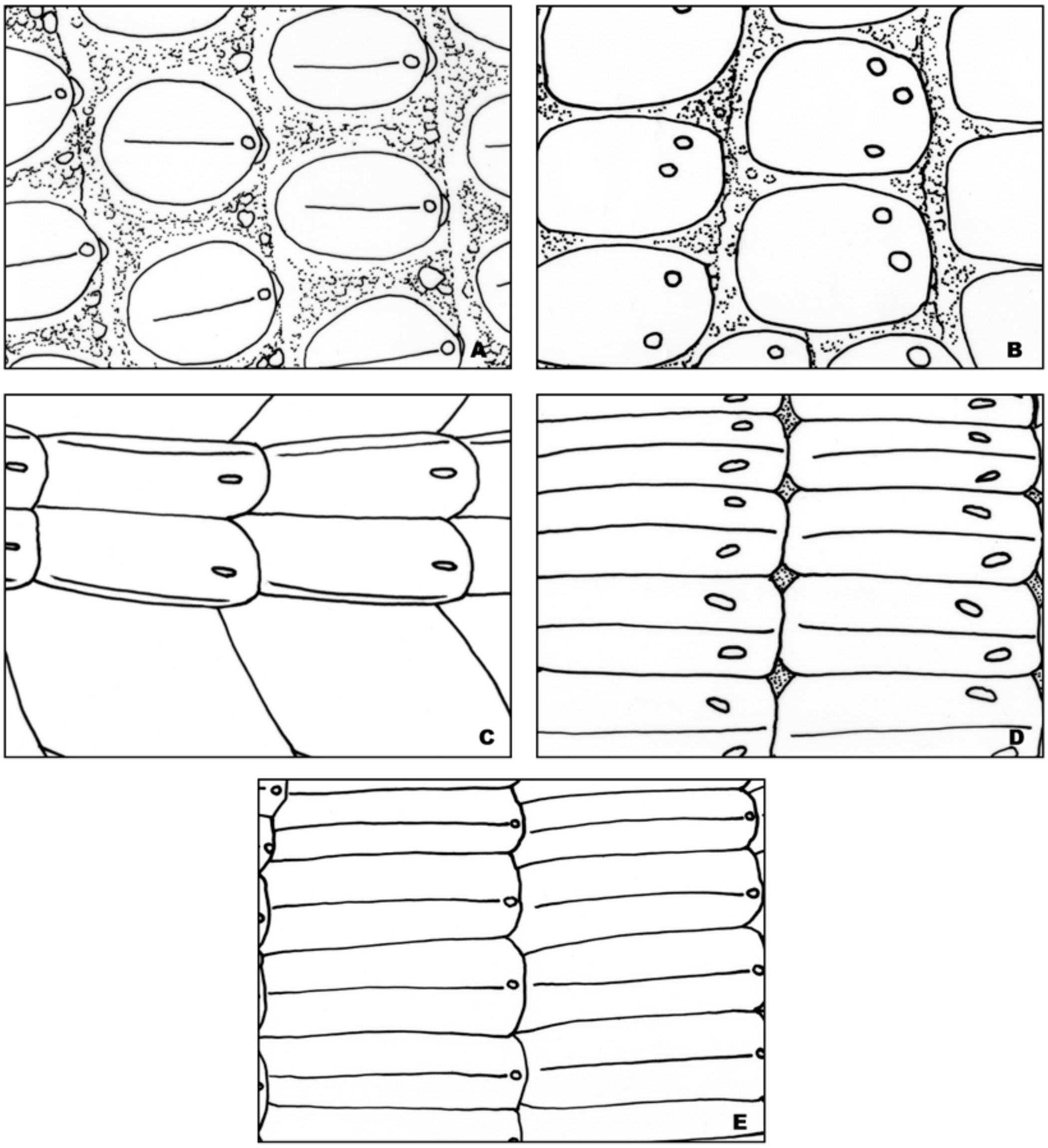

FIGURE 47. Number and distribution of scale organs on dorsals (character 109) of *Crocodilurus amazonicus* (USNM 200689, A) and *Tupinambis teguixin* (UF 130026, B) taken from upper left flank. Scale organs on caudals (character 110) of *C. amazonicus* (USNM 20689, C), *Tupinambis palustris* (UTA 59491, D), and *Ameiva ameiva* (FMNH 56030, E) from middorsal aspect of tail.

This character is most evident in adult males, although it is often present, albeit usually less pronounced, in females and even small juveniles (e.g., figure 78 of juvenile *Ameiva bifrontata* in Ugueto & Rivas 2010, page 193). In at least some species, the red snout undergoes seasonal shifts in intensity, probably related to breeding condition (G. N. Ugueto, personal observation on *A. bifrontata* in Venezuela).

We suspect that other seasonal color variation in teiids is also related to breeding condition. Males (and to a lesser degree females) of several species of northern *Cnemidophorus* show noticeable shifts in brilliance and color intensity (particularly on the flanks and sides of the head, Markezich *et al.* 1997; Ugueto *et al.* 2009). Although previously unreported, males from some populations of *C. arenivagus* and *C. gramivagus* develop noticeably deep reddish tones on the sides of the head, often at times when copulating pairs have been observed [G. N. Ugueto, personal observation. Readers might compare males in our figures 64 (A and B) to figure 13.A of Markezich *et al.* 1997]. Striking differences in coloration of males of other teiids such as *Dicrodon heterolepis* (Fig. 68 C and D) may also develop seasonally.

FIGURE 48. Snout coloration (character 113) of *Ameiva bifrontata bifrontata* from Isla Real, Los Frailes Archipelago, Venezuela (A, photo by T. Barros), *A. bifrontata* ssp. from Península de Paraguaná, Falcón, Venezuela (B, photo by G. van Buurt), *A. auberi sabulicolor* from Guantanamo, Cuba (C, photo by J. Burgess), and *A. griswoldi* from St. John, Antigua (D, photo by W. George).

Adult males of several other teiids (*Ameiva festiva*, *A. leptophrys*, *A. undulata*, *Kentropyx calcarata*, and some populations currently assigned to *Cnemidophorus ocellifer* and *Dicrodon heterolepis*) have orange, pink, or brick red color on the sides of the head. However, this coloration is not concentrated or more intense at the tip of the snout or the periphery of the eye, but usually extends along the sides of the head to the temporal region and towards the chin and throat. Brightly colored throats are common among many species of Teiinae, and the red head coloration in these species is more appropriately considered an expansion of the gular coloration (where red tones are usually brighter, 113.0). In these species, color on the sides of the head is sexually dimorphic, and in some species it may even disappear during non-breeding months.

This interesting aspect of teiid coloration has been under-studied, and additional research is required to document the full extent and significance of these seasonal shifts in color intensity.

114. *Condition of the Light Vertebral Stripe*.—In juveniles, a light vertebral stripe (Fig. 49) extending from the median occipitals to the base of the tail is solid and straight (0), split and straight (1), present and widening substantially on the posterior body (2), straight but broken into spots (3), present only from the mid-dorsum to the sacrum (4), or absent (5). We treated this character as unordered.

We scored several characters of coloration (Characters 114–121) only in juvenile specimens, because adults usually lose some or all of the patterns during ontogeny. The vertebral stripe of some *Cnemidophorus* (e.g., *C. gramivagus, C. murinus, C. ruthveni*) is usually absent or is only faintly indicated and was coded as absent (114.4).

115. *Paravertebral Stripe*.—In juveniles, a light stripe extending from the posterior corner of the parietals or occipitals to the base of the tail is present and solid (0), absent (1), or present and broken (2). We treated this character as unordered.

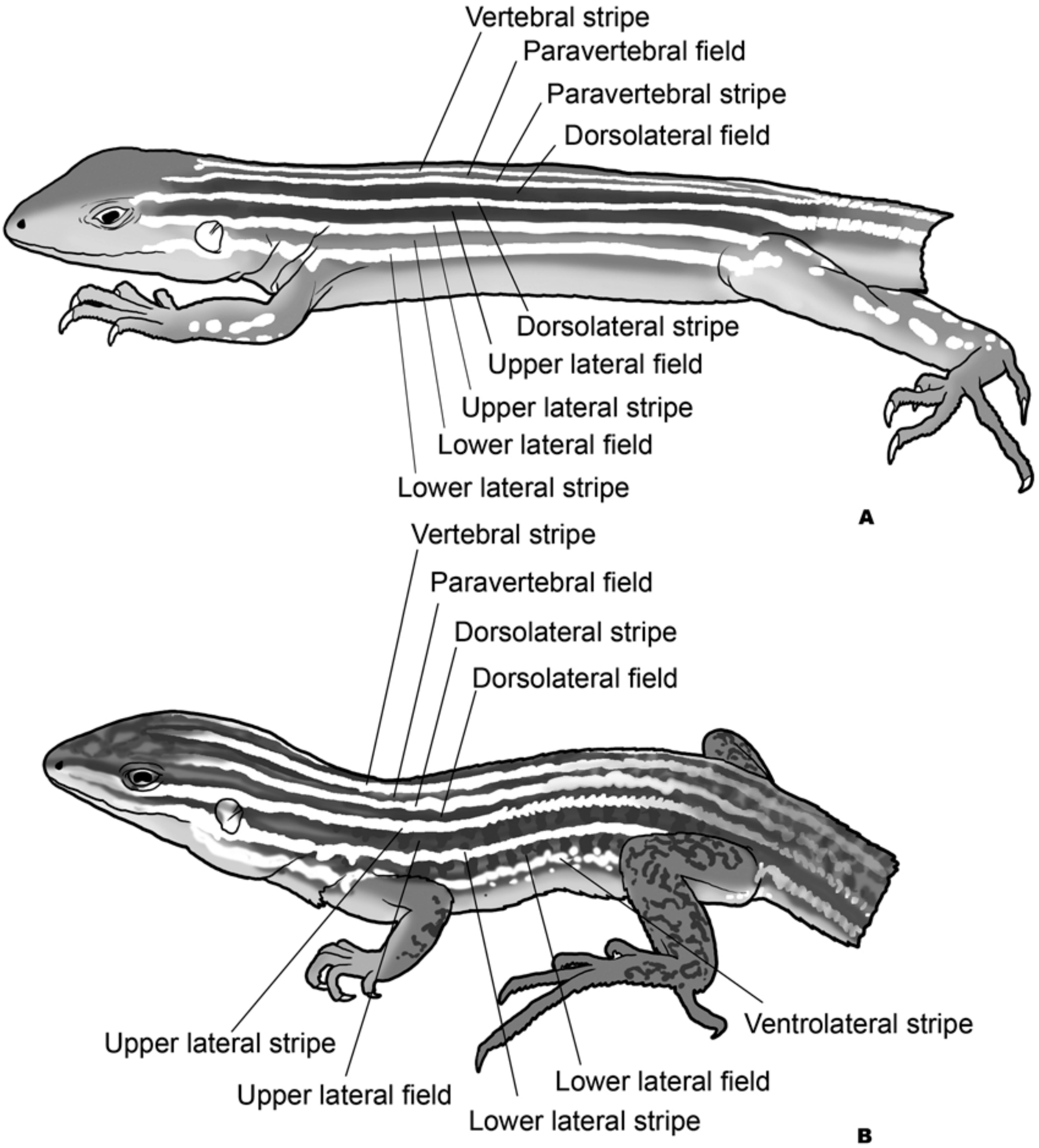

FIGURE 49. Nomenclature of dorsal stripes (characters 114–118 and 120) in *Cnemidophorus senectus* (top) and *Kentropyx striata* (bottom).

This character seems to be variable within populations currently assigned to *Cnemidophorus ocellifer*. Some specimens had distinct paravertebral stripes, whereas others had them broken or completely absent. The paravertebral stripe of *C. flavissimus* always breaks at different points along the dorsum; however, because most of the stripe remains solid, we scored it as present and solid (115.0).

116. *Dark Dorsolateral Field*.—In juveniles a darkly pigmented field usually forming a band edged by paravertebral and dorsolateral stripes is solid (0), solid anteriorly and breaking into spots posteriorly (1), completely broken into blotches (2), or absent (3). Based on morphological intermediacy, we ordered this character as follows: 0 > 1 > 2 > 3.

Juveniles of most *Cnemidophorus* and *Aspidoscelis* and some *Ameiva* have solid dark dorsolateral fields. The dark dorsolateral fields break up into discrete blotches in a few species such as *Ameiva bifrontata, A. edracantha, Cnemidophorus lacertoides*, *Teius teyou*, and *T. oculatus* (116.2). Species with solid fields anteriorly that break up into blotches posteriorly have an intermediate condition in some species such as *C. serranus* and *C. vittatus*.

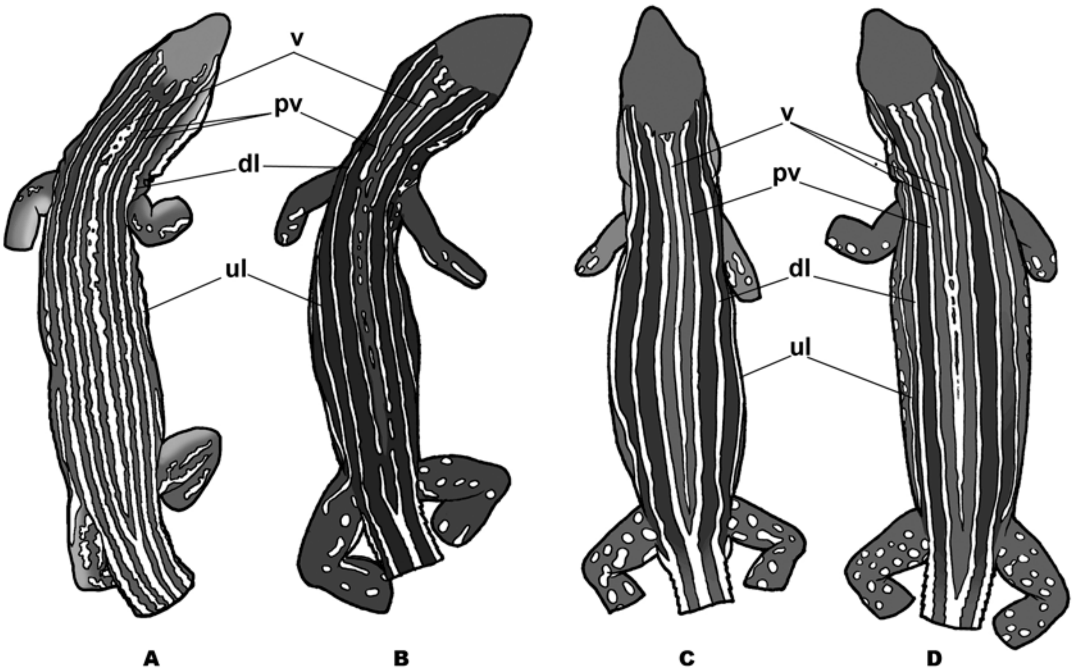

FIGURE 50. Condition of the light vertebral stripe (character 114) in *Aurivela longicauda* (A), *Cnemidophorus flavissimus* (B), *C. senectus* (C), and *C. lemniscatus* (D).

117. *Dorsolateral Light Stripes*.—In juveniles, a light stripe extending from the upper corner of the eye to the rump above the leg is solid to the tail (0), fading towards the head or sacrum (1), broken (2), or absent (3). We treated this character as unordered.

This stripe is only present on the head and anteriormost dorsum in many species of *Kentropyx* (*K. lagartija*, *K. vanzoi*, *K. viridistriga*), *Ameiva wetmorei* and the species of the *Tupinambis rufescens* group (117.1). The dorsolateral stripe of *Cnemidophorus flavissimus* often breaks at some point along the dorsum; however, since most of the stripe remains solid to the tail, we assigned this species state 0.

118. *Dark Lateral Field*.—In juveniles, a darkly pigmented field usually forming a band edged by dorsolateral and upper lateral pale stripes is solid (0), solid anteriorly and breaking into blotches posteriorly (1), completely broken into dark blotches (2), solid with light spots (3), or absent (4). Based on morphological intermediacy, we ordered this character as follows: 0 > 1 > 2 > 3 > 4.

When present, the lateral field begins behind the eye and extends to just above the leg. The field is solid in some species and broken into a series of blotches in others. *Cnemidophorus ocellifer* and *C. mumbuca* have rounded red, yellow, blue or white spots (118.3) within the dark lateral field. Similar brightly spotted lateral fields are present in adult male *Ameiva edracantha* but are absent from juveniles. Thus, this species was scored as not having spots within the lateral field. The dorsolateral fields of some specimens of *Tupinambis teguixin* seem to be broken into blotches at least anteriorly, but because they are rather irregular we decided to err on the side of caution and code this character as unknown (118.?) for *T. teguixin*.

119. *Upper Lateral Light Stripes*.—In juveniles, a light stripe extending from the lower corner of the eye is solid and extending to the groin (0), fading (1), broken to the groin (2), extending above the leg as either a broken or continuous stripe (3), or absent (4). We treated this character as unordered.

In most Teiinae, the upper lateral stripe extends to the groin (119.0–2), however it extends above the leg in *Kentropyx* (except in *K. altamazonica*), in *Ameiva wetmorei*, and in the *Tupinambis rufescens* group (119.3).

120. *Lower Lateral Light Stripes*.—In juveniles, a light stripe extending from the posterior supralabials or lower margin of the ear is solid to the groin (0), fading towards the groin (1), broken (2), or absent (3). We treated this character as unordered.

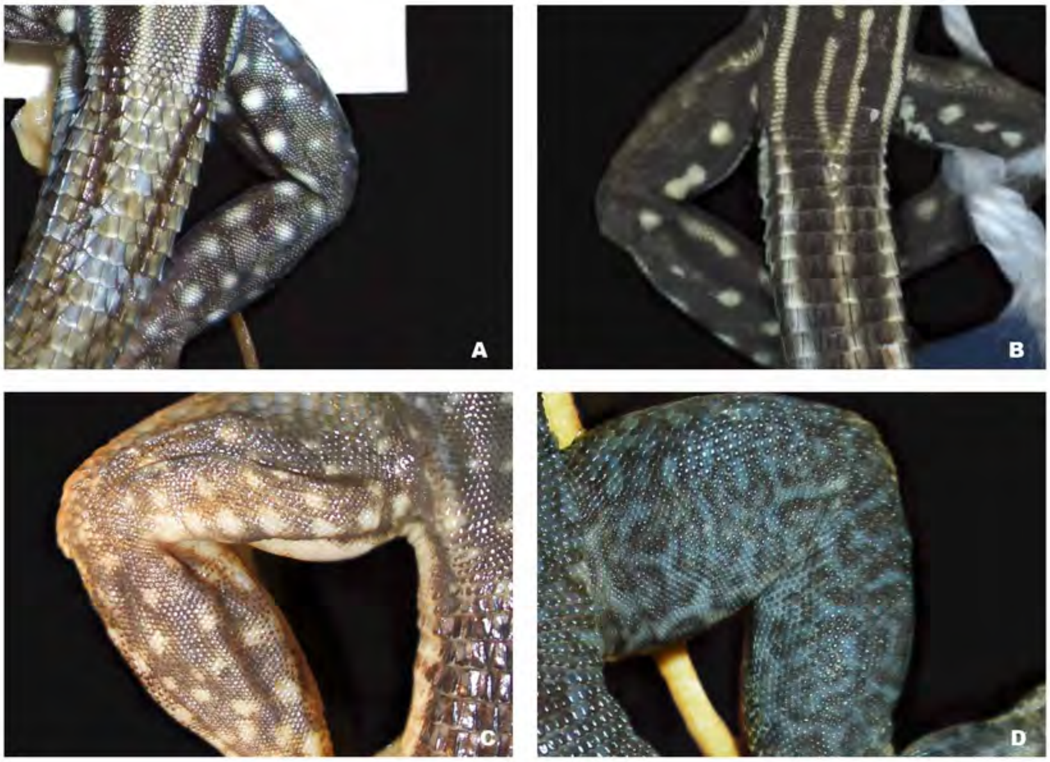

FIGURE 51. Light spots on thighs (character 121) of *Cnemidophorus lemniscatus splendidus* (FMNH 242236, A), *C. flavissimus* (MBUCV 985, B), *Dicrodon guttulatum* (FMNH 53856, C), and *Callopistes maculatus* (FMNH 9934, D).

121. *Light Spots on Thighs*.—In juveniles, round to oval spots on the dorsal aspect of the thighs are present (0) or absent (1).

Usually these spots (Fig. 51) are round, however in some species such as *Cnemidophorus flavissimus* they tend to elongate somewhat. Only species with well-defined spots were scored as having them; species with irregular blotching or marbling (e.g., *C. littoralis*) were scored as lacking spots. We do not consider black-edged ocelli on the thighs of *Callopistes maculatus* and cream specks on the thighs of *Dicrodon guttulatum* to be homologous with the spots of *Cnemidophorus*. The thigh pattern of both species is really just part of the overall dorsal pattern (121.0).

122. *Size of Spots on Flanks in Adult Males*.—Spots on the flanks of adult males (Fig. 52) are small (0) or large (1).

This character is not applicable (122.?) to species without spots. Large flank spots are only found in *Cnemidophorus murinus* and *C. ruthveni* (Ugueto & Harvey 2010). Spots on the flanks of *Kentropyx calcarata* and *K. pelviceps* often merge, forming larger spots or even short transverse bands, but we do not consider these markings to be homologous with the large spots of *C. murinus* and *C. ruthveni*. For this character, we coded *K. striata, Ameiva chrysolaema, A. exsul, A. plei analifera, Dicrodon guttulatum* and *D. heterolepis* as having small spots, however there is considerable variation among subspecies of *A. chrysolaema* and some lack spots on the flanks (e.g., *A. c. boekeri, A. c. ficta*).

123. *Count of Spots on Flanks in Adult Males*.—When present, spots are counted between the groin and axilla (Ugueto *et al*. 2009). In this analysis, we coded female and juvenile specimens as having the mean number of spots observed in males of the same species. Ugueto and Harvey (2010) provide ranges, means, and standard deviations for this character for species of *Cnemidophorus*.

Except for *Kentropyx striata* (22–46 spots, 36 ± 12, n = 7), we were unable to count spots in museum specimens of this genus. Consequently, we relied on good quality color photographs of live adult males. *Kentropyx altamazonica*, *K. lagartija*, *K. vanzoi*, and *K. viridistriga* apparently lack spots as adults. Adult male *K. calcarata* have 14–20 spots (18 ± 2, n = 6) and *K. pelviceps* have 24–35 spots (29 ± 4, n = 4) spots.

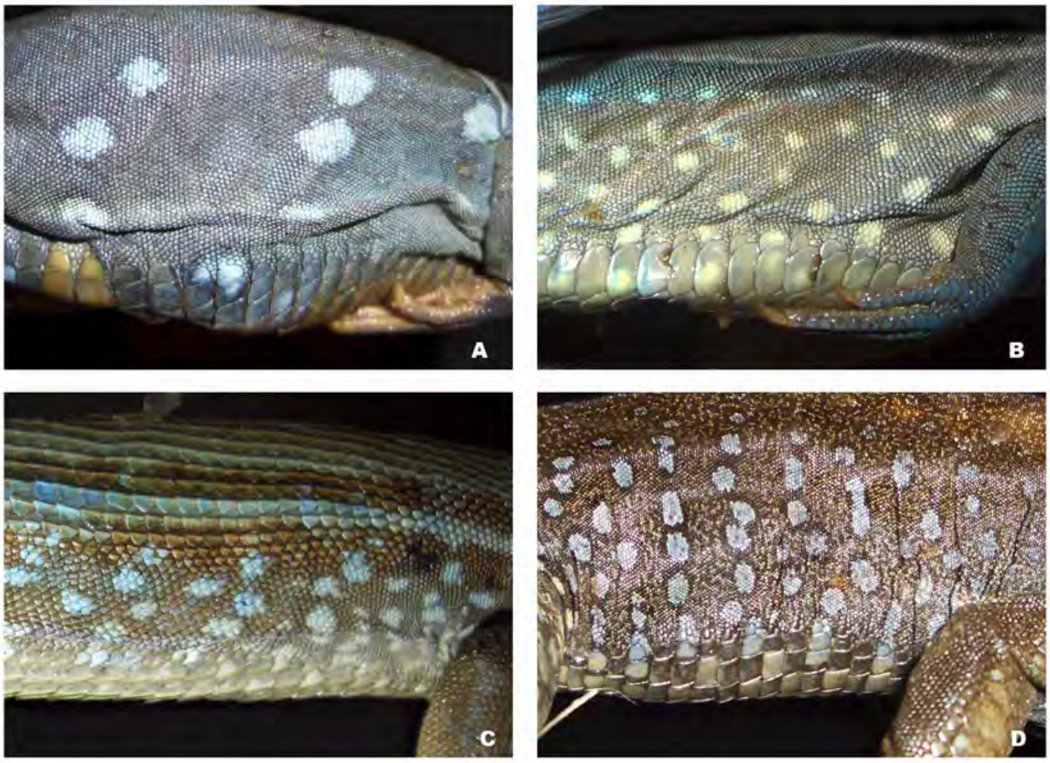

FIGURE 52. Size of spots on the flanks in adult males (character 122) of *Cnemidophorus murinus* (UMMZ 57251, A), *C. lemniscatus ssp* (CM 7271, B), *Kentropyx striata* (TCWC 44880, C), and *Ameiva atrigularis* (USNM 217052, D).

Most other Teiinae lack spots. Circular markings on the flanks of other species such as the ocelli of the *Ameiva ameiva* complex and light blue spots of *C. ocellifer* are probably not homologous with flank spots of northern *Cnemidophorus*. Nonetheless, to err on the side of caution, we coded these species as unknown (122.? and 123.?). *Dicrodon guttulatum* and some subspecies of *Ameiva chrysolaema* have similar spots, roughly arranged in transverse rows. We coded this character as not applicable to these species (123.?), because spots extend onto their dorsa, whereas the spots are restricted to the flanks in *Cnemidophorus*. Thus, counts in these species would not be comparable to those of *Cnemidophorus* and *Kentropyx*.

124. *Turquoise Ventrolateral Spots*.—In adult males, turquoise ventrolateral spots are absent (0) or present (1).

These spots are always absent from species of Tupinambinae. Adult males of many species of *Ameiva*, *Cnemidophorus* and *Teius* have light blue or turquoise spots along the lateralmost ventral scales. These spots usually occupy one or one-half of a ventral scale. In *Cnemidophorus parecis* the ventrolateral scales are blue, sharply differing from other ventral surfaces that are whitish in this species. Thus, we scored *C. parecis* as having turquoise ventrolateral spots (124.1) even though the color uniformly extends across the ventrolateral scales.

Photographs of some *Dicrodon guttulatum* and *D. heterolepis* show adult males with a bluish cast to the ventrolateral scales, however we were unable to obtain quality photographs or reliable descriptions of ventral coloration of *Dicrodon*. We scored these two species as unknown (124.?) for this character. Some teiids with pale to dark blue abdomens (like *Aspidoscelis sexlineata viridis* and *A. gularis*) have blue ventrolateral scales, however these are not spots but rather a continuation of the coloration of the belly (124.0).

125. *Ventral Blotches*.—The belly is immaculate to finely spotted (0) or mottled with large blotches (1).

Vanzolini and Valencia (1965) noted that the various species of Tupinambinae have mottled or blotched bellies, whereas species of Teiinae have immaculate bellies. In life, most species of Teiinae have white venters, however the venter of some species may be bright blue (e.g., *Ameiva septemlineata*), yellow (e.g., *Cnemidophorus vanzoi*), or reddish (at least some adult male *Kentropyx calcarata*). *Aspidoscelis marmorata*, *A. tigris*, and some populations currently assigned to *Ameiva praesignis* from the Llanos of Venezuela and Colombia have small black spots covering their bellies. This pattern is very different from the large blotches of Tupinambinae and we coded these species as having state 0.

126. *Black Pigmentation of Throat*.—In adult males, the throat is not (0) or is uniformly melanic (1).

Teiids having most of the chin and gular region uniformly black were scored as having melanic throats (e.g., *Ameiva atrigularis*). Melanic species that have a uniformly black coloration on all ventral surfaces of the head and body were also scored as having a black throat (e.g., *A. atrata, Cnemidophorus nigricolor, C. rostralis*). The various species of Tupinambinae we examined never have melanic areas on their ventral surfaces (126–128.0).

127. *Black Pigmentation of Chest*.—In adult males, the chest is not (0) or is melanic (1).

Some teiids (e.g., *Ameiva erythrocephala*, *Aspidoscelis gularis*, *Cnemidophorus vanzoi*) have a black chest contrasting with a pale throat and abdomen. Other species have uniformly melanic venters and, thus, were also scored as having a black chest (e.g., *C. nigricolor*). Finally, some taxa have only the throat and chest black and were also scored as having a melanic chest (e.g., *A. atrigularis*).

128. *Black Pigmentation of Abdomen*.—In life, the abdomen of adult males is not (0) or is melanic (1).

When we did not known the color in life, we coded species as unknown for this character (128.?), because the abdomen of some species such as *Ameiva praesignis* and *Dicrodon heterolepis* frequently darkens in preservative even though it is cream or blue in life.

129. *Ontogenetic Loss of Juvenile Color Pattern*.—In adult males, the juvenile dorsal color pattern is present with only slight modification (0) or completely absent (1).

Conspicuous ontogenetic changes in coloration are common among many genera of Teiinae (e.g.: *Ameiva*, *Cnemidophorus*, *Kentropyx*). Among Tupinambinae, only *Tupinambis merianae* and *T. rufescens* undergo moderate ontogenetic color changes. Green coloration on the heads and necks of juveniles of these species is completely lost in adults.

Hemipenis

Few studies of teiid hemipenes have been published. Cope (1896) described an organ with transverse laminae forming chevrons between the sulcus spermaticus and a "welt" on the opposite side in *Dracaena*, *Tupinambis*, *Cnemidophorus*, and *Ameiva*. He noted the presence of "a strong, fleshy papilla at the apex of each tract" in *Cnemidophorus* and *Ameiva* and "a large patch of flexible papillae" at the apex of the laminate organ of *Kentropyx pelviceps*. Dowling and Duellman (1978) illustrated hemipenes of *Ameiva maynardi*, *Teius teyou*, and "*Tupinambis nigropunctatus*" but did not describe the organs. Finally, as part of his review of saurian genital morphology, Böhme (1988) described and illustrated organs from 13 species in five genera accounting for much of teiid diversity. Here, we expand upon these data and identify additional characters of obvious phylogentic value.

Description of these organs requires introduction of new terminology. In the following account, we place these terms in bold print when first introduced.

Teiids have symmetrically bilobed hemipenes with the sulcus spermaticus extending to the crotch region and transverse **laminae** covering the sides (Fig. 53–55, Table 1). When everted, the sulcus enters from the ventromedial side of the specimen (i.e., it presumably extends along the ventromedial side of a retracted organ).

Nude **sulcate expansion pleats** separate the laminae from the sulcus spermaticus. In all teiids except *Kentropyx* and *Ameiva sp. F* (*A. bifrontata* complex), the sulcus spermaticus lies opposite from an **asulcate expansion pleat** separating the **distal laminae**. Usually, the asulcate pleat does not reach the base of the organ, being interrupted by several complete **proximal laminae**. Among species we examined, *Dicrodon guttulatum*, *Teius teyou, Cnemidophorus ocellifer,* and *A. exsul* are the only species that completely lack proximal laminae (Table 1). Most laminae extend unbroken between the asulcate and sulcate expansion pleats. In all species except *Callopistes flavipunctatus*, 2–4 proximal laminae terminate on the sides of the organ, so that there are slightly more laminae on the asulcate than on the sulcate side. In *C. flavipunctatus*, this pattern is reversed: FMNH 41588 has 3/3 more sulcate than asulcate laminae at the base of the organ. Many species have 1–3 **discontinuous distal laminae**, whereas larger numbers of these structures are relatively rare. In *Ameiva anomala, A. bridgesii,* and *A. septemlineata*, 5–7 discontinuous distal laminae extend from the asulcate expansion pleat to the sides of the organ where they terminate at a low **longitudinal fold** extending proximally from each awn. *Ameiva chrysolaema* and

Cnemidophorus ocellifer have four discontinuous laminae. *Callopistes flavipunctatus* has six similar discontinuous laminae in this area, although the fold is absent. In *Ameiva ameiva* and *A. praesignis* the longitudinal fold is present and interrupts 5–7 laminae on the side of the organ. The distalmost four of these are discontinuous, however they are positioned on the sulcate side of the organ rather than the asulcate side as in the other teiids with discontinuous laminae.

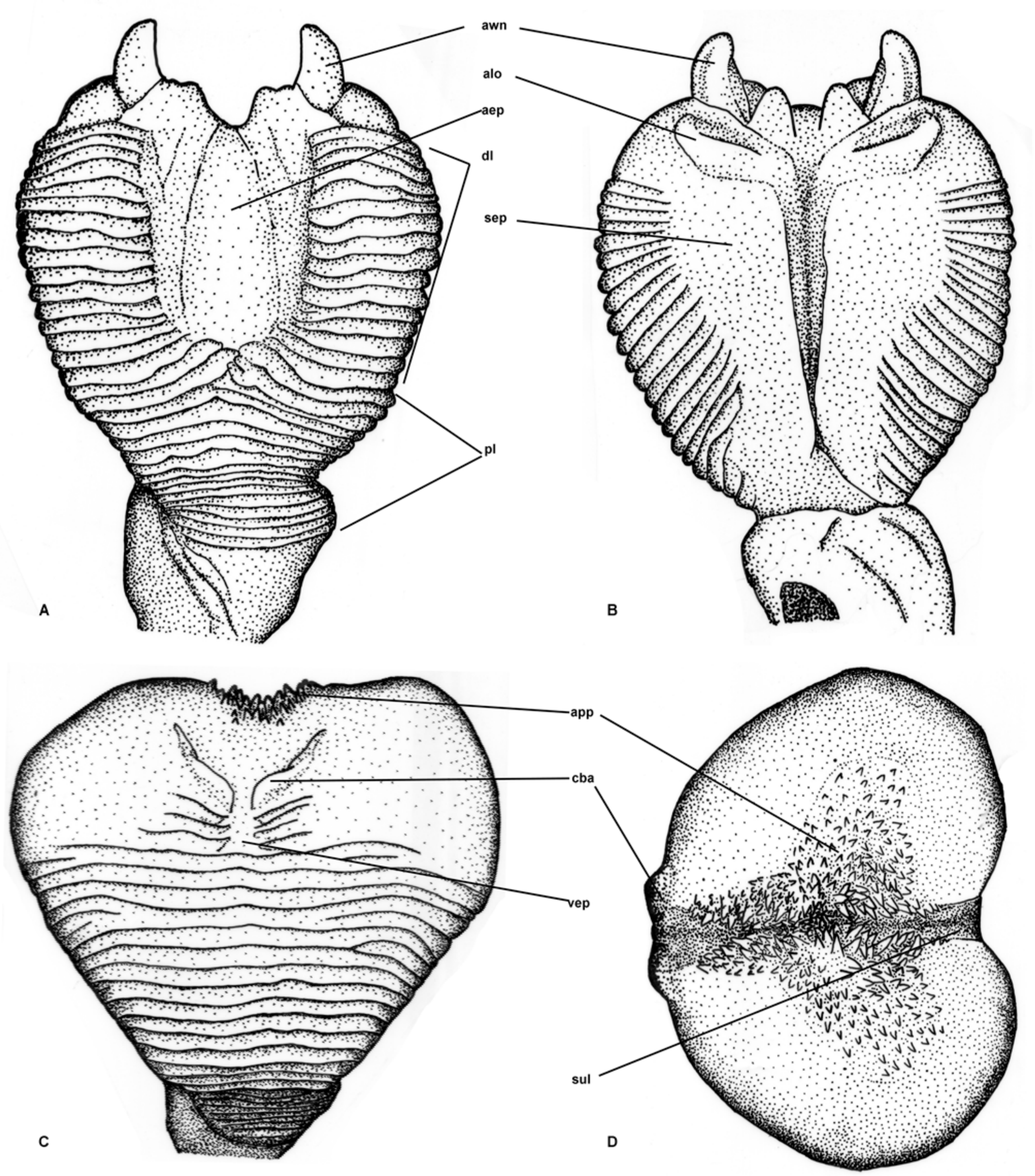

FIGURE 53 D. Asulcate (A) and sulcate (B) hemipenial morphology of *Contomastix vittata* (UTA 58475) and asulcate (C) and apical (D) hemipenial morphology of *Kentropyx altamazonica* (UTA 59488), showing asulcate expansion pleat (aep), apical lobe of sulcus spermaticus (alo), apical papillae (app), awns (awn), cup-shaped basin (cba), distal laminae (dl), proximal laminae (pl), sulcate expansion pleat (sep), sulcus spermaticus (sul), and vestigial asulcate expansion pleat (vep).

TABLE 1. Selected hemipenial characters of teiid lizards. Means ± standard deviation in parentheses follow ranges for counts of laminae when organs for more than two specimens were available for study. NA = not applicable.

Species	Proximal Laminae	Distal Laminae	Discontinuous Laminae	Awns	Apical Sulcate Structures	Apical Asulcate Structures
Callopistes flavipunctatus	6	19	Present (6, Asulcate)	Absent	Large Flat Expansions	Absent
Salvator merianae	33—40 (36 ± 2, *n* = 7)	56—71 (63 ± 6, *n* = 6)	Absent	Absent	Catchment Folds with Triangular Flaps	Rounded Lobes
Crocodilurus amazonicus	27—31	44	Absent	Styloid	Catchment Folds with Triangular Flaps	Rounded Lobes
Dicrodon guttulatum	0	17	Absent	Present		
D. heterolepis	6	17	Absent	Present	Low Ridges	Rounded Lobes
Teius teyou	0	13	Absent	Present on either side of Central Basin	Catchment Fold	High semicircular Ridge (Flap)
Kentropyx altamazonica	26 (*n* = 2)	Expansion Pleat Vestigial	Absent	Absent (apical papillae present)	Absent	Straight Ridges
K. calcarata	35	Expansion Pleat Vestigial	Absent	Absent (apical papillae present)	Absent	Straight Ridges
Cnemidophorus arubensis	12 (*n* = 2) (with basal papillae)	14 (*n* = 1)	Absent	Present	Catchment Fold	(not visible on partially evered organs)
Cn. lemniscatus espeuti	5 (with basal papillae)	19	Absent	Present	Catchment Folds	Subtriangular flaps
Cn. l. lemniscatus	6 (with basal papillae)	19	Absent	Present	Catchment Folds	Subtriangular flaps
Cn. murinus	13—14 (with basal papillae)	23	Absent	Present	Catchment Folds	Subtriangular flaps
Cn. vanzoi	8 (with basal papillae)	23	Absent	Present	Catchment Folds	Rounded Lobes
Ameivula ocellifera	0 (basal papillae absent)	7	Present (4, Asulcate)	Present: Papillate	Papillate Catchement Folds	Papillate Catchment Folds
Contomastix vittatus	14—15 (basal papillae absent)	18—19	Absent	Present	Subtriangular Lobes	Absent
Aspidoscelis gularis	7	10	Absent	Present	Subtriangular Lobes	Ridge with Subtriangular Flaps
As. sexlineata	5—7 (5 ± 1, *n* = 7)	12—16 (14 ± 2, *n* = 5)	Absent	Present	Low Ridges	Ridge with Subtriangular Flaps

Continued on next page...

TABLE 1. (Continued)

Species	Proximal Laminae	Distal Laminae	Discontinuous Laminae	Awns	Apical Sulcate Structures	Apical Asulcate Structures
As. tigris	10 (*n* = 3)	13—15 (14 ± 1, *n* = 3)	Absent	Present	Subtriangular Lobes	Straight Ridges
Ameiva ameiva	16	9	Present (4, Sulcate)	Present	Rounded Lobes	Rounded Lobes
Am. praesignis	14—23 (*n* = 3)	5—9 (*n* = 3)	Present (4, Sulcate)	Present	Rounded Lobes	Rounded Lobes
Holcosus anomalus	10	23	Present (7, Asulcate)	Present	Catchment Folds	Rounded Lobes
H. septemlineatus	10—15	12—15	Present (6, Asulcate)	Present	Catchment Folds	Rounded Lobes
H. festivus	8 (*n* = 2)	10	Absent	Present	Catchment Folds	Rounded Lobes
H. niceforoi	8	10	Absent	Present	Catchment Folds	Rounded Lobes
H. quadrilineatus	2	10	Absent	Present	Catchment Folds	Rounded Lobes
H. leptophrys	8	24	Absent	Present	Catchment Folds	Rounded Lobes
H. undulatus	49—50	10—11	Absent	Present	Catchment Folds	Rounded Lobes
Medopheos edracanthus	2	14	Absent	Present	Catchment Folds	Ridges with Subtriangular Flaps
Am. auberi	9 (*n* = 3)	16—18	Absent	Present	Subtriangular Lobes	Subtriangular Lobes
Am. dorsalis	8	14	Absent	Present	Subtriangular Lobes	Subtriangular Lobes
Am. lineolata	12—15 (14 ± 2, *n* = 4)	15—17	Absent	Present	Subtriangular Lobes	Subtriangular Lobes
Am. exsul	0 (*n* = 3)	22—24 (23 ± 1, *n* = 3)	Absent	Present	Subtriangular Lobes	Subtriangular Lobes
Am. chrysolaema	11	11	Present (4 asulcate)	Present	Subtriangular Lobes	Subtriangular Lobes
Am. taeniura	12	15	Absent	Present	Subtriangular Lobes	Subtriangular Lobes
Am. griswoldi	8—12 (10 ± 2, *n* = 7)	16—19 (18 ± 1, *n* = 5)	Absent	Present	Subtriangular Lobes	Subtriangular Lobes
Am. plei analifera	8—9 (8 ± 1, *n* = 5)	16—18 (17 ± 1, *n* = 5)	Absent	Present	Subtriangular Lobes	Subtriangular Lobes
Am. plei plei	7—8 (8 ± 1, *n* = 4)	18—19 (18 ± 1, *n* = 3)	Absent	Present	Subtriangular Lobes	Subtriangular Lobes
Am. erythrocephala	6—7 (6 ± 1, *n* = 3)	16	Absent	Present	Subtriangular Lobes	Subtriangular Lobes
Am. fuscata	6	16	Absent	Present	Subtriangular Lobes	Subtriangular Lobes
Am. bifrontata divisa	26	5	Absent	Present	Rounded Lobe	Longitudinal Ridge and Low Cup-shaped Basin
Am. bifrontata ssp.	23	5 (Asulcate Expansion Pleat Very Narrow)	Absent	Present	Rounded Lobe	Longitudinal Ridge and Low Cup-shaped Basin

Most laminae are unornamented structures. In some teiids such as *Aspidoscelis sexlineata*, laminae near the base of the organ are notched in several places. Small subtriangular **basal papillae** adorn proximal laminae in all species of northern *Cnemidophorus*. These small, flap-like, triangular structures are about as long as the laminae are wide. They are best developed on the medial side of the organ where the sulcus makes a curve before extending more or less straight along the organ. The basal papillae extend to the region immediately proximal to the asulcate expansion pleat, but are low and easily missed.

The most elaborate and variable features are concentrated on the apices of teiid hemipenes. Most teiids have a pair of extensible **awns** (we prefer this term to Cope's 1896, "fleshy papillae"), one located on either side of the crotch. A deep furrow separates each awn from laminae on the sides of the organ. Each awn typically bears a shallow groove in its center. The pair of grooves is continuous with the sulcus spermaticus and presumably allows seminal fluid to flow to the distal ends of the awns. In addition to the awns, **apical lobes** or **apical catchment folds** may be present. Both structures are usually continuous with lips of the sulcus spermaticus on the sulcate side and border the distal end of the asulcate expansion pleat on the asulcate side. When present, sulcate lobes form through thickening of the catchment fold. Moreover, there seems to be a continuum from very thin, sheet-like catchment folds to thickened lobes in the same location. A catchment fold is oriented more or less perpendicular to the sulcus. In contrast to the flap-like sulcate lobes, a pair of lobes on the asulcate side may form through thickening of the catchment fold or may simply result from outward bulging of the organ. In the latter instance, a ridge of tissue likely homologous with an asulcate catchment fold is usually visible atop the lobe.

Awns usually are prominent subcylindrical to taβ-shaped structures, rounded at their distal ends. Nonetheless, some extremes in awn morphology bear mention: (1) awns of western *Ameiva* are tiny, thin, triangular structures; (2) awns of *Ameiva leptophrys*, *A. undulata*, and *Dicrodon heterolepis* fan outward into flat areas with a raised fold of tissue continuous with the sulcate catchment fold; and (3) subtriangular awns of *Crocodilurus* overlap behind the pronounced sulcate catchment folds of this species. In *Crocodilurus*, the awns appear to effectively block the flow of seminal fluid from reaching the asulcate side of the organ (Fig. 55).

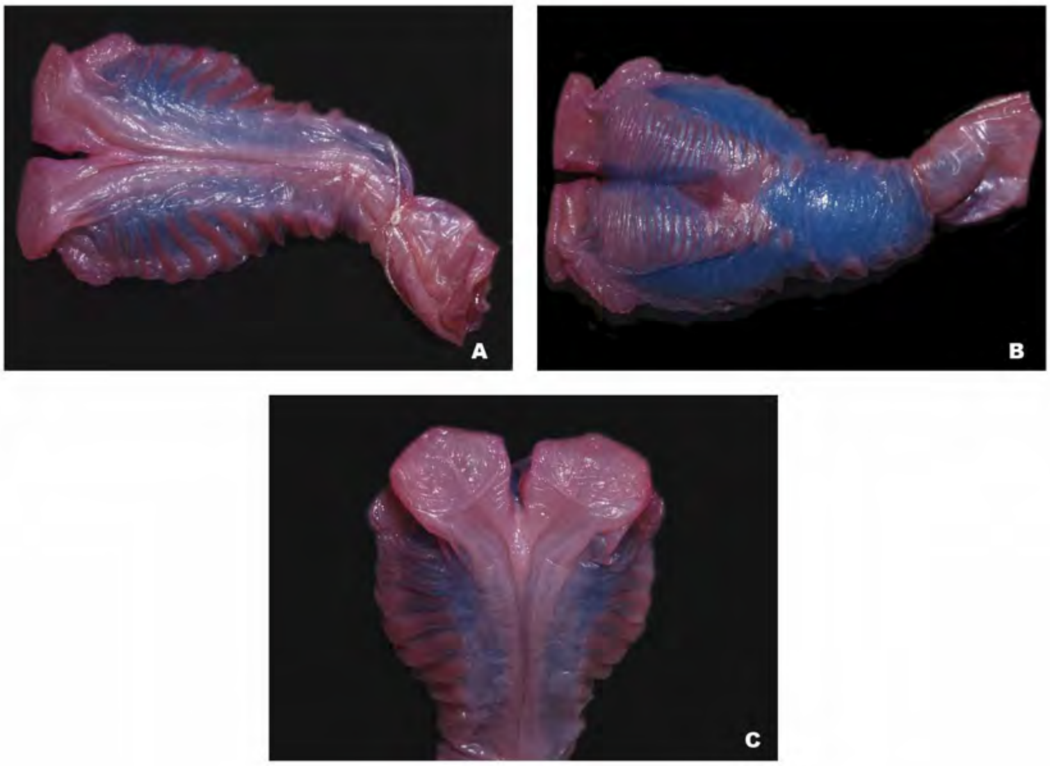

FIGURE 54. Sulcate (A), asulcate (B), and apical (C) morphology of hemipenis of *Callopistes flavipunctatus* (FMNH 41588) stained with Alizarin Red and injected with blue-stained petroleum jelly.

Apparent differences in the lobe-catchment fold continuum do not readily lend themselves to character coding. Therefore, we did not attempt to develop phylogenetic characters for these structures. Nonetheless, some patterns are evident (Table 1). Rounded to subtriangular sulcate lobes are present in Caribbean *Ameiva*, *Aspidoscelis* *gularis*, *A. tigris*, and *Cnemidophorus vittatus*. These lobes are much smaller than the well-developed awns of *Aspidoscelis*, about half as large as the awns in Caribbean *Ameiva*, and about the same size as the awns in *C. vittatus*. A pair of thin, sheet-like catchment folds is present in Central American and Western *Ameiva*, *Cnemidophorus vanzoi*, *Teius teyou*, *Tupinambis merianae*, and *Crocodilurus amazonicus*. The catchment folds of these species are extensions of the lips of the sulcus. Approaching the apex, each sulcal lip turns abruptly, so that the catchment fold is perpendicular to the sulcus. In *Aspidoscelis sexlineata*, *Dicrodon heterolepis*, and *Teius teyou*, each low sulcal lip arches far onto the side of the organ then distally to the awns. The most elaborate sulcate catchment fold occurs in *Crocodilurus* and *Tupinambis*. In these species, the portion of the fold close to the sulcus projects outward as a prominent triangular flap (Fig. 55). *Crocodilurus* is unique in having a **styloid process** positioned at the asulcate end of each sulcal catchment fold. A deep groove separates each of these long, pointed, and narrowly cylindrical structures from the rest of the fold.

On the asulcate side, most species have a pair of prominent lobes on either side of the asulcate pleat. *Aspidoscelis* (based on *gularis*, *sexlineata*, and *tigris*), *Ameiva edracantha*, *Callopistes flavipunctatus*, *Cnemidophorus vittatus*, and *Kentropyx* clearly lack asulcate lobes. In other species, a fold or flap of tissue is present. Each of these asulcate catchment folds borders the distal end of the asulcate pleat and often extends distally to the awn. Each fold usually is positioned atop a lobe. *Ameiva edracantha*, *Kentropyx*, and the three species of *Aspidoscelis* have asulcate folds, even though they lack lobes. The pair of folds in these species forms a V with the open point directed into the asulcate expansion pleat. The fold is low and straight in *A. tigris*, high and distally projecting in *Kentropyx*, and distally attenuate into a subtriangular flap in *Ameiva edracantha*, *Aspidoscelis sexlineata* and *A. gularis*. The fold is particularly well developed in *Teius teyou* where it is a large free semicircular structure. *Cnemidophorus vittatus* and *Callopistes flavipunctatus* bear no trace of the asulcate ridge or lobe.

In Caribbean *Ameiva*, the asulcate lobe is subtriangular and flat; it is usually about as large as the awn, whereas the awn is at least twice as large as the sulcate lobe. In Caribbean species, tissue forming the sulcate margin of the awn extends towards the crotch, slightly overlapping part of the sulcate lobe. Also, a flat sheet of tissue spans the area between the awn and asulcate lobe. Presumably, seminal fluid reaching the crotch would spread out across this sheet of tissue. The sheet forms a cup-like basin at the apex and presumably would prevent seminal fluid from flowing into the furrows around the awns.

The organs of *Callopistes*, *Kentropyx*, *Ameiva bifrontata ssp.*, *Cnemidophorus ocellifer*, *Teius*, and *Tupinambis merianae* differ substantially from those of other teiids. As in other teiids, the sulcus spermaticus of *Kentropyx* terminates at the crotch. However, species in this genus lack awns and lack apical lobes or catchment flaps on the sulcate side of the organ (Fig. 53). Distally, numerous, phylloid **apical papillae** interrupt the sulcus and extend onto the sides of the lobes. The papillae are most dense within the crotch where they presumably impede the flow of seminal fluid. *Kentropyx* bears only a **vestigial asulcate expansion pleat**. Instead, the V-shaped asulcate catchment folds have a narrow opening just distal to the proximal laminae. The asulcate folds are directed distally and thereby form a cup-shaped basin at the asulcate margin of the crotch in *Kentropyx*.

The hemipenes of *Ameiva bifrontata divisa* and *A. bifrontata ssp.* have very narrow asulcate expansion pleats, really just vestigial lines of tissue interrupting the distal five laminae. In most teiids, distal laminae outnumber proximal laminae. Aside from *Kentropyx*, the only other exceptions to this rule are *Ameiva ameiva* and *A. praesignis*. However, in these taxa the expansion pleats are relatively well developed and both species have nine distal laminae. As in *Kentropyx*, a low cup-shaped fold is present at the asulcate margin of the crotch in species of the *A. bifrontata* complex. This fold of tissue is oriented transversely and appears to block flow of seminal fluid into the asulcate expansion pleat. Nonetheless, as in other *Ameiva*, the species in this complex have a pair of taβ-shaped awns and lack apical papillae. The awns in these two species are deeply scalloped at the apex to accommodate short bifurcations of the sulcus. Approaching the sulcus spermaticus, the laminae extend out from the organ onto broad flaps that overlap the sulcate expansion pleat. At first glance, one might suspect these flaps are greatly distended lips of the sulcus, but this is not the case. The lips of the sulcus are comparable to those of most other teiids and are clearly discernible in the center of the sulcate expansion pleat. Distally, the lips of the sulcus lengthen and, at the apex, reach the free margin of the flaps.

The hemipenis of *Callopistes flavipunctatus* lacks asulcate lobes and apical awns (Fig. 54). Each sulcate lobe expands distally as a flat, circular structure deeply separated from the other lobe by the crotch of the organ. In this species, the sulcus spermaticus bifurcates at the crotch, sending a short branch to each of the sulcate lobes. In addition to the sulcate and asulcate expansion pleats, oval **lateral and medial expansion pleats** completely interrupt the laminae on the sides of the organ, thereby forming discrete series of sulcate and asulcate laminae. All other teiids lack these lateral and medial pleats. FMNH 41588 has 17 sulcate laminae, 19 distal asulcate laminae, and 6 proximal asulcate laminae. Three of the proximal laminae are continuous, interrupting the asulcate expansion pleat. The remaining three become progressively shorter moving toward the base and are interrupted by a smooth area.

None of the specimens of *Teius* examined in this study had fully everted organs. Our manually everted preparations are far from perfect, but all characters could be scored for a specimen of *T. teyou* (Fig. 55). Only some characters could be scored in a hemipenis removed from an old specimen of *T. oculatus*. Nonetheless, our observations agree well with illustrated organs of *T. teyou* (Böhme 1988; Dowling & Duellman 1978). In both species, the sulcus bifurcates at the apex, distal to the catchment folds. The sulcus sends a short branch to a depression in each cup-shaped awn. The branches of the sulcus pass on either side of a deep, subcircular **central apical basin** bordered by high fleshy walls. At the distal end of the asulcate expansion pleat, the walls of the basin are very low so that the basin appears to "open" into the expansion pleat. The two species of *Teius* are the only teiids with a central apical basin. The sulcal lips are highly degraded in our specimen of *T. oculatus*. In *T. teyou*, the sulcal lips are relatively low except where each expands into a prominent rounded lobe, about three-quarters of the distance to the apex. Distal to this lobe, the sulcus is low again and eventually fans outward as the sulcal catchment folds.

The hemipenis of *Tupinambis merianae* resembles that of *Callopistes flavipunctatus* in lacking apical awns. As in *Callopistes*, a single pair of apical lobes is present, however these structures are located on either side of the asulcate expansion pleat and appear to be homologous with the asulcate lobes of Teiinae. As in *Crocodilurus*, the lips of the sulcus spermaticus flare outward distally to form prominent triangular sulcal catchment folds. In both *T. merianae* and *Crocodilurus*, a series of 7–8 grooves run roughly perpendicular to the free edge of the sulcal catchment folds. Spaces, each roughly equal to the width of two laminae, separate the grooves. The relatively long hemipenis of *Tupinambis merianae* lacks lateral and medial expansion pleats and has more laminae than other teiids examined in this study (Table 1).

A partially everted organ (specimen's left side) from *Cnemidophorus ocellifer* (FMNH 44156) had some distal tears on the sulcate side and complete eversion was impossible. Nonetheless, the distinctive apical features are visible, albeit on only one of the lobes. The awns and both the asulcate and sulcate catchment folds are distally frayed into long papillae, about 15 on each lobe (also noted by Böhme 1988). Laminae are widely spaced, poorly developed, and visible only on the asulcate side where about seven lie adjacent to the broad asulcate expansion pleat. The distal four or so laminae in this species are clearly discontinuous, occurring more distally on the organ than the terminal lips of the sulcus. Proximal laminae and basal papillae are absent. We observed **papillate awns** and papillate catchment folds only in *C. ocellifer*, however Böhme (1988) described and illustrated similar structures on a hemipenis of *C. lacertoides*. Such a finding is surprising since these awns and catchment folds of the presumably closely related species *C. vittatus* are smooth. This character was excluded from the phylogenetic analysis since we observed it only on the single specimen of *C. ocellifer* with an everted organ. Additional study of an organ taken from *C. lacertoides* is required to determine if the papillae in *C. ocellifer* and *C. lacertoides* are homologous structures.

Alizarin staining and close inspection of everted organs failed to reveal any large calcified structures such as the spines embedded in the laminae of some microteiids (Uzzell 1970) or struts and spines of snakes (e.g., Harvey & Embert 2009). Nonetheless, a network of tiny **subcellular spinules** covers the laminae and absorbs alizarin red (Fig. 54. Red areas in the organ are covered in subcellular spinules). This material is visible at high magnification with a stereomicroscope and is present on the laminae of all teiid hemipenes. We mounted some of this material on a glass slide for light microscopy. The minute spinules are connected by struts and appear to be calcified, but a complete description of these structures will require advanced histological techniques and is beyond the scope of this study. Böhme (1988) first reported these spinules in teiids and published scanning electron micrographs (his figure 26) of them in situ.

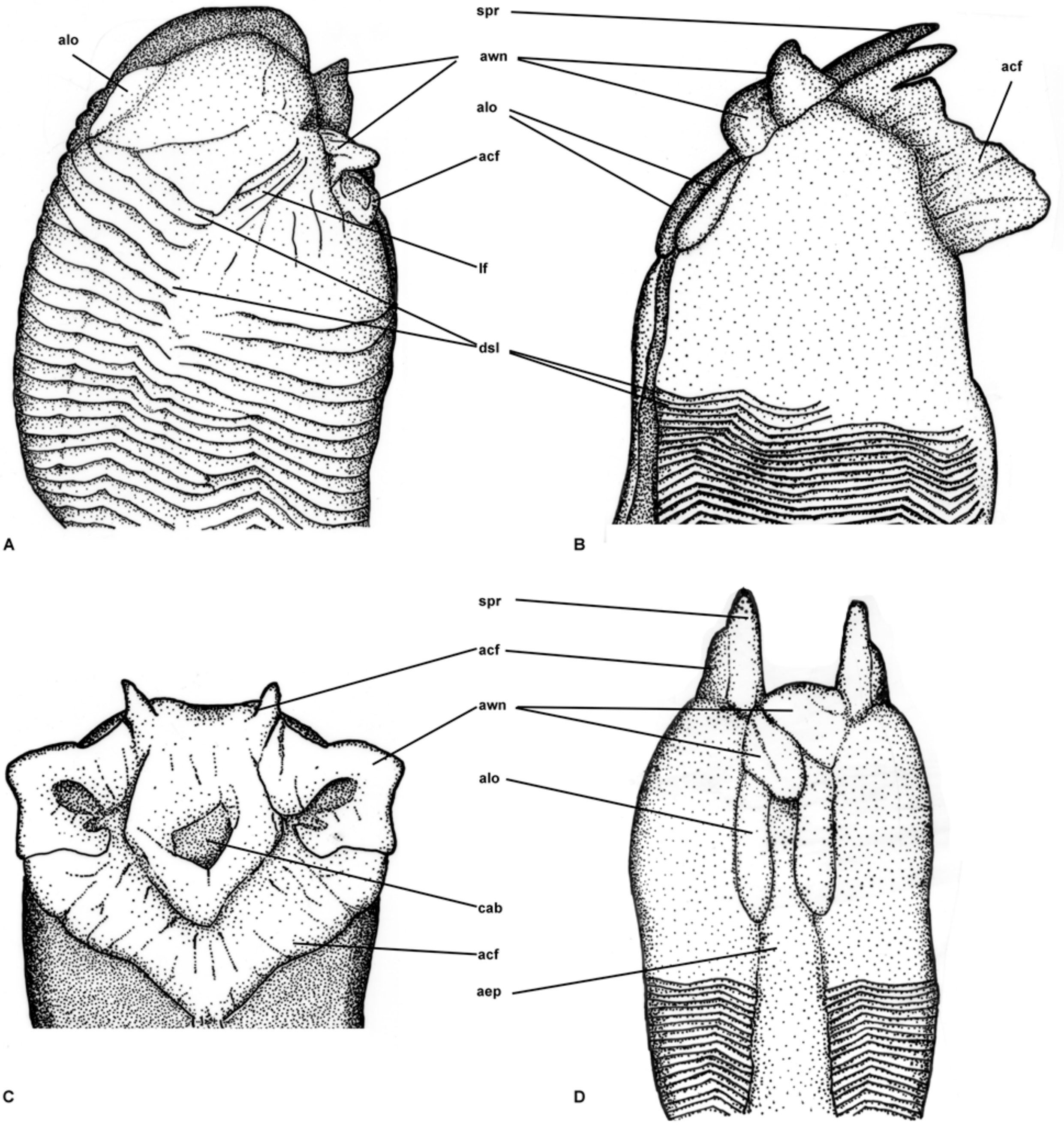

FIGURE 55 E. Lateral hemipenial morphology of *Holcosus anomalus* (AMNH 109694, A) and *Crocodilurus amazonicus* (USNM 200689, B), apical morphology of *Teius teyou* (FMNH 44155, C), and asulcate morphology of *C. amazonicus* (USNM 200689, D), showing apical catchment folds (acf), apical lobes (alo), awns (awn), central apical basin (cab), discontinuous laminae (dsl), longitudinal fold (lf), and styloid process of sulcate catchment fold (spr).

130. *Apical Papillae of Hemipenis*.—Apical papillae are absent (0) or present (1).

These structures appear to be a unique synapomorphy of the species of *Kentropyx*.

131. *Pairs of Apical Awns of Hemipenis*.—Apical awns are present (0) or absent (1).

Only *Kentropyx* and some Tupinambinae lack apical awns.

132. *Central Apical Basin of Hemipenis*.—A basin with high walls is absent (0) or centrally located between the awns (1).

This feature appears to be a unique synapomorphy of the species of *Teius*.

133. *Asulcate Expansion Pleat*.—On the asulcate side of the hemipenis, an expansion pleat separates the distal laminae (0) or is vestigial (1).

Vestigial expansion pleats occur only in *Kentropyx* and species of the *Ameiva bifrontata* Complex.

134. *Laminae Proximal to Asulcate Expansion Pleat*.—We counted the number of laminae proximal to the asulcate expansion pleat. We then averaged counts taken from more than one specimen (when available) and applied the mean number to all specimens of a species.

135. *Laminae Lateral to Asulcate Expansion Pleat*.—We counted the number of laminae lateral to the asulcate expansion pleat. We then averaged counts taken from more than one specimen (when available) and applied the mean number to all specimens of a species.

136. *Discontinuous Distal Laminae*.—Except for the most distal 1–3 laminae, the distal laminae are continuous (0), more distal laminae extend to the sides of the organ from the asulcate pleat than the sulcate pleat (1), or more distal laminae extend to the sides of the organ from the sulcate pleat than the asulcate pleat (2).

137. *Basal Papillae of Hemipenis*.—The proximal laminae are unornamented (0) or have small, flat papillae near the base of the organ (1).

This feature appears to be a unique synapomorphy of the species of northern *Cnemidophorus*.

Other Characters

We take this opportunity to discuss two potentially informative characters. We chose to exclude both characters from the phylogenetic analysis, because they require further study and data for them is incomplete.

Predator Monitoring and Anti-Predator Displays.—Most teiids, and particularly Teiinae, are very active foragers that move along elegantly with quick, often jerky motions while constantly flicking their tongues and often probing the substrate. Their jerky motions likely startle potential prey, but some behaviors may serve a dual role in predator monitoring. For example, *Ameiva ameiva*, *A. atrigularis*, and *A. bifrontata* nervously bob their heads while foraging, but they continue this activity when pursued by a predator. *Ameiva ameiva* and *A. atrigularis* also crash through leaf litter, so that they are frequently heard before being seen. The role of head bobbing in teiids is not known, and we do not know how common it is. In birds head bobbing occurs in pigeons, quail, cranes, and many other groups where this behavior may improve depth perception, sharpen vision, or stabilize the visual surroundings of birds in motion (Friedman 1975; Frost 1978; Troje & Frost 2000).

Unrelated groups of lizards commonly wave and undulate extremities in response to the presence of predators. Tail undulations of scincids, gekkonids, and other lizards are well known and thought to direct attacks to this expendable appendage. Foot shakes of lacertids (van Damme & Castilla 1996) and the arm movements of teiids are often interpreted to have an anti-predator or predator monitoring function. The movements may induce a predator to pursue and thus make it detectable to the lizard (Magnusson 1966; Cooper *et al*. 2003). In certain circumstances, these displays likely represent a form of honest signaling in which the lizard indicates to the predator that it has a high probability of escaping if attacked and that the predator would benefit by not attacking (Vega-Redondo & Hasson 1993; Cooper *et al*. 2003).

Arm waving has been well documented for *C. arubensis*, *C. murinus*, *C. ruthveni*, and most species of the *Cnemidophorus lemniscatus* complex, (e.g., Burt 1931; Hoogmoed 1973; Schall 1974; van Buurt 2005, 2011; Ugueto *et al*. 2009). It likely occurs in all northern *Cnemidophorus*. Ugueto has observed this behavior in *C. arenivagus*, *C. senectus*, and *C. lemniscatus*. In these lizards, arm waving appears to occur during short pauses while moving or immediately before moving. Unlike *Aspidoscelis* (see below), species of northern *Cnemidophorus* only wave one arm at a time. Usually the lizard waves only the arm facing the observer/predator when the latter approaches the lizard from the side. If a potential predator approaches the lizard from the front or behind, then *Cnemidophorus* species often wave both arms (one at a time). Furthermore, before waving, the lizard usually looks directly and even inclines its head towards the potential predator (Cooper *et al*. 2003; G. N. Ugueto personal observation). A good example of hand waving in *C. lemniscatus ssp.* can be observed in the following video (taxon misidentified by the author of the video as *Ameiva festiva*): http://www.youtube.com/watch?v=uI3CYvmmTq0. Another example can be observed in the following video of *C. ruthveni* from Bonaire: http://www.youtube.com/watch?v=JIQaubfB4bk&feature=fvwrel. Viewers should notice the female at the beginning of the video waving its right limb several times. Cooper et al (2003) found *C. ruthveni* only rarely waves when a predator retreats, and lizards habituated to human presence rarely wave their arms. Arm waving has been previously attributed to thermoregulation (Gorzula & Señaris 1999), but this seems unlikely since lizards often wave their forelimbs at shaded locations (Cooper *et al.* 2003; G. N. Ugueto personal observation). The hand waving in *Cnemidophorus* is so conspicuous that locals in many parts of Venezuela call them "guitarreros" (= guitar players). Similarly, locals in Surinam refer to this species as wai wai hannoe (= waving hand; Hoogmoed 1973). Markezich *et al.* (1997) reported an interesting legend pertaining to *C. lemniscatus splendidus*: locals at Monte Cano, Falcón, Venezuela, believe that large males lure and then kill snakes by putting a series of XXs on the ground in a ritualistic manner. The peculiar arm waving often displayed by *C. l. splendidus* may have inspired this legend.

In other teiids, arm waving has been reported for *Teius teyou* (Avila & Cunha-Avellar 2005). Like *Cnemidophorus, T. teyou* initially waves the arm closest to the observer and only waves one arm at a time (Avila & Cunha-Avellar 2005). A few authors have reported arm waving in *Aspidoscelis* (e.g., Boostic 1966; Cole & Townsend 1983). In addition to our observations on northern *Cnemidophorus*, we have observed arm waving in *Ameiva ameiva, Aspidoscelis sexlineata, A. tigris,* and *Dicrodon guttulatum.* The senior author noted this behavior while observing *D. guttulatum* near Pueblo Viejo, Manabí, Ecuador (May 2008). During Harvey's visit, *Dicrodon* was common around the town. When pursued, these lizards ran moderate distances only to pause and immediately begin waving one of their arms. Near Huarap, Río Mantaro valley, Ayacucho, Peru (June, 2010), two of us (MBH and RLG) collected *A. ameiva*. We noticed that stationary lizards taking refuge in thick brush often nervously shuffled their hands whenever we approached and tried to noose them. This behavior is not as obvious as the arm waving of *Dicrodon* and northern *Cnemidophorus*, but clearly serves a similar role of predator monitoring. At the Hobe Sound Nature Center, Florida, USA (April 2005), Ugueto observed several specimens of *A. sexlineata sexlineata* that while foraging would stop suddenly, look at the observer, and extend slightly then rapidly wave both forelimbs at the same time. The arm waving produced a pedaling-like movement in this species and was accompanied by quick and subtle vibrating of the tail. An example of the display by *A. s. sexlineata* can be viewed in the following video: http://www.youtube.com/watch?v=UpUKFg27QD4. At Anza-Borrego State Park, San Diego County, California, USA (September 2010), Ugueto followed several specimens of *A. tigris stejnegeri*. All specimens invariably darted across open areas between clumps of vegetation. When slowly approached, the specimens waved their arms like *A. sexlineata,* but the vibration of the tail was more conspicuous and sometimes even included undulation of the posterior body. Some individuals slightly raised the hind limbs while vibrating the tail. An example of the display of *A. tigris stejnegeri* can be observed in the following video: http://www.youtube.com/watch?v=jwaEqGFxjoU. We are unaware of reports of tail vibration in other teiids, but it clearly occurs in some *A. ameiva* as documented in the following video of an adult specimen from Brazil: http://www.youtube.com/watch?v=xurJUpWbi-I.

Prolonged observation may be necessary to detect arm waving and other forms of predator monitoring. Waving of the forelimbs and tail undulation are apparently absent from the display repertoire of Tupinambinae. These large lizards probably have fewer natural enemies and have no need for pursuit-deterrent signaling. They usually run far (often well out of sight) from potential predators, whereas most Teiinae run short distances then begin monitoring the predator. We have been unable to find any report of tail undulation or hand waving in southern *Cnemidophorus*. Although present in *Ameiva ameiva*, we have not observed arm waving or tail undulation in three congeners in spite of many hours observing the three species. Around La Unión, Miranda State, Venezuela (February, 2011), Ugueto specifically looked for arm waving when he followed several adult and juvenile *A. atrigularis* for relatively long periods of time (30–60 minutes). No hand waving was observed. He also followed various *A. bifrontata bifrontata* at Playa Guacuco, Isla de Margarita, Venezuela (October, 2006) for short periods of 10–15 minutes and failed to observe this behavior. At various times over the last year (2011), Harvey followed adult *A. festiva* in lowland rainforests around El Valle, Chocó, Colombia, and never observed arm waving in this species. Finally, we note that species of the *Cnemidophorus lemniscatus* complex, *C. murinus* and *C. ruthveni* do not undulate their tails in a manner similar to *A. ameiva* and *Aspidoscelis*. Nevertheless, juveniles of *C. lemniscatus* from la Unión, Miranda and Puerto La Cruz, Anzoátegui, Venezuela have bright bluish green tails. When foraging, small juveniles search for prey with a series of moves and pauses. Every time a lizard pauses, the posterior one or two thirds of the tail curls forward above the base of the tail exposing the brightest side of the tail coloration.

In summary, teiids exhibit a variety of predator monitoring behaviors. Documentation of these behaviors has been largely anecdotal and fragmentary. Arm waving is likely to be a synapomorphy of most, if not all, Teiinae, whereas it is difficult to predict at what point tail undulations evolved within the radiation of this subfamily. We have no data regarding basal Teiinae such as *Kentropyx*, *Cnemidophorus longicauda*, and *C. tergolaevigatus*. The tail curling behavior of some *C. lemniscatus* has not been previously reported, and we do not know if it occurs in congeners. As we emphasize in descriptions of our observations and document with video links, arm waving differs in important ways among teiids that exhibit this behavior. We urge future investigators to conduct controlled studies of these behaviors.

Tongue Morphology.—Two features of tongue morphology have long been the only characters used to diagnose *Cnemidophorus* from *Ameiva* (e.g., Boulenger 1885b, Burt 1931; Peters & Donoso-Barros 1970; Presch 1971; Ávila-Pires 1995). Species of *Cnemidophorus* were thought to have an arrow- or heart-shaped tongue and lack a lingual sheath around the base of the tongue, whereas *Ameiva* was thought to lack the deep notch (i.e., the posterior edge is more or less straight) and have a lingual sheath. Burt (1931) cited example of species from both genera that violate these criteria. He notes that *Ameiva taeniura* has a distinctly heart-shaped tongue and that the type species of *Cnemidophorus* has a weak lingual sheath. Of the two characters, Burt (1931, p. 13) concluded that "the sheath is not necessarily a fundamental character, but one subject to development and loss…" Presch (1971) stated that the lingual sheath of *Ameiva* is a derived character found in no other teiids, but this statement directly contradicts Boulenger (1885b) who reported a basal sheath in *Tupinambis*. Presch (1971) reported a sheath in 28 species of *Ameiva* including *A. edracantha*, but when describing the holotype of *C. armatulus* (= *A. edracantha*), Cope (1876, p. 164) explicitly described the tongue as "not furcated behind, but not received into a sheath as in *Ameiva*."

If older literature contains contradiction, recent studies have added to confusion about these characters. Tongue morphology has not been mentioned in descriptions of most new species of *Cnemidophorus*. Giugliano *et al.* (2006) note that a lingual sheath occurs in *Cnemidophorus parecis* but do not comment on whether the posterior end of the tongue is deeply or weakly notched. Cei and Scrocchi (1991) illustrated the tongues of *Ameiva ameiva*, *C. lacertoides*, *C. leachei*, *C. longicauda*, *C. ocellifer*, and *C. serranus*. Reeder *et al.* (2002, p. 20) stated that, " '*Cnemidophorus*' *lacertoides* possesses a distinctly forked posterior edge of the tongue (as in other "*Cnemidophorus*"), but also exhibits the tongue sheath characteristic of '*Ameiva*'." However, Cei and Scrocchi's (1991) illustrations show that the tongues of *C. lacertoides* and its close relatives, *C. leachei* and *C. serranus*, are not forked and lack a sheath.

Several specimens of *Cnemidophorus lacertoides*, *C. leachei*, and *C. vittatus* in our samples were preserved with their mouths open or had been cut open by previous workers. We confirm Cei and Scrocchi's (1991) report: a lingual sheath is absent in these species and the posterior margin of the tongue is straight rather than heart-shaped. Posteriorly, the tongue bears a medial depression to accommodate the glottis, perhaps explaining the report by Reeder *et al.* (2002) of a "forked posterior edge" in this species.

In practice, field biologists frequently confuse *Cnemidophorus* and *Ameiva*. The tongue characters used to distinguish these genera are unreliable and difficult to assess in museum specimens routinely preserved with their mouths tightly shut. Tongue morphology is an interesting source of characters deserving more careful study. As the preceding discussion shows, (1) tongue morphology is not diagnostic of *Ameiva* and *Cnemidophorus* as currently defined, (2) tongue morphology has not been described for many species of *Ameiva* and *Cnemidophorus* and existing descriptions are often contradictory, and (3) tongue morphology cannot be studied without damaging specimens except when specimens were preserved with their mouths open.

Polyphyly of *Tupinambis* and Status of *Salvator*

Systematics of the tegus has received considerable interest in recent years. Four species recognized by earlier authors (Peters & Donoso-Barros 1970: *Tupinambis duseni*, *T. nigropunctatus*, *T. rufescens*, and *T. teguixin*) were reduced to two by Presch (1973) who reviewed older synonyms and recognized only *Tupinambis rufescens* and *T. teguixin* as valid. Although Presch (1973) referred most specimens of *T. merianae* to *T. rufescens*, he nonetheless placed Duméril and Bibron's (1839) name in the synonymy of *T. teguixin*. Avila-Pires (1995) rejected Presch's (1973) results, recognized the four species listed by Peters and Donoso-Barros (1970), and redescribed *T.*

merianae. Her (Avila-Pires 1995) careful review of older names, detailed morphological comparisons, and designation of various lectotypes resolved many persisting problems with the alpha taxonomy of *Tupinambis.*

After 1995, several new species were described: *Tupinambis longilineus* (Avila-Pires 1995), *T. palustris* (Manzani & Abe 2002), and *T. quadrilineatus* (Manzani & Abe 1997). Almost concurrently, Colli *et al.* (1998) described *Tupinambis quadrilineatus* under the junior synonym *T. cerradensis*. Although one study (Fitzgerald *et al.* 1991) found relatively little divergence between *T. duseni* and *T. rufescens* among mitochondrial DNA sequences, recent multivariate analysis of mensural and meristic data (Fitzgerald *et al.* 1991; Péres & Colli 2004) identified a suite of characters that effectively distinguish these superficially similar species.

Fitzgerald *et al.* (1991) identified two deeply divergent clades within *Tupinambis*: a "southern clade" including *T. duseni, T. merianae,* and *T. rufescens* and a "northern/Amazonian clade" of the remaining species. These authors did not explicitly test *Tupinambis* monophyly but used three species of Teiinae (*Ameiva ameiva, Cnemidophorus ocellifer,* and *Kentropyx viridistriga*) to root the tree. Noting the deep split within *Tupinambis*, Fitzgerald *et al.* (1991) acknowledged that a broader study including other macroteiid genera would be required to test its monophyly.

We show that *Tupinambis* is polyphyletic. The "southern clade" of Fitzgerald *et al.* (1991) is evidently closely related to *Dracaena*, whereas the northern/Amazonian clade is related to *Crocodilurus*. To resolve this problem of polyphyly, we here resurrect *Salvator* Duméril and Bibron for the southern clade.

Unlike *Crocodilurus* and *Tupinambis sensu stricto* (characters in parentheses), *Dracaena* and *Salvator* share character 5.0 round pupils (reniform); 26.2 two loreals (one); 28.3 a scale inserted between the first subocular, supralabials and posterior loreal (first subocular contacting supralabials or rarely separated from them by anterior expansion of second subocular); 32.1 a complete row of lateral supraocular granules (lateral supraocular granules absent); a high number of supraciliaries (23–28 vs. 14–19); 48.2 chinshields usually separated from infralabials by row of granular sublabials (usually in contact); 54.1/54.0 intertympanic sulcus incomplete medially or absent (complete); 68 a high number of longitudinal rows of ventrals (30–39 vs. 20–28); 83.1 keeled proximal subcaudals (smooth); and 108.0 macrohoneycomb on dorsals (loss of macrohoneycomb from dorsals and evolution of long aligned macroridges on supracaudal scales). *Salvator* and *Dracaena* are larger lizards, exceeding 400 mm SVL (usually less than 350 mm SVL) with strongly molariform teeth (at least in adults).

Some obvious differences in coloration also distinguish *Salvator* from *Tupinambis*. In *Salvator*, the dorsolateral stripe starts on the posterior supraciliary and extends to a paravertebral position on the body where it is mostly broken. In contrast, the dorsolateral stripe of *Tupinambis* starts at the same location on the supraciliary but remains in the dorsolateral position. As in *Salvator*, the stripe is difficult to see and broken in most species, but it is distinct in *T. quadrilineatus*. In *Salvator*, the upper lateral stripe is distinct, starts below the eye, and extends (often broken) to a point above the leg as in *Kentropyx*. In contrast, the upper lateral stripe of *Tupinambis* is very indistinct or absent, and it is not present on the flanks except in *T. quadrilineatus*. Nonetheless, even in *T. quadrilineatus* the stripe is broken and extends to the groin rather than above the leg as it does in *Salvator*. Finally, juvenile *Salvator* have white spots on the thighs and a bright green (*S. merianae*) or somewhat olivaceous (*S. rufescens*) color on the head, whereas juvenile *Tupinambis* lack white spots, basically resemble adults, and do not exhibit an ontogenetic change in dorsal head coloration.

Our conclusions regarding the relationships of *Crocodilurus, Dracaena, Salvator,* and *Tupinambis* are at odds with some other phylogenetic analyses (Presch 1974a; Sullivan & Estes 1997; Teixeira 2003). Presch's (1974a) analysis was phenetic, but Sullivan and Estes (1997) included his characters in a more modern analysis and found *Crocodilurus* to be sister to a clade containing *Dracaena* and the extinct genus *Paradracaena*. *Tupinambis* was placed outside this clade as sister to these three genera. But *Crocodilurus* and *Dracaena* shared only two synapomorphies: a robust quadrate and fewer than sixty caudal vertebrae. On the other hand, Sullivan and Estes's character 5 (biconodont or triconodont premaxillary teeth present) contradicted this arrangement, evolving in *Tupinambis* and *Crocodilurus* under their hypothesis. Sullivan and Estes (1997, p. 111) state that a robust quadrate is "also present in *Callopistes*," although they did not map this character on the branch leading to *Callopistes* in their figure 7.3. A problem with the osteological studies of Presch (1974a) and Sullivan and Estes (1997) is that some specimens (e.g., BMNH 1853.3.7.27 and SDSNH 65496 and 66269) lack locality information and may be specimens of *Salvator* rather than *Tupinambis*. Nonetheless, SDSNH 64932 from Guyana and BMNH 1964.1825 from Trinidad or Tobago can only be *T. teguixin*.

Teixeira (2003) added high infralabial scale (her character 123) and fourth toe lamellae counts (her character 126) to the list of characters shared by *Dracaena* and *Crocodilurus*. However, these suggestions contradict the data presented in her Table 2 where *Crocodilurus* has the lowest mean fourth toe lamellae (29.68 ± 1.94) of all Tupinambinae (more than 30 in the other genera) and infralabial counts (12.00 ± 0.55) comparable to *Tupinambis* (11.80 ± 1.57) rather than *Dracaena* (20.43 ± 2.40). Data in her Table 2 reflects the same pattern that we observed. Uncertainty regarding the alpha taxonomy of tegus affected other early studies. Gorman (1970) described three distinctive karyotypes within the Tupinambinae. He reports that *Dracaena* and *Tupinambis* have an acrocentric chromosome 6 (vs. submetacentric in the other Tupinambinae) that is intermediate in size between macro and microchromosomes (vs. large in *Crocodilurus*). He did not provide catalogue numbers for his material. Preliminary work was performed on *Tupinambis teguixin* from Trinidad, however he also studied "*Tupinambis nigropunctatus* from Brazil." Unless this last specimen can be located, it is impossible to know if it is *Tupinambis* or *Salvator*; this name has certainly been applied to *S. merianae* in the past. Examining trigeminal muscles, Rieppel (1980) reached similar conclusions, finding more similarities between *Dracaena* and *Tupinambis*. For example, these genera share (1) a broad based bodenaponeurosis (narrow-based in *Callopistes*, *Crocodilurus*, and the Teiinae) attached to the caudomesial edge of the coronoid process and the dorsomesial edge of the surangular (vs. attached to coronoid process only), and (2) the pseudotemporalis profundus muscle spreading posteriorly below the mandibular ramus of the trigeminal nerve (vs. the muscle located entirely in front of the mandibular ramus in *Callopistes*, *Crocodilurus*, and Teiinae). Rieppel (1980) evidently examined two species of tegus (identified as *Tupinambis nigropunctatus* and *T. teguixin*) and reported no interspecific differences between them.

Some of our own characters contradict a close relationship between *Dracaena* and *Salvator.* The various species of *Tupinambis* and *Salvator* share 24.4/24.5 the nostril posterior or somewhat posterior to the nasal suture (slightly anterior to the suture in *Dracaena*, centered in *Crocodilurus*), 31.2 fourth supraocular larger than first (smaller than), and 110.1 paired scale organs on supracaudals positioned to the sides of the keel (organs single and positioned atop keel). Finally, *Crocodilurus* and *Dracaena* are both aquatic genera and share several adaptations for swimming. Most notably, their tails are flattened and possess dorsolateral crests of high, heavily keeled scales. Reduction in the number of caudal vertebrae (Sullivan & Estes 1997) also may be associated with swimming.

A posterior position of the nostril relative to the narial suture also occurs in *Callopistes* and is likely to be a symplesiomorphy of *Salvator* and *Tupinambis*, whereas character 31 is difficult to interpret since it is not applicable to *Callopistes*. Under our hypothesis, the aquatic genera would have evolved independently from relatively unspecialized terrestrial macroteiids like *Callopistes, Salvator,* and *Tupinambis*. Aquatic behavior would impose a strong selective pressure for convergent evolution of flattened tails with paired dorsolateral crests, reduced numbers of caudal vertebrae, and movement of lenticular scale organs to the tops of high keels. In these characters, the tails of aquatic macroteiids resemble tails of crocodilians and other aquatic lizards such as the gymnophthalmid *Neusticurus*, scincid *Tropidophorus*, and shinisaurid *Shinisaurus*. In the context of this discussion, some possible adaptations for aquatic habits have evolved in one of the aquatic macroteiids, but not the other. Like the other aquatic lizards mentioned above, *Dracaena* has heterogeneous dorsals, whereas the dorsals of *Crocodilurus* are homogeneous. Moreover, *Dracaena* lacks the long fifth toe of *Crocodilurus,* and *Crocodilurus* lacks the keeled ventrals of *Dracaena*. Both species have accessory dorsolateral crests at the base of the tail, although the arrangement of enlarged scales is different.

In summary, we recognize *Salvator* and *Tupinambis* as two highly divergent and clearly monophyletic genera. Our conclusions regarding relationships among the genera of Tupinambinae deserve further study. Limited surveys of osteology, chromosomes, and trigeminal jaw adductors suggest different relationships, but were hampered by the previously confused alpha taxonomy of tegus. Nonetheless, these studies identified potentially informative characters that should be assessed for more species of *Salvator* and *Tupinambis*.

Generic Boundaries within *Cnemidophorus*

Until recently, the Teiinae included two large polyphyletic genera, *Ameiva* and *Cnemidophorus*. Recent phylogenetic analyses of these lizards (Giugliano *et al.* 2006, 2007; Giugliano 2009; Hower & Hedges 2003; Reeder *et al.* 2002) have shed light on interspecific relationships, but several key taxa were not included in these analyses and few steps have been taken to resolve polyphyly of these two unwieldy genera. Before 2002, about 50 species of whiptails were partitioned into six groups of *Cnemidophorus* (Lowe *et al.* 1970); South American species were lumped into the *C. lemniscatus* species group (Wright 1993). Reeder *et al.* (2002) resurrected *Aspidoscelis* Fitzinger and transferred all except the polyphyletic *C. lemniscatus* group to this genus. Reeder *et al.* (2002) further identified four unrelated lineages of *Cnemidophorus* within South America: (1) *Cnemidophorus lemniscatus* complex (represented by *C. gramivagus*, *C. l. lemniscatus*, *C. l. splendidus*, and *C. arenivagus* in their analysis) + *C. murinus*, (2) *C. lacertoides*, (3) *C. ocellifer*, and (4) *C. longicauda*. Although their analysis placed *C. longicauda* at the base of the *Aspidoscelis* radiation, Reeder *et al.* (2002) preferred not to include it in that genus. Reeder *et al.* (2002) also found *Ameiva* to be polyphyletic, although their analysis included few species of that genus (Fig. 56). Two species from the Caribbean were found to be sister to *Aspidoscelis* + *C. longicauda* and four other species were nested in a radiation of South American cnemidophorines. The results of Giugliano *et al.* (2006) are largely congruent with those of Reeder *et al.* (2002). Importantly, these authors had genetic data for *C. parecis*, a species not considered by Reeder *et al.* (2002). Reeder *et al.* (2002) did not have molecular data for *C. ocellifer*, but unambiguously placed it within the South American clade based on a small (10 characters) morphological data set. Giugliano *et al.* (2006) found that *C. parecis* is more closely related to *Ameiva ameiva* than it is to *C. ocellifer* and that both of these *Cnemidophorus* are more closely related to *Ameiva* than either is to northern *Cnemidophorus*. Hower and Hedges (2003) analyzed relationships of most Caribbean *Ameiva*, however they only included three species from the mainland. Whereas Reeder *et al.* (2002) found that *Ameiva ameiva* is closely related to the Central American species *A. quadrilineata*, Hower and Hedges found that this species is more closely related to Caribbean *Ameiva* than to *A. ameiva*.

Our own phylogenetic analyses confirm polyphyly of both *Ameiva* and *Cnemidophorus*. Moreover, we note that neither genus has been adequately diagnosed. Presence in *Ameiva* and absence in *Cnemidophorus* of a tongue sheath appeared to be the only character to distinguish these genera (e.g., the key in Peters & Donoso-Barros 1970; Presch 1971). However, we show that even this character is problematic, requires considerable study, and has led to frequent misinterpretation and contradictory conclusions. Thus, a serious obstacle to resolving problems of polyphyly has been a lack of characters.

In this study, we identified many additional characters that allow us to unequivocally diagnose monophyletic units within the large, polyphyletic genera *Ameiva* and *Cnemidophorus* (Table 2–3). The former "*lemniscatus* complex" and *Cnemidophorus* from the Caribbean form a cohesive genus unrelated to the various species from south and east of Amazonia. Moreover, the southern species comprise three unrelated groups for which we propose the new generic names *Ameivula*, *Aurivela*, and *Contomastix*. Unlike these southern species (characters in parentheses), *Cnemidophorus sensu stricto* has a single pair of preanal spurs in males (spurs absent), a subtriangular to round nostril (oval except in *Contomastix lacertoides*), a long first supralabial with a straight to curved ventral margin (small, toothy first supralabial except in *Contomastix*), divided subarticular lamellae of the hand (entire), a serrate row of keeled scales between the digital lamellae of Toes II–V (granules restricted to phalangeal articulations at least on Toe V), and basal hemipenial papillae (absent). As redefined here *Cnemidophorus* lacks nasal-prefrontal contact (in contact) and an auricular flap (present in *Aurivela*, absent in other southern genera) and usually has the nasal suture passing through the nostril (behind or touching nostril).

Aurivela longicauda and *A. tergolaevigata* comprise one of the most distinctive lineages of Neotropical Teiinae. Unlike other lineages placed previously in *Cnemidophorus*, these two species share an auricular flap (absent), broad medial contact between the second pair of chinshields (completely separated by anterior gulars), a serrate row of keeled scales separating digital lamellae of Toes II–IV (granules restricted to phalangeal articulations or with serrate scales also present on the fifth toe), and a single large medial preanal plate, much larger than the scale in front of it (preanals paired but smaller than the scale in front of them).

The various species of the former *Cnemidophorus ocellifer* complex are here transferred to the new genus *Ameivula*, whereas *C. lacertoides* and similar species are transferred to the new genus *Contomastix*. Our review of morphological characters and available molecular data supports the results of Giugliano *et al.* (2006) that *C. parecis* is closely related to *Ameiva* and we formally transfer this species to that genus. From *Contomastix* (characters in parentheses), the various species of *Ameivula* have relatively longer tails (usually relatively short), five parietals (three), short toothy first supralabials (long first supralabials with straight to curved ventral margins), small and numerous scales at the heel (three large scales), and reduced fifth toes (fifth toe well-developed).

We have uncovered additional characters that strengthen the diagnosis of *Aspidoscelis*, as resurrected by Reeder *et al.* (2002). *Aspidoscelis* lacks the various distinctive morphological characters of *Aurivela* and *Cnemidophorus sensu stricto* such as the auricular flap, serrated scales between pedal lamellae, broad medial contact between the second pair of chinshields, and preanal spurs. Unlike all the species formerly placed in

Cnemidophorus, *Aspidoscelis* has postanal plates in males (absent) and a short first supraciliary and long third or fourth supraciliary (first supraciliary usually long). Interestingly, both of these characters ally *Aspidoscelis* with Central American *Ameiva*.

TABLE 2. Selected diagnostic characters of genera formerly confused with *Cnemidophorus*. In some genera, variation occurs at low frequencies for some characters, viz. nasal-prefrontal contact, position of nasal suture, shape of nostril, and parietals.

	Ameivula	*Aspidoscelis*	*Aurivela*	*Cnemidophorus*	*Contomastix*
Relative Tail Length (Tail length/ SVL)	Long (2.1–2.3)	Very Long (2.3–2.8)	Very Long (about 2.6)	Usually Long to Very Long (2.0–2.7)	Usually Relatively Short (1.5–2.1)
Nasal-Prefrontal	In Contact	In Contact	In Contact	Separate	In Contact
Parietals	Five	Three	Three	Five	Three
Position of Nostril Relative to Nasal Suture	In Front of Suture	In Front of Suture	In Front of Suture	Passing Through, Occasionally in Front of and Touching Suture	In Front of Suture
Shape of Nostril	Oval	Oval	Oval	Subtriangular to Round	Oval (round in *C. lacertoides*)
Pattern of Supraciliary Fusion	Long First Supraciliary (divided in some species)	Short First, Long Third Supraciliary	Supraciliaries More or Less Subequal (long first in *A. longicauda*)	Long First Supraciliary	Long First Supraciliary
Auricular Flap	Absent	Absent	Present	Absent	Absent
Ventral Margin of First Supralabial	Toothy	Curved or Toothy	Toothy	Straight to Curved	Straight to Curved
Relative Size of First Supralabial	Small	Small	Small	Longer than or Subequal to Second	Subequal to Second
Second Pair of Chinshields	Separate	Separate	In Broad Medial Contact	Separate	Separate
Preanal Spurs	Absent	Absent	Absent	One Pair Present in Males	Absent
Postanal Plates	Absent	Present	Absent	Absent	Absent
Subdigital Lamellae of Fingers	Homogenous	Homogenous	Homogenous	Subarticular Lamellae Divided	Homogenous
Separation of Pedal Lamellae	Granules Restricted to Phalangeal Articulations	Usually separated except distally on Toes 2–4.	Serrate Row of Keeled Scales on Toes 2–4.	Serrate Row of Keeled Scales on Toes 2–5.	Granules Restricted to Phalangeal Articulations
Fifth Toe	Reduced	Long/Reduced	Long	Long	Long

TABLE 3. Selected diagnostic characters of genera formerly confused with *Ameiva*. In some genera, variation occurs at low frequencies for some characters, viz. nasal-prefrontal contact, parietals, and rostral groove.

	Ameiva	Central American *Holcosus* and *H. orcesi*	*Holcosus septemlineatus* Group	*Medopheos*
Nasal-Prefontal	Separate	Variable	In Contact	Separate
Fracturing and Texture of Cephalic Roofing Scales	Entire, Smooth	Mostly Entire, Smooth	Heavily Fractured, Keeled	Entire, Smooth
Key-hole Shaped Depression of Frontoparietal Region	Absent	Absent	Present	Absent
Parietals	Five	Usually Three	Fractured	Five
Rostral Groove	Present	Absent (except in *H. niceforoi*)	Absent	Present
Longitudinal Ventral Rows	10—20 (8 in few Caribbean Species)	8	6	8
Preanal Spurs	Absent	Absent	Absent	5—6 Pairs in Males
Postanal Plates	Absent	Present	Present	Absent
Dorsolateral Row of Serrated Caudals	Absent	Present	Present	Absent
Subdigital Lamellae of Fingers	Homogenous	Subarticular Lamellae Noticeably Enlarged	Subarticular Lamellae Noticeably Enlarged	Homogenous
Scales at Heel	Small and Numerous	One Very Wide Ventral Shield Present (three large scales in *H. orcesi*)	One Very Wide Ventral Shield Present	Three Relatively Large Subequal Scales Present
Distal Subdigital Lamellae of Fourth Toe	Smooth	Sharply Keeled	Sharply Keeled	Smooth
Scale Surface Microstructure	Macrohoneycomb	Macrohoneycomb	Short Aligned Microridges	Macrohoneycomb

Generic Boundaries within *Ameiva*

Until recently, the large Neotropical genus *Ameiva* was both polyphyletic and ill defined. In this study, we identify three geographically cohesive groups formerly lumped in *Ameiva*. We identify suites of characters to define these groups and show that inclusion of all species within a single genus would render that genus polyphyletic. Our revised taxonomy more accurately reflects phylogenetic relationships and biogeography of these species. *Ameiva edracantha* does not appear to be closely related to other congeners. Accordingly, we propose the new genus *Medopheos* for this species. We resurrect *Holcosus* Cope to accommodate Western and Central American species. Finally, we demonstrate monophyly of cis-Andean and West Indian *Ameiva* and retain them in this genus.

As in many other Neotropical reptiles and amphibians, species once lumped in *Ameiva* comprise trans-Andean and cis-Andean groups. *Holcosus* and the predominantly Nearctic lizards of the genus *Aspidoscelis* are the only other teiids with postanal plates in males. Unlike *Ameiva* (characters in parentheses), the species of *Holcosus* share a suite of derived characters including a dorsolateral row of serrated caudals (serrated row absent), noticeably enlarged subarticular lamellae of the hands (manual subdigital lamellae homogeneous), two large scales at the heel (scales at heel small and numerous), and sharply keeled distal subdigital lamellae.

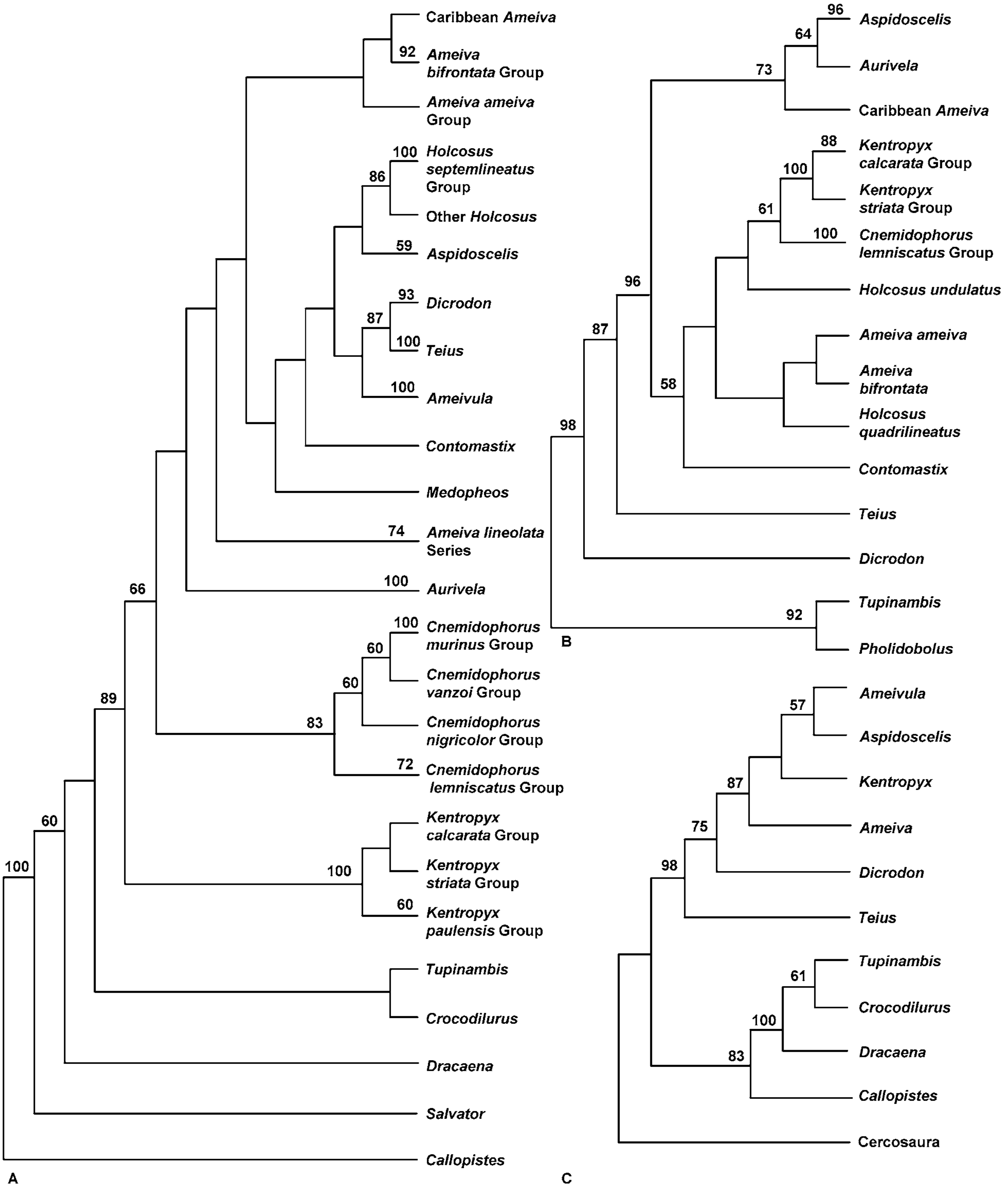

FIGURE 56 T. Intergeneric relationships of the Teiidae based on morphology (A, this study, ordered analysis with all characters included), on combined allozyme, mtDNA, and 10 morphological characters (B, Reeder *et al.* 2002), and mtDNA (C, Giugliano *et al.* 2007). Numbers indicate bootstrap support.

Of the various apomorphic characters uniting *Holcosus*, the plesiomorphic states occur in *Ameiva* and the enigmatic monotypic genus *Medopheos*. *Medopheos edracanthus* should not be included within *Ameiva* because derived features of *Medopheos* suggest that it may be more closely related to other teiids. *Medopheos* occurs in geographic proximity to *Holcosus orcesi* and shares three large scales at the heel with this species. On the other hand, *Medopheos, Cnemidophorus,* and *Kentropyx* are the only teiids with anal spurs. If *Medopheos* truly is related to one of the other genera with anal spurs or to *Ameiva*, uplift of the Andes is the most likely vicariant event to explain its current isolation and high level of divergence.

Phylogeny of Teiid Genera

Our ordered phylogenetic analysis of all characters recovered a single shortest tree (Figs. 56, 60, 66, 70, 72) with 19192760 weighted steps. Subsequent analyses excluding color and meristic characters differed in minor details from this tree and each of these analyses also recovered single trees. Intergeneric relationships in all morphology-based phylogenies differ substantially from similar phylogenies based on molecular characters (Giugliano *et al.* 2007; Reeder *et al.* 2002).

We find no support for a "cnemidophorine" clade sensu Reeder *et al.* (2002) who coined this term. Morphologically, *Kentropyx* is the most divergent genus of Teiinae. This divergence cannot be easily explained as adaptation to some specialized niche, because the extreme divergence vis-à-vis other Teiinae includes characters that have no obvious adaptive connections with one another. There is no apparent connection among fracturing of the antebrachial scales, the unusual hemipenis of this genus, the aligned microridges on the scale surfaces, and the keyhole shaped depression. Such a highly divergent group might be expected to be older than more similar groups. Of course, some young groups of species have undergone rapid and remarkable diversification, but these instances are rare. We found *Kentropyx* to be the most basal genus of Teiinae contra Reeder *et al.* (2002, Fig. 56 B) and Giugliano *et al.* (2007, Fig. 56 C) who found *Kentropyx* to be deeply nested within this subfamily.

As for *Kentropyx*, both *Cnemidophorus* and *Aurivela* possess numerous distinctive morphological traits and were placed near the base of the Teiinae. In ordered analyses, the remaining species comprise two large clades: one composed of *Ameiva* and the other composed of *Holcosus*, *Aspidoscelis*, *Dicrodon*, *Teius*, *Ameivula*, *Contomastix*, and *Medopheos*. As we discuss in greater detail in the generic account for *Ameiva*, placement of the *A. lineolata* Series outside of *Ameiva* is likely due to numerous distinctive autapomorphies of the small, unusual species in this series.

Teius (with 2n = 54) and *Dicrodon* (2n = 56) have more chromosomes than the various other genera of Teiinae. Although karyotypes of these genera markedly differ from one another, hypothetical pericentric inversions and centric fissions led Gorman (1970) to propose common ancestry of *Teius* and *Dicrodon*. Reeder *et al.* (2002) and Giugliano *et al.* (2007) found these genera to be basal Teiinae, but not sister taxa. However, in addition to the chromosomal characters, they share a frontal ridge (also present in *Ameiva bifrontata*) and transversely oriented and bicuspid mandibular and maxillary teeth. Together, *Teius* and *Dicrodon* are the sister group of *Ameivula* in our ordered phylogeny. The closest relatives of this clade are *Holcosus* and *Aspidoscelis*, whereas *Contomastix* and *Medopheos* occupy basal positions in the group.

In our analyses, the Tupinambinae is consistently paraphyletic, whereas the Teiinae is monophyletic. *Tupinambis* and *Crocodilurus* appear to be sister taxa, whereas *Dracaena* and *Salvator* occupy more basal positions in the phylogeny. Ordering and meristic and color characters affect placement of *Dracaena* in the phylogeny. When either set of characters is excluded or when all characters are unordered, *Dracaena* is the sister taxon of *Salvator.* Even though Tupinambinae is paraphyletic in our analysis, this result is contradicted by molecular data (e.g., Giugliano *et al.* 2007) and internal morphological characters not included in our study. Until conflict among these diverse data sets can be resolved, we recognize Tupinambinae for *Crocodilurus, Dracaena, Salvator,* and *Tupinambis*.

The unordered analysis found two equally parsimonious trees. These trees do not differ from the ordered trees in the placement of *Callopistes,* the various genera of Tupinambinae, *Kentropyx,* or *Cnemidophorus.* However, some genera move between the two deeply nested clades of the remaining teiid genera. In the unordered tree, *Cnemidophorus* is sister to two large clades as follows: (((*Ameiva, Ameivula*) (*Dicrodon, Teius*)) ((((*Holcosus, Medopheos*) *Contomastix) Aspidoscelis) Aurivela*)) *Cnemidophorus*). This topology makes some sense on biogeographic grounds in that the very similar cis-Andean genera *Ameiva* and *Ameivula* are sister taxa and in that the trans-Andean genera *Holcosus* and *Medopheos* are sister taxa. Importantly, neither unordered nor ordered analysis recovered monophyletic *Ameiva* or *Cnemidophorus* as defined prior to this study.

Revised Taxonomy of Extant Teiidae

Callopistinae New Subfamily

Type Genus.—*Callopistes* by original designation.

Diagnosis.—Characters in the generic diagnosis of *Callopistes* distinguish the Callopistinae from the Teiinae and Tupinambinae. Unlike the Chamopsiinae, the Callopistinae has strong heterodonty and flat (non-concave) frontal and parietal bones. The Callopistinae lacks a parietal foramen and surangular fenestra (Sullivan & Estes 1997).

Remarks.—In an unpublished doctoral dissertation, Teixeira (2003) assigned *Callopistes* to the Teiinae based on phylogenetic analysis of morphological data. Nonetheless as noted by Teixeira (2003) and Giugliano *et al.* (2007) this conclusion was only weakly supported. Teixeira's data matrix and characters have several problems that raise questions regarding her results. For example, she incorporated data directly from several earlier studies (Moro & Abdala 2000; Presch 1970; Vanzolini & Valencia 1965; Veronese & Krause 1997), in some cases perpetuating errors in those studies. She miscoded characters 43 and 44 (intertympanic and interangular sulci both coded as present in *Tupinambis* and absent in *Crocodilurus* based on Vanzolini & Valencia's misunderstanding of these characters. Interangular sulci are absent in both genera, whereas intertympanic sulci are present in *Tupinambis* and *Crocodilurus*, but absent from *Salvator*). As we point out elsewhere in this publication, some of these data matrices may include misidentified species and Teixeira apparently did not address this problem. Many of her new characters are not described except in brief one-line statements, and this problem is particularly acute in the hemipenial descriptions where variation appears to be over interpreted. Teixeira (2003) listed presence of teeth on the pterygoid (her character 6.1) as a synapomorphy of Teiinae + *Callopistes*, and she coded the various Teiinae genera as being fixed for this character (i.e., she assigned them state 1 rather than 0/1). This coding contradicts Presch's (1974a, p. 347) observations that, "pterygoid teeth are present in *K. intermedius* but variably present in *K. calcaratus* and absent in all other species examined," and "of the species of *Ameiva* that I have examined, only *Ameiva bifrontata* and *Ameiva ameiva* have pterygoid teeth."

Our study did not consider most synapomorphies that Teixeira (2003) identified for Teiinae + *Callopistes*. Regarding 38.1 (supraoculars not in contact with supraciliaries), we suspect that this character is a synapomorphy of Teiidae rather than Teiinae + *Callopistes*; a reversal is likely a shared character of the *Tupinambis teguixin* group and *Crocodilurus*. Scales between the supraoculars and supraciliaries rarely occur in gymnophthalmids (*Amapasaurus* has them, for example). Teixeira (2003) examined specimens of *Salvator merianae* and *S. duseni* in her analysis. Both species invariably have her character 38.1, yet she coded *Tupinambis* as having 38.0. She coded *Dracaena* as polymorphic (0/1); all specimens we examined have 38.1.

Teixeira's (2003) study remains unpublished and some of the problems might be resolved during any future review process. However, we think it inadvisable to uncritically accept her conclusions or incorporate her data into any type of combined analysis. For this reason, we do not have much confidence in the combined analysis of Giugliano *et al.* (2007).

Phylogenetic analysis of mitochondrial DNA supports assignment of *Callopistes* to a separate subfamily. *Callopistes* differs considerably from other Tupinambinae and is likely the sister genus of the remaining Teiidae or Tupinambinae. This conclusion is consistent with our survey of coloration, hemipenes, and external morphology. Furthermore, it is well supported by earlier morphological (Presch 1974a; Sullivan & Estes 1997) studies. The parsimony analysis of 12S sequences by Giugliano *et al.* (2007) recovered *Callopistes* as the sister genus of all other Teiidae, whereas analysis of 16S and combined 12S and 16S sequences recovered *Callopistes* as the sister genus of the Tupinambinae. Finally, we note that *Callopistes* is an ancient lineage. Giugliano *et al.* (2007) concluded that *Callopistes* diverged from other teiids in the Paleocene, perhaps through vicariance related to formation of the Salamancan Sea.

In summary, a separate subfamily should be recognized for four reasons: (1) *Callopistes* is basal to one or both other extant subfamilies, (2) its exact relationship to the other subfamilies has yet to be resolved, (3) it likely represents a very old lineage distinguished from other teiids by a suite of novel characters, and (4) recognition of the subfamily does not render either the Teiinae or Tupinambinae paraphyletic, but failure to do so would produce a taxonomy inconsistent with teiid phylogeny.

FIGURE 57. Adult *Callopistes flavipunctatus* from Piura, Peru (A, photo by A. Catenazzi) and from Desierto de Sechura, Piura, Peru *(*B, photo by P. Venegas); adult *C. maculatus* from Quebrada de la Plata, ca. 30 km SW Santiago, Chile (C, photo by T. Poch) and juvenile from Calderilla, III región, Chile (B, photo by J. Jerez).

Callopistes Gravenhorst
Figure 57

Callopistes Gravenhorst 1837: 738. Type species *Callopistes maculatus* Gravenhorst, by monotypy.
Aporomera Duméril and Bibron 1839: 69. Type species *Aporomera ornata* Duméril and Bibron, by monotypy.
Tejovaranus Steindachner 1877: 93. Type species *Tejovaranus Branickii* Steindachner, by monotypy.

Diagnosis.—Unlike all other extant Teiidae, *Callopistes* lacks femoral and abdominal pores and has three or more loreals, 2–3 complete rows of lorilabials separating the suboculars from the supralabials, heavily fractured prefrontals, and a vertical fold of skin in front of the auditory meatus.

Content.—*Callopistes flavipunctatus* (Duméril & Bibron), *Callopistes maculatus atacamensis* Donoso-Barros, *Callopistes maculatus maculatus* Gravenhorst, *Callopistes maculatus manni* Donoso-Barros.

Definition.—Medium to large lizards reaching 166 (*Callopistes maculatus*) to 325 (*C. flavipunctatus*) mm SVL; tail about 2.3X as long as body; posterior maxillary and dentary teeth longitudinally compressed, anteriorly unicuspid and recurved, becoming tricuspid posteriorly; pupil round.

Prefrontal fractured; frontal entire or transversely divided in *Callopistes maculatus*, heavily fractured in *C. flavipunctatus*, lacking longitudinal ridge; scales of frontoparietal region smooth, outwardly convex to flat in *C. maculatus*; key-hole shaped depression between eyes and in parietal region of *C. flavipunctatus*; frontoparietals paired in *C. maculatus*, fractured in *C. flavipunctatus*; parietals consisting of three regular scales in *C. maculatus*, heavily fractured in *C. flavipunctatus*; interparietal of *C. maculatus* entire, smaller than flanking parietals; medial pair of enlarged occipitals absent; occipitals 11–14 (in *C. maculatus*), usually larger than first row of dorsals; supratemporals slightly to moderately enlarged, separated from parietals by one or more scales.

Rostral groove absent; nostril subcircular to subtriangular, positioned somewhat posterior to nasal suture; loreals three (*Callopistes maculatus*) or heavily fractured; supraoculars 10–14; first supraocular heavily fractured; circumorbital semicircles consisting of 16–27 small scales, extending to posterior border of first supraocular; supraciliaries subequal, 24–33, separated from supraoculars by 1.5–4.5 rows of 38–45 (in *C. maculatus*; character not applicable to *C. flavipunctatus*) granular scales; angulate keel extending from first subocular to elongate subocular below eye; suboculars 6–8, separated from supralabials by 2–3 rows of lorilabials; first subocular entire in *C. maculatus*, its ventral margin parallel to ventral margin of second subocular in this species; first subocular contacting (*C. maculatus*) or separated from (*C. flavipunctatus*) first supraciliary; scales in front of auditory meatus slightly enlarged; auricular flap absent; vertical preauricular fold partially projecting posteriorly over anterior margin of auditory meatus.

Supralabials 19–24; first supralabial subequal to second, its ventral margin straight; infralabials 19–22; first pair of chinshields contacting infralabials (*Callopistes flavipunctatus*) or partially separated from them (*C. maculatus*) by small granular scales; first and second pairs of chinshields in medial contact; interangular sulcus absent; anterior gulars 23–41; gular patch absent; posterior gulars 15–26; intertympanic sulcus complete medially, containing scales distinctly smaller than anterior and posterior gulars; larger anterior gulars undergoing transition to smaller posterior gulars at intertympanic sulcus; mesoptychials not to slightly enlarged, not forming differentiated transverse row, not forming serrated edge of gular fold.

Dorsals smooth; scales on flank subequal to middorsals, supported by small apical granules and not projecting laterally (*Callopistes maculatus*) or supported by noticeably enlarged apical granules and projecting laterally giving flanks "bristly" appearance (*C. flavipunctatus*); scales on rump much smaller than proximal subcaudals; scales of chest large and flat; pectoral sulcus absent; ventrals smooth, in 42–66 transverse and 25–56 longitudinal rows; subrectangular scales lateral to ventrals gradually decreasing in size on flanks, bordering transverse folds of skin; preanals 7–10; preanal plate absent; preanal spurs and postanal plates absent; postcloacal buttons present in males; scales on dorsolateral edge of tail like those on top and sides, denticulate edge and dorsolateral crests absent; some caudal annuli divided, but pattern irregular; divided caudal annuli short and usually restricted to dorsal surface of tail, always separated by at least two rows of complete annuli; proximal subcaudals smooth.
Preaxial, dorsal, and postaxial sides of brachium and antebrachium covered in scales longer than wide, noticeably enlarged series absent from arm; scales on proximal, ventral surface of antebrachium granular; subdigital lamellae of hand homogeneous in size, mostly divided, 18–23 under fourth finger.

Prefemorals 13–16 in *Callopistes maculatus*, not differentiated in *C. flavipunctatus*; femoral and abdominal pores absent; scales at heel relatively small and numerous; tibiotarsal spurs and shields absent; lamellae under fourth toe 32–35; distal lamellae of fourth toe smooth; continuous row of small granular scales separating digital lamellae along postaxial edge of each toe; noticeably enlarged postaxial scales between fourth and fifth toe absent; fifth toe well-developed, base of its claw extending beyond level of skin between third and fourth toes when adpressed, but not surpassing proximal free phalangeal articulation of fourth toe.

β-keratin containing layers of dorsal scales folded into macrohoneycomb; dorsal and caudal scales with one subterminal lenticular scale organ; ventrals lacking scale organs; generation glands present; gland-bearing scales collapsed and callused distally.

Snout same color as dorsal head scales; head and throat of some adult *Callopistes maculatus* with bright orange or reddish sides, but this color not restricted to nor more conspicuous on snout. In juveniles, light vertebral, paravertebral, dorsolateral, upper and lower lateral stripes absent; dark dorsolateral and lateral fields absent, instead all dorsal surfaces of *C. flavipunctatus* covered by dark-bordered pale ocelli and blotches, and all dorsal surfaces of *C. maculatus* covered by light-bordered black ocelli; thigh lacking light spots but with conspicuous light, black-bordered ocelli. Adult males lacking light spots on flanks but with light (*C. flavipunctatus*) or black (*C. maculatus*) ocelli; turquoise ventrolateral spots absent; venter with moderately sized melanic areas or blotches; juvenile dorsal color pattern present in adult males with no or only slight modification.

Hemipenis bilobed; apical papillae, awns, and basin absent; sulcate lobes expanded and flat, deeply separated by crotch. In *Callopistes flavipunctatus*, asulcate expansion pleat interrupting about 19 distal laminae; six distal laminae discontinuous; oval lateral and medial expansion pleats completely interrupting distal laminae on sides of organ; 5–6 laminae proximal to expansion pleat; basal papillae absent; lips of sulcus rounded, lacking distal triangular expansions.

Distribution.—Western coast and Andean foothills of South America from Loja, Ecuador to Central Chile.

Remarks.—The two species of *Callopistes* are strikingly different from one another in body proportions and squamation. Based on mitochondrial DNA data, Giugliano *et al.* (2007) concluded that the two species diverged in the Oligocene. This event predates hypothesized divergences among some genera of Teiinae. The name *Tejovaranus* Steindachner is available for *C. flavipunctatus*. Nonetheless, even though the species are very old and clearly divergent from one another, we do not advocate erection of monotypic genera, except when continued recognition of a single genus produces obvious paraphyly. We identified a suite of distinctive synapomorphies of *Callopistes*. Based on chromosome morphology, Gorman (1970, p. 238) reached a similar conclusion remarking that the karyotypes of the two species are "indistinguishable" and "unique among lizards."

Böhme (1988, his figure 24 n, p. 79) illustrated the hemipenis of *Callopistes maculatus*. The organ differs substantially from that of *C. flavipunctatus* in being deeply bifurcate with an asulcate expansion pleat on each lobe. In contrast, the expansion pleat of *C. flavipunctatus* lies proximal to the lobes as in all other Teiidae. Both Böhme's illustration and description of the organ indicate that the laminae are more closely spaced than in *C. flavipunctatus*. We count 15 distal and 16 proximal laminae in his figure.

Teiinae Estes, de Queiroz, and Gauthier

Teiinae Estes, de Queiroz, and Gauthier 1988: 215.

Type Genus.—*Teius* Merrem, designated herein.

Diagnosis.—From the characters we surveyed, the Teiinae are defined by femoral pores continuous with abdominal pores, caudal annuli complete, ventrals in 6–20 longitudinal rows at midbody, postcloacal buttons absent, interangular and intertympanic sulci absent, preaxial and postaxial patches of enlarged brachial scales differentiated, and venter without large melanic blotches. Other defining characters of the subfamily include 25 presacral vertebrae (Presch 1974a; Veronese & Krause 1997), a single thin pair of infralingual plicae with 0–7 much smaller swollen pairs behind it (Harris 1985), and 2n = 46–56 chromosomes, with most large chromosomes acrocentric and with no distinct break between macro and microchromosomes (Gorman 1970). The Teiinae share two apparent synapomorphies of the trigeminal jaw musculature (Rieppel 1980): (1) a large sheet of temporal fascia arising from the entire temporal arch (postorbital and squamosal; the same fascia is much less extensive in the Tupinambinae, arising only from the dorsolateral edge of the squamosal and the cephalic condyle of the quadrate) and (2) a more lateral (i.e., relative to the Tupinambinae) position of the vertical sheet of the quadrate aponeurosis. Unlike the Callopistinae and Tupinambinae, the Teiinae share fusion of the postorbital and postfrontal, an expanded pterygoid process of the quadrate, a pterygoid flange, presence of a dorsal squamosal process, an expanded clavicle, presence of clavicular hooks, presence of a scapular fenestra, 12 postxiphisternal ribs, and a low median crest on the caudal vertebrae (Presch 1974a).

Remarks.—The subfamily names Tupinambinae and Teiinae are attributed to Estes *et al.* (1988) who elevated Teiini Presch and Tupinambini Presch to subfamilial rank when defining Teiidae. These authors did not designate a type genus of the subfamily. Accordingly, we here designate *Teius* as the type genus of Teiinae Estes, de Queiroz, and Gauthier. In earlier publications (1983a, b), Estes recognized two subfamilies of Teiidae: Polyglyphanodontinae including several extinct genera and Teiinae including Teiini and Tupinambini sensu Presch (1974a).

***Ameiva* Meyer**

Figure 58–59

Ameiua Meyer 1795: 27. Type species *Ameiua americana* Meyer by subsequent designation (see remarks). [Original spelling emended by Bechstein 1800]
Cnemidotus Wagler 1828: 860. Type species *Lacerta ameiva* Linnaeus.
Pachylobronchus Wagler 1833: 891. Type species *Lacerta ameiva* Linnaeus.
Pholidoscelis Fitzinger 1843: 20. Type species *Ameiva major* Duméril and Bibron by original designation.
Tiaporus Cope 1892: 132. Type species *Tiaporus fuliginosus* Cope by monotypy.

Diagnosis.—From all other Teiinae, *Ameiva* can be distinguished by the combination of the following characters: first supraciliary short, third or fourth supraciliary usually elongate (except in *A. wetmorei*), five regular parietals (except in *A.wetmorei*), the prefrontal separated from the nasal, small numerous scales at the heel (except in *A. lineolata* series), homogeneous manual subdigital lamellae, smooth ventrals and subcaudals, and males lacking preanal spurs.

FIGURE 58. Adult *Ameiva ameiva* from Mato Grosso, Brazil (A, photo by P. Bernardo); adult male *A. atrigularis* from Fuentidueño, Isla de Margarita, Nueva Esparta, Venezuela (B, photo by G. N. Ugueto); adult *A. auberi felis* from Half Moon Cay, Cat Island, Bahamas (C, photo by B. Lindsay); adult *A. bifrontata ssp.* from La Vela de Coro, Falcón, Venezuela (D, photo by Y. Surget-Groba) and Aruba (E, photo by G. van Buurt); adult *A. dorsalis* from Port Royal, Jamaica (F, photo by J. Burgess); adult male *A. erythrocephala* from Saint George Basseterre, St. Christopher (G, photo by M. Dalzell); adult male *Ameiva exsul* from Anegada, British Virgin Islands (H, photo by J. Burgess).

Content.—Twenty-five named species, each assigned herein to one of five species groups.

Definition.—Small to large lizards reaching 243 (*Ameiva praesignis*) mm SVL; tail 1.9–2.6X as long as body; posterior maxillary and dentary teeth longitudinally compressed, tricuspid; pupil reniform.

Prefrontal usually separated from nasal and contacting (except in *Ameiva lineolata* Series) first supraciliary; frontal entire (transversely divided in *A. bifrontata* complex and in few specimens of *A. ameiva*), lacking longitudinal ridge (except *A. bifrontata* complex); posterior suture of frontal usually contacting third supraocular in most species, frequently or usually contacting second supraocular in *A. ameiva* complex, *A. dorsalis*, and *A. fuscata*; scales of frontoparietal region smooth, outwardly convex to flat (key-hole shaped depression absent); frontoparietals paired; parietals consisting of five regular scales (three in *A. wetmorei*); interparietal entire, variable in size; medial pair of enlarged occipitals usually absent; occipitals usually larger than first row of dorsals; supratemporals slightly to moderately enlarged, separated from parietals by one or more scales (except in *A. lineolata* series).

Rostral groove usually present; nostril oval and oriented anteroventrally, its position relative to nasal suture varying among species groups; loreal single; supraoculars eight (rarely 6, 7, 9, or 10); first supraocular entire, larger than fourth supraocular (except *Ameiva maynardi*), and usually broadly contacting second supraocular; circumorbital semicircles consisting of 2–40 small scales, their anterior extent varying among species; supraciliaries 11–18, separated from supraoculars by 1–3 rows of 17–81 granular scales; first supraciliary small, second and third enlarged and subequal in size or third greatly enlarged (first and second supraciliaries subequal and longer than rest in *A. wetmorei*); angulate keel extending from first subocular to elongate subocular below eye; suboculars usually four; first subocular usually contacting first supraciliary, usually contacting supralabials in most Caribbean species or usually separated from supralabials by anterior expansion of second supralabial in *A. ameiva*, *A. bifrontata*, and *A. parecis* Groups; scales in front of auditory meatus variable in size; auricular flap and preauricular fold absent.

Supralabials 11–17; first supralabial smaller than or subequal to second, its ventral margin curved in *Ameiva ameiva* Group and *A. lineolata* Series, toothy in other groups; infralabials 10–15; first pair of chinshields broadly contacting infralabials (frequently partially to completely separated by small granular scales in *A. auberi*, *A. dorsalis*, and *A. exsul*) and usually forming a medial suture greater than or equal to half their length in all species except *A. dorsalis* Group where variable in length in several species; interangular sulcus absent; anterior gulars 18–55; gular patch absent; posterior gulars 7–29; intertympanic sulcus absent; larger anterior gulars undergoing sharp transition to smaller posterior gulars at intertympanic crease except in *A. lineolata* Series, *A. auberi*, and *A. dorsalis*; mesoptychials not to moderately enlarged, not forming differentiated transverse row; gular fold lacking serrated edge.

Dorsals smooth; scales on flank subequal to middorsals, not projecting laterally, supported by small apical granules; scales on rump much smaller than proximal subcaudals; scales of chest large and flat; pectoral sulcus present in *Ameiva erythrocephala* Group and some specimens of *A. bifrontata* Group, absent in other groups; ventrals smooth, in 29–37 transverse and 8–20 longitudinal rows; lateral-most ventrals often gradually decreasing in size on flanks; preanals 4–17 (generally highest counts in *A. erythrocephala* Group); preanal plate present, bordered by subtriangular scales; preanals one-half as large to slightly larger than scale anterior to them; preanal spurs, postcloacal buttons, and postanal plates absent; scales on dorsolateral edge of tail like those on top and sides, denticulate edge and dorsolateral crests absent; caudal annuli complete; proximal subcaudals smooth.

Enlarged scales of brachium connected by continuous band of subtriangular plates on dorsal surface of arm of *Ameiva lineolata* Series, separated by small granular scales in all other species; preaxial brachial scales 1–2X as wide as long (except in *A. corvina*, *A. erythrocephala*, and *A. pluvianotata* where scales are not enlarged, longer than wide), usually not extending beyond middle of arm; postaxial brachial scales variable in size, both extending to or beyond center of arm; antebrachial scales enlarged and smooth, separated from brachial scales by large gap on proximal antebrachium in *A. erythrocephala* Group and *A. dorsalis*, narrowly separated from or in continuous row with preaxial brachial scales in all other species; postaxial antebrachial scales slightly enlarged to granular; subdigital lamellae of hand homogeneous in size, entire (except *A. lineolata* with scattered divided subdigital lamellae, not restricted to phalangeal articulations), 13–22 (counts lower in *A. ameiva* Group than in other groups) under fourth finger.

Prefemorals 4–14; femoral and abdominal pores 22–78 (higher in *Ameiva erythrocephala* Group than other species) in continuous row on each side (abdominal pores not separated from femoral pores by gap); each compound pore-bearing scale consisting of partially fused prefemoral or abdominal scale and 2–6 granular scales; 4–26 (usually higher in *A. dorsalis* Group than in other species) scales separating right and left pore rows; scales at heel relatively small and numerous (except *A. lineolata* and holotype of *A. wetmorei*, both with three relatively large subequal scales); tibiotarsal shields absent; tibiotarsal spurs absent in most species (two rows of about eight total spurs with elongate mucrons present in *A. dorsalis* and some populations of *A. auberi*); lamellae under fourth toe 29–46; distal lamellae of fourth toe smooth in most species (keeled in *A. plei*); scales between subdigital and supradigital lamellae of toes small and mostly restricted to phalangeal articulations in most Caribbean species, keeled and separating lamellae in *A. fuscata* and the *A. ameiva* and *A. bifrontata* Groups; noticeably enlarged postaxial scales between fourth and fifth toe absent; fifth toe well-developed in Caribbean species, reduced in some *A. griswoldi* and all specimens of the *A. ameiva* and *A. bifrontata* Groups.

FIGURE 59. Adult male *Ameiva fuscata* eating a crab (A, photo by J. Burgess) and juvenile (B, photo by W. Wüster), both from Dominica; adult *A. griswoldi* from Antigua (C, photo by W. Wüster); adult *A. plei plei* from Phillipsburg, St. Martin (D, photo by J. Burgess); adult male *A. praesignis* from Zulia, Venezuela (E, photo by L. A. Rodríguez); juvenile *A. provitaae* from Lagunillas, Merida, Venezuela (F, photo by J. E. García-Pérez); adult *A. taeniura* from near La Romana, Dominican Republic (G, photo by J. Finch); adult *A. ameiva tobagana* from Bequia Island, St. Vincent and the Grenadines (H, photo by J. Burgess).

β-keratin containing layers of dorsal scales folded into macrohoneycomb; dorsal and caudal scales with one subterminal lenticular scale organ; ventrals lacking scale organs; generation glands present in most Caribbean species and the *A. bifrontata* Group, absent in *A. fuscata, A. pluvianotata,* and the species of the *A. ameiva* Group. Snout of adults usually red or with reddish cast except few species with snout of same color as dorsal head scales (*Ameiva ameiva*, *A. atrigularis, A. dorsalis, A. lineolata, A. pantherina, A. parecis, A. praesignis, A. wetmorei*). In juveniles (characters of juvenile coloration of *A. corvina, A. maynardi,* and *A. pluvianotata* unknown), light vertebral stripe absent (most species), or solid and straight (*A. auberi* species complex, *A. bifrontata* species complex, at least some subspecies of *A. chrysolaema, A. wetmorei*), or split and straight (*A. lineolata*), or widening substantially on the posterior body (*A. dorsalis*), or straight but breaking into spots posteriorly (*A. plei*), or present only from mid-dorsum to sacrum (*A. praesignis*); light paravertebral stripes absent (most species), or present and straight (at least some subspecies of *A. chrysolaema*, A. *lineolata*), or broken into spots (*A. plei*), or absent (*A. abaetensis*); dark dorsolateral field absent (most species), solid (at least some subspecies of *A. chrysolaema*, *A. exsul, A. lineolata*), or completely broken into blotches (*A. bifrontata* species complex, *A. parecis, A. plei*); dorsolateral light stripe solid and extending to tail (most species), or fading towards sacrum (*A. ameiva* Group, *A. fuscata, A. griswoldi, A. wetmorei*), or broken (*A. dorsalis*), or absent (*A. pluvianotata*); dark lateral field solid (most species), or solid anteriorly and breaking into spots posteriorly (*A. bifrontata divisa* and other members of the *bifrontata* complex not currently assigned to a particular subspecies), or completely broken into blotches (most taxa of the *A. bifrontata* complex, *A. dorsalis, A. exsul, A. griswoldi, A. parecis*); upper lateral light stripe solid and extending to groin (most species), or broken to groin (some taxa of the *A. bifrontata* complex, *A. dorsalis, A. exsul*), or extending above the leg as either a broken or continuous stripe (*A. wetmorei*), or absent (*A. pluvianotata*); lower lateral light stripe absent (most species), or solid and extending to groin (*A. lineolata, A. wetmorei*), or broken (*A. exsul*); thighs lacking light spots (most species), or with light spots (*A. chrysolaema complex, A. exsul, A. griswoldi, A. lineolata, A. plei, A. wetmorei*). In adult males, turquoise ventrolateral spots present (most species), absent in *A. lineolata* and *A. wetmorei*; venter immaculate to finely spotted, except in some specimens of *A. praesignis* from Venezuelan and Colombian Llanos with moderately large black blotches; juvenile dorsal color pattern present in adult males with only slight modification in most species, but some species undergo considerable ontogenetic changes (*A. ameiva, A. atrigularis, A. exsul, A. fuscata, A. griswoldi, A. pantherina, A. parecis, A. plei, A. praesignis*).

Hemipenis with pair of taβ-like and smooth apical awns; apical papillae and apical basin absent; asulcate expansion pleat vestigial in the *Ameiva bifrontata* Group, well-developed in other groups; asulcate expansion pleat interrupting about 11–24 distal laminae in Caribbean species and about 5–9 distal laminae in *A. ameiva* and *A. bifrontata* Groups; discontinuous distal laminae approximately 4 in *A. chrysolaema* and species of the *A. ameiva* Group; 0–15 laminae proximal to expansion pleat in Caribbean species, 14–26 in the *A. ameiva* and *A. bifrontata* Groups; basal papillae absent.

Etymology.—We do not know the derivation of *Ameiva*. Duméril and Bibron (1839) remark that the name had been used by earlier authors and was said to be a common name used somewhere in the New World as was the case with *Teius*.

Distribution.—The genus *Ameiva* occurs in eastern South America and the Caribbean Islands with one species (*Ameiva praesignis*) extending into northern Colombia, Panama, and extreme southern Costa Rica. *Ameiva ameiva* and *A. praesignis* have been introduced to South Florida (Ugueto & Harvey 2011).

Interspecific Relationships.—In all of our analyses, *Ameiva* forms a monophyletic group containing four clades. We used suites of morphological characters (Table 4) to define geographically and morphologically cohesive groups of species. Species groups are consistent with well-established biogeographic patterns and, except for the *A. dorsalis* Group, demonstrably monophyletic (Fig. 60).

The West Indian *Ameiva* form a monophyletic group in all recent analyses of both morphological (this study) and molecular characters (Giugliano *et al.* 2009; Hower & Hedges 2003; Reeder *et al.* 2002). Unlike other *Ameiva* (characters in parentheses), the West Indian species share the narial suture positioned behind the nostril (passing through nostril or located in front of it), the first subocular usually contacting the supralabials (usually separated from supralabials), a long fifth toe (reduced), and supradigital and subdigital lamellae usually in contact along the postaxial margin of the toes (separated).

TABLE 4. Selected characters useful in the recognition of species groups within *Ameiva*.

Characters	*A. ameiva* Group	*A. bifrontata* Group	*A. dorsalis* Group	*A. erythrocephala* Group
Frontal	Usually entire	Always divided	Entire	Entire
Usual Position of Posterior Frontal Suture	Contacting 2nd supraocular, or aligned with suture of 2nd and 3rd supraoculars	Contacting 3rd supraocular	Contacting 3rd supraocular, or aligned with suture of 2nd and 3rd supraoculars (except *A. dorsalis*)	Contacting 3rd supraocular, or aligned with suture of 2nd and 3rd supraoculars (except *A. fuscata*)
Frontal ridge	Absent (slightly visible in some *A. ameiva atrigularis*)	Present	Absent	Absent
Interparietal	Usually entire	Entire	Usually entire	Often divided (except *A. erythrocephala*)
Parietals	Long	Long	Long	Short
Position of nostril relative to narial suture	Suture passing through nostril	Suture in front of nostril	Suture behind nostril (except type of *A. wetmorei*)	Suture behind nostril
1st supralabial	Curved	Toothy	Toothy (curved in *A. lineolata* series)	Toothy
1st subocular	Separated from supralabials	Usually separated from supralabials	Contacting supralabials (except in *A. chrysolaema* and *A. taeniura*)	Usually Contacting Supralabials (except *A. erythrocephala*)
Intertympanic crease	Present	Present	Present or absent	Present
Pectoral sulcus	Absent	Usually absent	Absent (except *A. chrysolaema*)	Present
Longitudinal rows of ventrals	10–12	10	8–10 (some *A. auberi* with 12)	10–20
Continuation of antebrachial and brachials	Continuous or narrowly separated	Continuous or narrowly separated	Continuous or narrowly separated (except *A. dorsalis*)	Separated by large gap of distinctly smaller scales
Femoral pores (combining counts for both legs)	28–45	26–40	20–48	39–78
5th toe	Reduced	Reduced	Long	Long (except some *A. griswoldi)*
Scales separating lamellae along postaxial edge of toes	Completely separating lamellae	Completely separating lamellae	Lamellae in contact	Lamellae in contact (except *A. fuscata)*
Generation glands	Absent	Present	Present	Present (except *A. fuscata, A. pluvionotata)*
Red or reddish color on tip of snout of adult males	Absent	Present	Present (except *A. lineolata* Series)	Present
Ontogenetic changes in coloration	Present, conspicuous	Absent or inconspicuous	Absent or inconspicuous	Absent or inconspicuous (except in *A. fuscata, A. plei,* and *A. pluvionotata)*
Ocelli on flanks of adult males	Present	Absent	Absent	Absent (except *A. fuscata)*
Hemipenial Laminae	Fewer distal than proximal	Fewer distal than proximal	More distal than proximal	More distal than proximal
Asulcate Expansion Pleat	Present	Vestigial	Present	Present

The West Indian *Ameiva* most likely evolved from a South American ancestor and are most closely related to the *Ameiva bifrontata* Group in all our trees. The West Indian species and the *A. bifrontata* Group (characters of *A. ameiva* Group in parentheses) share the frontal suture usually contacting the third supraocular (usually contacting second), “toothy” first supralabials (curved), presence of generation glands (absent), and a red or reddish snout (snout same color as rest of head). Moreover, some species in both groups have a pectoral sulcus. The red snout and pectoral sulcus occur in no other Teiidae. South American ancestry of the West Indian *Ameiva* contrasts with conclusions of recent molecular studies that found West Indian species to be related to *Holcosus* (Hower & Hedges 2003, Giugliano 2009) or *Aspidoscelis* (Reeder *et al.* 2002). We judge a South American origin and common ancestry with the *A. bifrontata* Group to be likely for three reasons: (1) most West Indian radiations of other groups of animals arose from ancestral species in northern South America, (2) alternative hypotheses require convergent evolution of two characters (the red snout and pectoral sulcus) unique to these lizards among Teiidae, and (3) alternative phylogenetic analyses (Giugliano 2009; Hower & Hedges 2003; Reeder *et al.* 2002) included fewer species of *Ameiva*.

Analyses of morphological (this study) and mtDNA (Hower & Hedges 2003) both identified a Lesser Antillean clade (Fig. 60) including *Ameiva erythrocephala, A. fuscata, A. griswoldi, A. plei*, and *A. pluvianotata.* We found *A. corvina* to be nested within this clade, and Hower and Hedges (2003) found *A. corax* to be nested within this clade. Both studies found *A. auberi* and *A. dorsalis* to be sister taxa, and distinctive tibiotarsal spurs in these two species support this conclusion. On the other hand, we found these species to be closely related to the Greater Antillean *A. taeniura*, whereas the molecular phylogeny placed these two species at the base of the Lesser Antillean radiation.

Both analyses found that *Ameiva lineolata* and *A. maynardi* are sister species. These two species share a suite of distinctive characteristics and are both relatively small. Perhaps because of their unusual traits, our analyses consistently placed these two species outside of *Ameiva*. However, they possess the diagnostic characters of our *Ameiva dorsalis* group; they are the closest relatives of *A. taeniura* in the molecular phylogeny (Hower & Hedges 2003).

Our analysis and that of Hower and Hedges differ in placement of *A. chrysolaema* and *A. exsul*. These large Greater Antillean species were placed at the base of the Lesser Antillean clade in our ordered analysis and at the base of a Greater Antillean clade in the molecular analysis. On the other hand, in our unordered analysis, *A. chrysolaema* moved to the base of the Greater Antillean clade, whereas *A. exsul* moved deeper into the Lesser Antillean clade as the sister species of *A. griswoldi*. Both species lack most defining characters of the Lesser Antillean clade such as short parietals, frequent longitudinal division of the interparietal, and a wide gap between the enlarged brachials and antebrachials. Nonetheless, *A. chrysolaema* is the only Greater Antillean species with a pectoral sulcus, whereas this trait is always present in the Lesser Antillean species.

In summary, the Lesser Antillean *Ameiva* share distinctive derived traits, many found in no other Teiidae, and clearly form a monophyletic group. Uncertainty persists regarding the interrelationships of the Greater Antillean species, because they lack distinctive morphological traits. Although morphological and molecular data sets agree on many points, further study is required to resolve persisting uncertainty about the relationships of Greater Antillean *Ameiva*.

Much of the diversity within the *Ameiva bifrontata* and *A. ameiva* Groups has not been adequately described. Ugueto and Harvey (2011) recently reviewed the *A. ameiva* Group in Venezuela and showed that some subspecies of *A. ameiva* are full, evolutionary species. In this analysis, we found that *A. praesignis* is the sister taxon of *A. ameiva* and *A. atrigularis* is the sister taxon of the recently described *A. pantherina*.

Ruthven (1924) thought a new taxon from Peru was a subspecies of *Ameiva bifrontata*, because it has a transversely divided frontal and similar habitus. Nonetheless, Ugueto and Harvey (2011) showed that the interparietal is frequently divided in some populations of upper Amazonian *A. ameiva*. Known only from the Peruvian Andes, *A. bifrontata concolor* is distantly allopatric from all other populations of *A. bifrontata*, which are restricted to a few southern Caribbean islands and northern Venezuela and Colombia.

As part of our ongoing revisions of species in this genus, we examined the type series of *Ameiva bifrontata concolor* (Appendix). These lizards differ substantially from other populations of *A. bifrontata*. Perhaps not surprisingly, the phylogenetic analysis assigned this taxon to the *A. ameiva* Group when all characters were included in both the ordered and unordered analyses, but placed *A. b. concolor* at the base of the *A. bifrontata* Group when meristic characters were excluded. Striking morphological differences between *A. b. concolor* and other *A. bifrontata*, the results of the phylogenetic analysis, and the wide geographic hiatus between *A. b. concolor* and other *A. bifrontata* convince us that *A. b. concolor* is a full species, and we here formally recognize it as *Ameiva concolor* Ruthven. A complete redescription of the species will be published elsewhere.

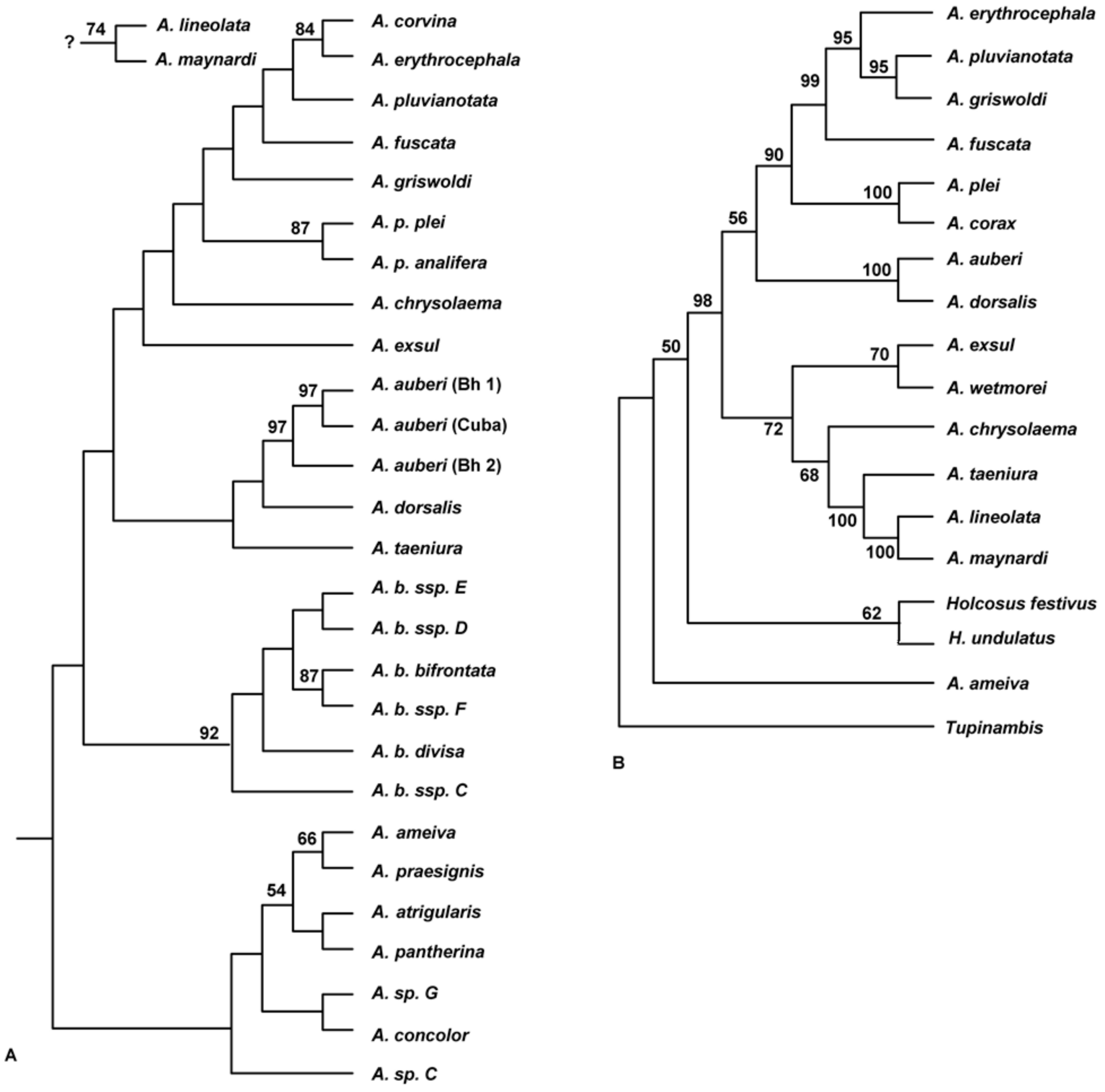

FIGURE 60. Phylogeny of *Ameiva* based on morphology (this study, ordered analysis of all characters, A) and phylogeny of West Indian *Ameiva* based on 12S and 16S mtDNA (from Hower & Hedges 2003, B). In both trees, numbers indicate bootstrap support.

Remarks.—In our taxonomy, we chose the oldest species name as the group or series name in accordance with well-established precedent. Hower and Hedges (2003) named four species groups without following this convention. Their *plei* Group is essentially equivalent to our *Ameiva erythrocephala* Group, whereas the other groups recognized by them (*auberi*, *exsul*, and *lineolata* Groups) together comprise our *A. dorsalis* Group.

Regarding the generic synonymy, two issues require comment. Meyer (1795) proposed *Ameiua* to accommodate fourteen species listed by Gmelin (1789), including several species no longer included in this genus such as *Lacerta Teguixin* Linnaeus (= *Tupinambis teguixin*). Meyer further proposed *Ameiua americana* as a replacement name for *Lacerta ameiva* Linnaeus and this name was listed as the type species of *Ameiva* by Peters and Donoso-Barros (1970).

Earlier synonymies of *Ameiva* (e.g., Peters & Donoso-Barros 1970) have included *Amieva*, with the “i" and “e” interposed, based on Gray (1840). If available, Gray’s name could be used as a subgenus or genus for lizards here placed in the *Ameiva dorsalis* Group. This name would be pronounced differently than *Ameiva* and, therefore, could not be considered a secondary homonym. *Amieva* was clearly a misspelling and not proposed as a new name. We suspect that Peters and Donoso-Barros (1970) concluded otherwise, because Gray did not place an author after *Amieva*, and, following the practices of the day, this omission usually meant that the author intended to formally name a new genus. We interpret “*Amieva*” to be an incorrect subsequent spelling of *Ameiva*, because, when discussing *A. trilineata*, Gray (1840, p. 115) mentions, “this species differs from all the other species of the genus that we have in the British Museum in colour…” Gray (1840) misspelled other genera, notably *Anolis*, which he twice misspelled “*Anolius*” on page 110 only to correctly spell the genus again on page 112. As for *Amieva* he does not list the author of *Anolis* on p. 112 even though he does so for other genera of this section such as “*Chamaeleolis*, Cocteau” on p. 111. As an incorrect subsequent spelling not in prevailing usage, Gray’s name is removed from the synonymy of *Ameiva* and is not available for the species of the *Ameiva dorsalis* Group.

Ameiva ameiva Group

Definition.—The following combination of characters distinguishes the *Ameiva ameiva* Group (Table 5) from other groups of *Ameiva*: frontal usually entire, its posterior suture usually contacting second supraocular or aligned with suture between second and third supraoculars; frontal ridge absent (faint indication of frontal ridge evident in some specimens of *A. atrigularis*); interparietal entire with rare exceptions; parietal series (including interparietal) composed of five (only in rare occasions three) relatively long plates; narial suture passing through nostril; first supralabial usually curved; first subocular usually separated from supralabials by anterior expansion of the second subocular; intertympanic crease present; pectoral sulcus absent; ventral scales in 10–12 longitudinal rows (usually 10); plate-like antebrachials continuous with or narrowly separated from brachial scales; combined femoral and abdominal pores 28–45; fifth toe reduced; complete row of scales separating supradigital and subdigital lamellae along postaxial edge of each toe; generation glands absent; tip of snout of adult males never reddish; conspicuous ontogenetic changes in coloration; adults without dorsolateral and vertebral stripes, or only vertebral stripe apparent on posterior dorsum; flanks with pale ocelli; hemipenis with fewer distal (5–9) than proximal laminae (14–23); about four discontinuous laminae present on sulcate side of hemipenis; asulcate expansion pleat well-developed.

Content.—*Ameiva ameiva ameiva* (Linnaeus), *A. a. fuliginosa* Cope, *A. a. tobagana* (Cope), *A. atrigularis* Garman, *A. pantherina* Ugueto and Harvey, *A. praesignis* (Baird & Girard).

Distribution.—Most of South America east of the Andes south to Bolivia, also present in northern Colombia, Panama, extreme southern Costa Rica, Trinidad, Tobago, Isla de Providencia, St. Vincent, Grenada, and The Grenadines; apparently extinct on Swan Island.

Remarks.—Status of the insular species *Ameiva ameiva fuliginosa* from Providencia Island and *A. a. tobagana* from the Grenada Bank should be reconsidered. The first taxon was originally described by Cope (1892) as *Tiaporus fuliginosus*. He remarked that *Tiaporus* was identical to *Ameiva* except that it lacked femoral pores. Burt and Burt (1931) added Cope’s name to the synonymy of *Ameiva* after they revised the four cotypes of *T. fuliginosus* and found that all have femoral pores (17–18 on each leg). Lizards from the Swan Islands were also found to be conspecific with those from Providencia formerly described as *A. panchlora* by Barbour (1921). Dunn and Saxe (1950) could not differentiate these insular populations from continental *A. ameiva* and thus preferred to treat *panchlora* as a subspecies. The same authors reported that the population on the Swan Islands was extinct by 1914. Cope (1879) also described another insular population, *Ameiva surinamensis* (=*ameiva*) *tobaganus* purportedly collected on the island of Tobago. Almost a decade later, Garman (1887) named another insular variant of *A. surinamensis*, *A. s.* var. *aquilina*, based on a series of eight specimens from Grenada and 39 from St. Vincent. Apparently, Garman was unaware of Cope’s description of *A. s. tobaganus* and did not compare his specimens with the taxon described from neighboring Tobago. In their revision of the genus *Ameiva*, Barbour and Noble (1915) considered the population purportedly from Tobago and the one from the Grenada Bank as full species closely associated with *A. ameiva*. Peters and Donoso-Barros (1970) considered both populations to be subspecies of *A. ameiva*. Tuck and Hardy (1973) concluded that *A. a. tobagana* was likely collected in Grenada, the Grenadines or

St. Vincent (populations previously allocated to *A. a. aquilina*) rather than on Tobago but continued to regard it as a subspecies of the widespread mainland species *A. ameiva*.

We have observed photographs of both *Ameiva ameiva fuliginosa* and *A. a. tobagana* and they sharply differ in coloration from other *Ameiva* of the *A. ameiva* Group. Additionally, both taxa are isolated on islands far from the range of *A. ameiva* (Ugueto & Harvey 2011) and thus likely represent separate evolutionary lineages. Accordingly, we continue to recognize these taxa as subspecies until they can be reviewed.

***Ameiva bifrontata* Group**

Definition.—The following combination of characters distinguishes the *Ameiva bifrontata* Group (Table 5) from other groups of *Ameiva:* frontal always divided, its posterior suture usually contacting third supraocular or aligned with suture between second and third supraoculars; frontal ridge well-developed; interparietal entire; parietal series (including interparietal) composed of five, relatively long plates; narial suture passing in front of nostril; first supralabial distinctly toothy; first subocular usually separated from supralabials by anterior expansion of the second subocular; intertympanic crease present; pectoral sulcus usually absent; ventral scales in 10 longitudinal rows; plate-like antebrachials continuous with or narrowly separated from brachial scales; combined femoral and abdominal pores 26–40; fifth toe reduced; complete row of scales separating supradigital and subdigital lamellae along postaxial edge of each toe; generation glands present; tip of snout of adult males red or reddish; ontogenetic changes in coloration absent or very limited; adults usually with dorsolateral and vertebral stripes (obscured only in *A. bifrontata* ssp.); flanks without pale ocelli; hemipenis with much fewer distal (five) than proximal laminae (23–26); discontinuous laminae absent; asulcate expansion pleat vestigial.

Content.—*Ameiva bifrontata bifrontata* Cope, *A. b. divisa* (Fischer), *A. b. insulana* Ruthven, *A. b.* ssp., *A. provitaae* García-Pérez.

Distribution.—Disjunctly distributed in northern Colombia and Venezuela, including the islands of Margarita, Coche, Cubagua, La Tortuga (García-Pérez personal comment) and the archipelagos of Los Frailes and Los Testigos; also present on the island of Aruba.

***Ameiva dorsalis* Group**

Definition.—The following combination of characters distinguishes the *Ameiva dorsalis* Group (Table 6) from other groups of *Ameiva:* frontal entire, its posterior suture usually contacting third supraocular (except in *A. dorsalis*) or aligned with suture between second and third supraoculars; frontal ridge absent; interparietal entire with very rare exceptions; parietal series (including interparietal) composed of five (only three in *A. wetmorei*) relatively long plates; narial suture behind nostril and touching it (except in the type of *A. wetmorei*); first supralabial usually toothy (except in *A. lineolata* series); first subocular usually contacting supralabials (except *A. chrysolaema* and *A. taeniura*); intertympanic crease present or absent; pectoral sulcus absent (except *A. chrysolaema*); ventral scales in 8–10 longitudinal rows (some *A. auberi* specimens with 12 longitudinal rows); plate-like antebrachials continuous with or narrowly separated from brachial scales (except *A. chrysolaema* and *A. dorsalis*); combined femoral and abdominal pores 20–48; fifth toe well-developed; supradigital and subdigital lamellae contacting one another, at least on toes 4 and/or 5; generation glands present; tip of snout of adult males red or reddish in most species (except in *A. dorsalis*, *A. lineolata* and *A. wetmorei*; condition unknown in *A. maynardi*); ontogenetic changes in coloration absent or very limited; adults with dorsolateral and vertebral stripes, or only vertebral stripe present and broadening conspicuously on posterior dorsum; flanks without pale ocelli (adult *A. exsul* and some races of *A. chrysolaema* have pale spots but without black margins); hemipenis with more distal (11–24) than proximal (0–15) laminae (as many distal as proximal laminae in some specimens of *A. chrysolaema*); discontinuous laminae absent (except *A. chrysolaema*); asulcate expansion pleat well-developed.

Content.—*Ameiva alboguttata* Boulenger, *A. auberi* Cocteau, *A. chrysolaema* Cope, *A. dorsalis* Gray, *A. exsul* Cope, *A. lineolata* Duméril and Bibron, *A. maynardi* Garman, *A. polops* Cope, *A. taeniura* Cope, *A. wetmorei* Stejneger.

Distribution.—Greater Antilles from the Bahamas and Cuba to St. Croix in the U. S. Virgin islands.

TABLE 5. Meristic data of selected mainland *Ameiva* examined by us. Means ± standard deviation follow ranges.

	Ameiva b. bifrontata (*n* = 9)	*Ameiva b. divisa* (*n* = 4)	*Ameiva ameiva* (*n* = 22)	*Ameiva atrigularis* (*n* = 40)	*Ameiva pantherina* (*n* = 31)	*Ameiva praesignis* (*n* = 52)
Occipitals	17–20 (19 ± 1)	18–21 (19 ± 1)	11–17 (15 ± 1)	10–18 (14 ± 2)	14–18 (15 ± 1)	12–21 (16 ± 2)
Lateral Supraocular Granules	48–64 (58 ± 5)	29–72 (49 ± 18)	19–44 (28 ± 7)	17–47 (28 ± 7)	24–41 (30 ± 5)	15–36 (22 ± 5)
Circumorbitals	27–40 (33 ± 4)	21–29(26 ± 4)	6–17 (11 ± 3)	6–17 (13 ± 2)	9–17 (12 ± 2)	8–17 (11 ± 2)
Supraciliaris	12–13 (12 ± 0)	12–14 (13 ± 1)	12–14 (12 ± 1)	12–16 (13 ± 1)	12–14 (13 ± 1)	12–17 (13 ± 1)
Supralabials	12	12	12–17 (13 ± 1)	12–15 (12 ± 1)	11–14 (12 ± 1)	12–16 (13 ± 1)
Infralabials	10–11 (10 ± 0)	10	12–15 (13 ± 1)	10–15 (12 ± 1)	12–14 (12 ± 1)	10–14 (12 ± 1)
Anterior Gulars	25–31 (27 ± 2)	26–31 (28 ± 2)	18–32 (27 ± 4)	22–40 (30 ± 4)	20–36 (29 ± 4)	22–40 (29 ± 4)
Posterior Gulars	16–18 (17 ± 1)	13–24 (17 ± 5)	7–16 (12 ± 2)	13–23 (16 ± 2)	14–20 (17 ± 2)	9–18 (13 ± 2)
Transverse Ventral Rows	31–33 (32 ± 1)	31–34 (33 ± 2)	29–32 (31 ± 1)	29–34 (31 ± 1)	29–35 (32 ± 1)	29–34 (32 ± 1)
Longitudinal Ventral Rows	10	10	10–12 (10 ± 1)	10	10	10–12 (10 ± 1)
Preanals	4–5 (5 ± 0)	5	6–8 (6 ± 1)	6–7 (6 ± 0)	5–7 (6 ± 0)	5–8 (6 ± 1)
Lamellae Under Fourth Finger	17–19 (18 ± 1)	17–18 (18 ± 1)	14–16 (15 ± 1)	14–17 (16 ± 1)	14–17 (15 ± 1)	13–18 (16 ± 1)
Prefemorals	6–7 (7 ± 0)	5–7 (7 ± 1)	8–12 (9 ± 1)	7–10 (9 ± 1)	7–8 (8 ± 1)	7–9 (8 ± 1)
Femoral and Abdominal Pores	26–34 (30 ± 3)	25–36 (31 ± 5)	30–45 (38 ± 4)	31–42 (36 ± 3)	32–40 (36 ± 2)	28–42 (34 ± 3)
Scales Separating Pore Rows	6–7 (6 ± 0)	5–6 (6 ± 1)	6–14 (9 ± 2)	6–16 (9 ± 2)	7–13 (10 ± 2)	5–13 (8 ± 2)
Lamellae Under Fourth Toe	38–46 (40 ± 3)	33–40 (36 ± 3)	32–40 (36 ± 2)	32–41 (36 ± 2)	30–37 (33 ± 2)	29–40 (34 ± 3)

Remarks.—As currently understood, *Ameiva auberi* is a polytypic taxon composed of as many as 40 subspecies distributed throughout Cuba and the Bahamas (Schwartz & Henderson 1991). There is considerable morphological and color variation among these populations, even among our very limited sample. Development of the distinctive tibiotarsal spurs also varies among populations. Among the specimens we examined, tibiotarsal spurs were well developed on specimens of *A. auberi* from Cuba but present in only one specimen from the Bahamas. Regarding coloration, Schwartz and Henderson (1991) describe the throat as “varying from cream or yellow to solid black, often extending posteriorly onto abdomen for various distances.” There can be little doubt that some of the currently recognized subspecies of *A. auberi* are distinct evolutionary lineages and their conspecificity should be rigorously tested.

Similarly, *Ameiva chrysolaema* is a polytypic taxon composed of 16 subspecies distributed throughout Hispaniola and adjacent keys (Gifford *et al*. 2004; Schwartz & Henderson 1991). We examined photographs of lizards from different localities within Haiti and the Dominican Republic that show conspicuous variation among localities. Schwartz and Henderson (1991) note similar variation when describing the ventral coloration of *A.*

chrysolaema: "venter whitish, pink, bluish to grayish, very pale orange, rust or even black; throat and/or chest often with a black band; throat white, yellow, orange, dull pinkish gray, grayish orange, dull purplish, often with a black area." As with *A. auberi*, *A. chrysolaema* almost certainly contains more than one species.

TABLE 6. Meristic and mensural data of *Ameiva* from the Greater Antilles examined by us. Means ± standard deviation follow ranges.

	Ameiva auberi (*n* = 15)	*Ameiva dorsalis* (*n* = 10)	*Ameiva maynardi* (*n* = 5)	*Ameiva lineolata* (*n* = 9)	*Ameiva exsul* (*n* = 6)	*Ameiva taeniura* (*n* = 5)	*Ameiva chrysolaema* (*n* = 10)
Occipitals	13–17 (15 ± 2)	13–16 (14 ± 1)	11–13 (12 ± 1)	8–13 (11 ± 2)	13–18 (16 ± 2)	12–16 (14 ± 2)	12–16 (15 ± 1)
Lateral Supraocular Granules	24–66 (37 ± 13)	38–54 (48 ± 5)	23–28 (25 ± 2)	18–25 (21 ± 2)	32–57 (41 ± 10)	24–46 (38 ± 9)	26–55 (38 ± 10)
Circumorbitals	2–14 (7 ± 3)	8–14 (11 ± 2)	2	2–4 (3 ± 1)	12–19 (15 ± 2)	8–9 (8 ± 1)	12–22 (16 ± 3)
Supraciliaris	12–16 (12 ± 1)	11–16 (13 ± 2)	10–13 (12 ± 1)	10–12 (12 ± 1)	12–15 (13 ± 1)	11–15 (13 ± 2)	13–16 (14 ± 1)
Supralabials	12–13 (12 ± 0)	12–15 (13 ± 1)	12	12–14 (12 ± 1)	12–14 (13 ± 1)	12–14 (13 ± 1)	12–14 (12 ± 1)
Infralabials	10–11 (10 ± 0)	12–14 (13 ± 1)	10	10	11–12 (12 ± 1)	10–12 (10 ± 1)	10–12 (11 ± 1)
Anterior Gulars	31–47 (39 ± 5)	36–55 (49 ± 5)	23–32 (29 ± 4)	18–23 (20 ± 2)	41–52 (47 ± 4)	33–38 (36 ± 2)	41–51 (44 ± 3)
Posterior Gulars	15–23 (17 ± 2)	12–26 (19 ± 4)	14–18 (16 ± 2)	10–16 (12 ± 2)	20–24 (22 ± 2)	13–19 (16 ± 3)	17–26 (22 ± 3)
Transverse Ventral Rows	32–37 (35 ± 1)	34–37 (35 ± 1)	33–35 (34 ± 1)	32–33 (33 ± 1)	34–35 (35 ± 1)	33–35 (34 ± 1)	34–37 (36 ± 1)
Longitudinal Ventral Rows	10–12 (10 ± 1)	10	8–10 (10 ± 1)	8	10	10	10
Preanals	5–9 (6 ± 1)	5–6 (6 ± 0)	4–5 (5 ± 1)	6	6–7 (6 ± 0)	6–7 (6 ± 1)	6–8 (7 ± 1)
Lamellae Under Fourth Finger	17–20 (19 ± 1)	18–21 (19 ± 1)	19–22 (21 ± 1)	17–18 (17 ± 0)	17–19 (18 ± 1)	17–20 (18 ± 1)	18–21 (20 ± 1)
Prefemorals	6–9 (7 ± 1)	6–9 (8 ± 1)	5–6 (5 ± 0)	4–7 (5 ± 1)	6–7 (6 ± 0)	6–7 (7 ± 1)	9–11 (10 ± 1)
Femoral and Abdominal Pores	22–33 (28 ± 3)	39–48 (44 ± 2)	24–26 (25 ± 1)	24–30 (27 ± 2)	27–33 (31 ± 2)	30–36 (33 ± 2)	32–39 (36 ± 2)
Scales Separating Pore Rows	8–16 (13 ± 2)	9–13 (11 ± 1)	10–13 (11 ± 1)	4–6 (5 ± 1)	18–26 (22 ± 4)	9–12 (11 ± 1)	9–14 (11 ± 2)
Lamellae Under Fourth Toe	34–39 (37 ± 2)	38–46 (41 ± 3)	34–39 (37 ± 2)	29–33 (31 ± 2)	35–38 (37 ± 2)	33–40 (36 ± 3)	37–43 (40 ± 2)
Tail Length/ SVL	1.9–2.6 (2.2 ± 0.3, *n* = 7)	2–2.4 (2.2 ± 0.2, *n* = 4)	2.1–2.5 (2.2 ± 0.2, *n* = 3)	2.2–2.4 (2.3 ± 0.1, *n* = 3)	2.3 (*n* = 2)	2.3–2.5 (*n* = 2)	2.2–25. (2.3 ± 0.1, *n* = 6)

Ameiva lineolata Series

Definition.—The following characters distinguish the *Ameiva lineolata* Series from other *Ameiva*: first supralabial usually curved; prefrontal usually separated from first supraciliary (vs. in contact); only 2–4 circumorbital scales restricted to posterior border of last supraocular (vs. reaching or extending beyond third); first supratemporal usually contacting parietal (vs. usually separate); intertympanic crease absent; supra and subdigital lamellae on toes in broad contact with postaxial granules restricted to 0–1 scales at phalangeal articulations; scales on dorsal surface of arm enlarged and triangular (*A. lineolata*) or small and triangular (*A. maynardi*, *A. wetmorei*) (vs. granular).

Content.—*A. lineolata*, *A. maynardi*, *A. wetmorei*.

Remarks.—We include this distinctive series of species in the *Ameiva dorsalis* Group.

We did not borrow specimens of *Ameiva wetmorei*, and our coding of this species is based solely on photographs of the holotype posted on the UMMZ website. We assign *A. wetmorei* to the *A. lineolata* Series, because it shares several unequivocal synapomorphies with other members. Hower and Hedges (2003) found that *A. lineolata* and *A. maynardi* were sister species. However, surprisingly they concluded that *A. wetmorei* is the sister species of *A. exsul*. Both species occur together on islands of the Puerto Rican Bank, but they could not be more different from one another morphologically. We note that this conclusion is based on a single tissue sample and can only be verified by collecting additional samples. Additional work is required to resolve the apparently contradictory morphological and molecular evidence.

***Ameiva erythrocephala* Group**

Definition.—The following combination of characters distinguishes the *Ameiva erythrocephala* Group (Table 7) from other groups of *Ameiva:* frontal entire, its posterior suture usually contacting third supraocular (except in *A. fuscata*) or aligned with suture between second and third supraoculars; interparietal frequently divided longitudinally (except *A. erythrocephala*); parietal series (including interparietal) composed of five (only three in single specimen of *A. major* examined), short and somewhat irregularly round plates; narial suture behind nostril and touching it; first supralabial usually toothy; first subocular usually contacting supralabials (except *A. erythrocephala*); intertympanic crease present; pectoral sulcus separating 2–4 transverse rows of ventrals; ventral scales in 10–20 longitudinal rows (most taxa with 10 rows, *A. pluvianotata* with 12, *A. fuscata* with 12–14, *A. cineracea* and *A. major* with 18–20 rows); plate-like antebrachial scales broadly separated from brachial scales; combined femoral and abdominal pores 39–78; fifth toe well-developed (except some *A. griswoldi*); supradigital and subdigital lamellae contacting one another, at least on Toes IV and/or V (except *A. fuscata*); generation glands present (except *A. fuscata* and *A. pluvianotata*); tip of snout reddish in adult males (only with slight reddish cast in *A. plei*; condition of melanic species *A. atrata, A. corvina* and *A. corax* unknown); ontogenetic changes in coloration absent or very limited in all species except *A. fuscata, A. plei* and *A. pluvianotata* which undergo considerable changes (condition not corroborated in *A. griswoldi,* but Schwartz and Henderson [1991] do not mention juveniles as having different coloration than adults); adult males completely melanic or without dorsolateral and vertebral stripes, except *A. erythrocephala* which has relatively distinct dorsolateral and upper lateral pale stripes; flanks without pale ocelli (except *A. fuscata* which has black-margined pale blue ocelli rather reminiscent of those in the *A. ameiva* Group) but most species with pale spots, sometimes merging and forming short transverse bands (e.g., *A. griswoldi*, *A. plei*); hemipenis with more distal (16–19) than proximal (7–13) laminae; discontinuous laminae absent; asulcate expansion pleat well-developed.

Content.—*Ameiva atrata* Garman, *A. cineracea* Barbour and Noble, *A. corax* Censky and Paulson, *A. corvina* Cope, *A. erythrocephala* Daudin, *A. fuscata* Garman, *A. griswoldi* Barbour, *A. major* Duméril and Bibron, *A. plei* Duméril and Bibron, *A. pluvianotata* Garman.

Distribution.—Lesser Antilles from Sombrero Island south to Dominica.

Remarks.—Species of this group have short and somewhat irregularly rounded parietal scales that are unlike those of any other species in the remaining groups of *Ameiva.* Among other teiids, frequent longitudinal division of the interparietal only occurs in the *Cnemidophorus murinus* and *C. vanzoi* Groups. *Ameiva chrysolaema* is the only other teiid that shares a pectoral sulcus with the *A. erythrocephala* Group.

Ameiva cineracea and *A. major* are included in this group with slight reservation. Both are Lesser Antillean endemics considered extinct on the island of Guadeloupe and the Grand Îlet off Petit-Bourg on the east coast of Basse-Terre, Guadeloupe (Schwartz & Henderson 1991; Breuil 2002). Both taxa have noticeably more longitudinal rows of ventral scales than other members of the group (*A. cineracea* has 18–20 rows and *A. major* has 18 rows according to Schwartz & Henderson 1991, vs. 10–14 in all other members of the group). We were only able to examine photographs of the head from the type specimen of *A. major* (MNHN 1491) and, thus, these elevated counts could not be verified. However, examination of the head squamation of *A. major* reveals similarities with other species of the *A. erythrocephala* Group. With the group, *A. major* shares a longitudinally divided interparietal, conspicuously short parietals, narial suture behind nostril, first supralabial toothy and first subocular contacting supralabials. Additionally, the drawing of the type specimen in the original description clearly shows that the enlarged antebrachial scales are separated from the brachial scales by a wide gap of small scales, as in all other members of the *A. erythrocephala* Group. Therefore, it seems appropriate to include *A. major* in the *A. erythrocephala* Group.

Ameiva fuscata from Dominica is the southernmost member of the *A. erythrocephala* Group and the closest geographically to the *A. ameiva* Group represented by *A. ameiva tobagana* on St. Vincent, Grenada, and the Grenadines. Interestingly, *A. fuscata* also shares several morphological similarities with the *A. ameiva* Group such as the posterior suture of the frontal usually contacting the second supraocular, scales separating the supradigital and subdigital lamellae along the postaxial edge of each toe, a pectoral sulcus separating only two transverse rows of ventrals in this species whereas it separates 3–4 in all other *A. erythrocephala* Group species, a distinct ontogenetic change in coloration, presence of pale blue ocelli on the flanks of males, and absence of generation glands. However, other characters such as a longitudinally divided interparietal, short parietal scales, nostril in front of the narial suture, a toothy first supralabial, contact between the first subocular and supralabials, a large gap of smaller scales separating the enlarged series of brachials from enlarged antebrachials, and a long fifth toe indicate that this species is related to the other *Ameiva* of the Lesser Antilles.

Ameiva fuscata and *A. pluvianotata* share preanals 10–17 (vs. 4–8 in other *Ameiva*), preanal plate single and much larger than the scale in front of it (paired or variable in other *Ameiva*), and generation glands absent (also in *A. ameiva* Group).

Ameiva **Incertae Sedis**

Remarks.—Although they are clearly species of *Ameiva*, we refrain from assigning *Ameiva concolor* Ruthven and *A. parecis* (Colli *et al.*) to species group.

Ameiva parecis is known only from Fazenda Cachoeira, 50 km NW of Vilhena, Estado de Rondônia, Brazil. It most closely resembles species of the *A. ameiva* Group. Unfortunately many important characters were not mentioned in the original description or in a subsequent publication (Giugliano *et al.* 2006) about this rare species. To our knowledge, it remains known from the type series and a few other specimens in Brazilian museums. *Ameiva concolor* resembles species in the *A. bifrontata* Group in overall habitus. As mentioned above, this species was assigned to the *A. ameiva* Group by a phylogenetic analysis of all characters, but assigned to the *A. bifrontata* Group when meristic characters were excluded.

Ameivula **New Genus**

Figure 61

Type Species.—*Tejus ocellifer* Spix by original designation.

Diagnosis.—Although the hemipenis of *Ameivula ocellifera* has at least one unique character (the papillate catchment folds and awns), hemipenes of other species in this genus have never been described and were unavailable for study. *Ameivula* differs from *Ameiva* (characters in parentheses) in having a long first supraciliary (shorter than second; but see remarks regarding species allied to *A. litoralis* where the first supraciliary is divided), the prefrontal usually contacting the nasal (separated from nasal), and the prefrontal separated from the first supraciliary (in contact, except in the *A. lineolata* series).

Content.—*Ameivula abaetensis* (Dias, Rocha, & Vrcibradic), *Ameivula confusioniba* (Arias *et al.*), *Ameivula cyanura* (Arias *et al.*), *Ameivula jalapensis* (Colli *et al.*), *Ameivula litoralis* (Rocha *et al.*), *Ameivula mumbuca* (Colli *et al.*), *Ameivula nativo* (Rocha, Bergallo, & Peccinni-Seale), *Ameivula nigrigula* (Arias et al.), *Ameivula ocellifera* (Spix), and *Ameivula venetacauda* (Arias *et al.*).

Definition.—Small to medium lizards reaching about 85 mm SVL; tail about 1.9–2.4X as long as body (Table 8); posterior maxillary and dentary teeth longitudinally compressed, tricuspid; pupil reniform.

TABLE 7. Meristic and mensural data of *Ameiva* from the Lesser Antilles examined by us. Means ± standard deviation follow ranges.

	Ameiva griswoldi (*n* = 10)	*Ameiva p. plei* (*n* = 5)	*Ameiva p. analifera* (*n* = 9)	*Ameiva corvina* (*n* = 5)	*Ameiva erythrocephala* (*n* = 5)	*Ameiva pluvionotata* (*n* = 3)	*Ameiva fuscata* (*n* = 3)
Occipitals	15–20 (17 ± 2)	13–18 (15 ± 2)	15–21 (18 ± 2)	16–18 (17 ± 1)	15–17 (16 ± 1)	18–21	11–12
Lateral Supraocular Granules	22–41 (34 ± 6)	29–38 (35 ± 4)	25–42 (34 ± 6)	26–43 (33 ± 6)	54–81 (66 ± 10)	15–40	40–60
Circumorbitals	13–18 (15 ± 2)	18–23 (21 ± 2)	20–27 (24 ± 2)	15–21 (18 ± 2)	17–29 (22 ± 5)	12–22	19–21
Supraciliaris	12–16 (14 ± 1)	14–15 (14 ± 1)	14–17 (15 ± 1)	14	16–18 (17 ± 1)	13–16	12–15
Supralabials	12–14 (13 ± 1)	12–13 (12 ± 0)	12–13 (12 ± 0)	12–13 (12 ± 0)	12	12	14–16
Infralabials	10	10	10	10	10	10	10–12
Anterior Gulars	30–43 (36 ± 4)	33–39 (35 ± 2)	35–39 (37 ± 1)	33–36 (35 ± 1)	47–53 (50 ± 2)	40–48	34–40
Posterior Gulars	16–20 (19 ± 1)	21–24 (23 ± 1)	17–24 (21 ± 2)	17–25 (22 ± 3)	23–29 (26 ± 2)	21–28	15
Transverse Ventral Rows	33–35 (34 ± 1)	32–34 (33 ± 1)	31–34 (32 ± 1)	35–37 (36 ± 1)	34–37 (35 ± 1)	34–36	32–33
Longitudinal Ventral Rows	10	10	10	10	10	12	12–14
Preanals	8–10 (9 ± 1)	6–8 (7 ± 1)	6–8 (6 ± 1)	6–7 (6 ± 1)	8–13 (10 ± 2)	6–8	12–17
Lamellae Under Fourth Finger	16–21 (18 ± 1)	17–19 (18 ± 1)	17–20 (18 ± 1)	17–19 (18 ± 1)	19–21 (20 ± 1)	18–20	19–21
Prefemorals	5–7 (6 ± 1)	6–8 (7 ± 1)	6–8 (7 ± 1)	8–10 (9 ± 1)	11–14 (12 ± 2)	8–10	12–13
Femoral and Abdominal Pores	45–55 (50 ± 3)	43–52 (47 ± 4)	39–50 (45 ± 4)	54–58 (56 ± 2)	69–78 (73 ± 4)	59–62	54–64
Scales Separating Pore Rows	5–9 (7 ± 1)	4–6 (5 ± 1)	6–11 (7 ± 2)	7–8 (7 ± 0)	9–14 (11 ± 2)	7	8–12
Lamellae Under Fourth Toe	33–39 (36 ± 2)	34–36 (35 ± 1)	33–38 (35 ± 1)	37–38 (37 ± 1)	42–46 (44 ± 2)	38–41	38–43
Tail Length/ SVL	2.1–2.3 (2.2 ± 0.1, *n* = 4)	2.3–2.4 (*n* = 2)	2.2–2.3 (2.2 ± 0.1, *n* = 4)	Not Available	2.3 (*n* = 1)	Not Available	2.2 (*n* = 1)

Prefrontal usually in contact with nasal, separated from first supraciliary; frontal entire, lacking longitudinal ridge, its posterior suture contacting third supraocular; scales of frontoparietal region smooth, outwardly convex to flat (key-hole shaped depression absent); frontoparietals paired; parietals consisting of five regular scales (rarely three, i.e., holotypes of *Ameivula jalapensis* and *A. confusioniba* and some specimens of *A. littoralis*, Roca *et al.* 2000); interparietal entire, larger to narrower than flanking parietals; medial pair of enlarged occipitals absent (*A. ocellifera* and type specimens of *A. confusioniba*, *A. cyanura*, *A. nigrigula*, *A. venetacauda*) or present (type specimens of *A. abaetensis*, *A. jalapensis*, and *A. mumbuca*); occipitals 13–18, subequal to first row of dorsals; supratemporals slightly to moderately enlarged, separated from parietals by one or more scales.

FIGURE 61. *Ameivula abaetensis* from Parque Nacional Serra de Itabaiana, Sergipe, Brazil (A, photo by C. B. de Carvalho); adult male *A. jalapensis* from Jalapão, Tocantins, Brazil (B, photo by M. Texeira Jr.); adult male *A. mumbuca* from Jalapão, Tocantins/Bahia, Brazil (C, photo by M. Texeira Jr.); adult female *A. nativo* from Trancoso, Bahia, Brazil (D, photo by M. Texeira Jr.); adult *A.* cf. *ocellifera* from Parque Nacional de Sete Cidades, Piauí, Brazil (E, photo by L. Cavalcanti); adult males of *A.* cf. *ocellifera* from Nova Xavantina, Mato Grosso (F, photo by C. Rodrigues Vieira) and Rio Grande do Piauí, Piauí, Brazil (G, photo by F. Delfim); adult *C. ocellifera* from Bahia, Brazil (H, photo by M. Travassos).

Rostral groove present; nostril oval and oriented anteroventrally, positioned anterior to nasal suture; loreal single; supraoculars usually eight (6–10); first supraocular entire, larger than fourth supraocular, contacting

(*Ameivula ocellifera,* types of *A. abaetensis, A. confusioniba, A. nigrigula, A. venetacauda*) or separated from (types of *A. cyanura, A. jalapensis, A. mumbuca*) second supraocular; circumorbital semicircles consisting of 21–35 scales (15 in illustration of type of *A. littoralis*), usually extending to posterior margin of first supraocular; supraciliaries 10–14, separated from supraoculars by 1–2 rows of 26–56 granular scales; first supraciliary long (*A. confusioniba, A. mumbuca, A. nativo, A. nigrigula, A. jalapensis,* and *A. ocellifera*) and greater than one-half length of second or divided (*A. abaetensis, A. litoralis,* and *A. venetacauda*) so that third supraciliary longest; angulate keel extending from first subocular to elongate subocular below eye; suboculars four; first subocular contacting or separated from first supraciliary, separated from supralabials by second subocular; patch of distinctly enlarged scales in front of auditory meatus; auricular flap and preauricular fold absent.

Supralabials 10–14; first supralabial usually smaller than second, its ventral margin "toothy"; infralabials 10–12; first pair of chinshields broadly contacting infralabials or partially separated from them by row of granular scales, forming medial suture greater than or equal to half their length; interangular sulcus absent; anterior gulars 14–22; gular patch absent; posterior gulars 9–14; intertympanic sulcus absent; larger anterior gulars undergoing sharp transition to smaller posterior gulars at intertympanic crease; mesoptychials moderately enlarged; gular fold lacking serrated edge.

Dorsals smooth; scales on flank subequal to middorsals, not projecting laterally, supported by small apical granules; scales on rump much smaller than proximal subcaudals; scales of chest large and flat; pectoral sulcus absent; ventrals smooth, in 27–32 (24–38 in species not examined by us, Arias *et al.* 2011a,b) transverse and eight (*Ameivula jalapensis, A. mumbuca, A. nativo, A. nigrigula, A. ocellifera;* possibly 6–8 according to Arias *et al.* 2011a,b, whose method of counting ventrals may differ from ours) or 8–10 (*A. abaetensis, A. cyanura, A. venetacauda, A. littoralis*) longitudinal rows; lateral-most ventrals flanked by small scales (i.e., ventrals not gradually decreasing in size on flanks); preanals 4–5; preanal plate present, bordered by subtriangular scales; preanals one-half as large to larger than scale anterior to them; preanal spurs, postcloacal buttons, and postanal plates absent; scales on dorsolateral edge of tail like those on top and sides, denticulate edge and dorsolateral crests absent; caudal annuli complete; proximal subcaudals smooth.

Enlarged scales of brachium connected by continuous band of subtriangular plates on dorsal surface of arm; preaxial and postaxial brachial scales 1.5–2X as wide as long, both extending proximally to or beyond center of arm; antebrachial scales enlarged and smooth, narrowly separated from or in continuous row with preaxial brachial scales; postaxial antebrachial scales slightly enlarged; subdigital lamellae of hand homogeneous in size, 14–20 (13–24 in specimens not examined by us; Arias *et al.* 2011a,b) under fourth finger.

Prefemorals 4–5; femoral and abdominal pores 12–45 in continuous row on each side (abdominal pores not separated from femoral pores by gap); each compound pore-bearing scale consisting of partially fused prefemoral or abdominal scale and 2–6 granular scales; 1–3 (usually 2) scales separating right and left pore rows; scales at heel relatively small and numerous; tibiotarsal shields absent; tibiotarsal spurs present in some populations of *Ameivula ocellifera* and in *A. abaetensis, A. cyanura, A. litoralis,* and *A. venetacauda*; lamellae under fourth toe 25–34 (24–38 in species not examined by us; Arias *et al.* 2011a,b); distal lamellae of fourth toe smooth; scales between subdigital and supradigital lamellae of toes small and mostly restricted to phalangeal articulations; noticeably enlarged postaxial scales between fourth and fifth toe absent; fifth toe shortened, base of its claw not passing level of skin between third and fourth toes when adpressed.

β-keratin containing layers of dorsal scales folded into macrohoneycomb; dorsal and caudal scales with one subterminal lenticular scale organ; ventrals lacking scale organs; generation glands absent.

Snout same color as dorsal head scales, males of some populations currently assigned to *Ameivula ocellifera* with reddish heads and throats but color not restricted to snout. In juveniles (color of juvenile *A. confusioniba* and *A. venetacauda* unknown), light vertebral stripe absent (*A. jalapensis, A. mumbuca, A. nigrigula, A. ocellifera*) or solid and straight (*A. cyanura, A. littoralis*), or present only from mid-dorsum to sacrum (*A. abaetensis*); light paravertebral stripes present though often broken (*A. cyanura, A. jalapensis, A. littoralis, A. mumbuca, A. nigrigula, A. ocellifera,* some specimens of *A. abaetensis*) or absent (some specimens of *A. abaetensis,* some populations currently assigned to *A. ocellifera*); dark dorsolateral field solid (*A. jalapensis, A. littoralis, A. mumbuca, A. nigrigula,* some populations assigned to *A. ocellifera*), solid and broken into blotches posteriorly (some populations of *A. ocellifera*), or absent (*A. abaetensis, A. cyanura*); dorsolateral light stripe solid and extending to tail; dark lateral field solid (*A. abaetensis, A. cyanura, A. jalapensis, A. littoralis, A. nativo*) or with light spots (*A. mumbuca, A. nigrigula, A. ocellifera*); upper lateral light stripe solid and extending to groin; lower lateral light stripe broken (*A. jalapensis, A. littoralis, A. mumbuca, A. nativo, A. nigrigula, A. ocellifera*) or absent/faded (*A. abaetensis, A. cyanura*); thigh lacking light spots, with some light marbling but not spots in *A. littoralis*; lacking spots on flanks. Adult males with (*A. ocellifera, A. nigrigula*) or without (*A. abaetensis, A. confusioniba, A. cyanura, A. jalapensis, A. littoralis; A. mumbuca, A. venetacauda*) turquoise ventrolateral spots; venter immaculate, lacking melanic areas in adult males (most species) or with black throat (*A. nigrigula*).

Hemipenis (based on *Ameivula ocellifera*) with pair of taβ-like apical awns; awns and catchment folds papillate; apical papillae and apical basin absent; asulcate expansion pleat well-developed, interrupting about seven distal laminae; discontinuous distal laminae four on sulcate side; no laminae proximal to expansion pleat; basal papillae absent.

Etymology.—The new name *Ameivula* is a feminine noun in the nominative singular and a diminutive form of *Ameiva*. Arias *et al.* (2011a,b) did not state whether their new specific epithets (*confusionibus, cyanurus*, and *venetacaudus*) are adjectives or nouns in apposition. We consider these names to be adjectives and accordingly emend them to agree in gender with the feminine genus *Ameivula*.

Distribution.—Cis-Andean lowlands south of the Amazon in Argentina, Bolivia, Brazil, and Paraguay.

Remarks.—Most species of *Ameivula* have only recently been described through revisions of the *A. ocellifera* complex, and many species have not reached museums outside of Brazil. Although we refer to our specimens as *A. ocellifera*, the ten specimens coded for phylogenetic analysis likely comprise three species: one from Bahia, another from Mato Grosso, and a third from the Chaco of Bolivia and Paraguay. Conceivably, all three could be undescribed. We base this assertion on presence/absence of tibiotarsal spurs and variation in other characters assessed in this study. Many of our characters were not assessed in recent descriptions of species in this genus. Thus, our definition is based primarily on the three species we examined and data gleaned from photographs and descriptions of other species not available for study.

Although similar in many ways to *Ameiva*, most species of the former *Cnemidophorus ocellifer* Complex are placed in the new genus *Ameivula* based on the long first supraciliaries of most species, small size, distinctive spinules on the apex of the hemipenis of *A. ocellifera*, and phylogenetic analyses of morphological (this study) and molecular data (Giugliano 2009; Giugliano *et al.* 2006). Unlike all *Ameiva* except for the *A. lineolata* series, species of *Ameivula* have the prefrontal separated from the first supraciliary and most specimens have the prefrontal in contact with the nasal. The prefrontal is separated from the nasal in the holotype of *A. mumbuca* and variation in this character remains unreported for this species (Colli *et al.* 2003). Nonetheless, these scales were also separated in one specimen of *A. ocellifera* from Paraguay and low levels of polymorphism in this character should not come as a surprise.

Among the species of *Ameivula*, Arias *et al.* (2011a, b) recognized two "subgroups." Specimens in their samples of *A. confusioniba, A. mumbuca, A. nigrigula, A. jalapensis*, and *A. ocellifera* lacked tibiotarsal spurs and had an enlarged scale behind the fourth subocular, five supraciliaries, ventrals in 6–8 longitudinal and 24–29 transverse rows, and 11–21 femoral pores. In contrast, specimens of *A. abaetensis, A. cyanura, A. littoralis*, and *A. venetacauda* lacked an enlarged scale behind the fourth subocular and had tibiotarsal spurs, 6–7 supraciliaries, ventrals in 8–10 longitudinal and 29–38 transverse rows, and 21–45 femoral pores. *Ameivula nativo* is a unisexual species that likely formed through hybridization involving a member of each group, *A. ocellifera* and *A. abaetensis* being the most likely candidates (Dias *et al.* 2002).

This publication appeared after we had returned about half of the specimens of *Ameivula ocellifera*. However, we could not confidently assign the 10 specimens coded for phylogenetic analysis or two additional specimens to either subgroup defined by Arias *et al.* (2011a,b). Arias *et al.* (2011a) illustrate an enlarged temporal scale positioned behind the suboculars and bordering the rictal fold. Apparently, this scale varies somewhat in size even in their material: it is almost as large as the fourth subocular in a specimen of *A. ocellifera* illustrated in their figure 9, but only about half as large and longitudinally divided on the right side of the type of *A. confusioniba* (their figure 3). According to Arias *et al.* (2011a,b), species of the *A. ocellifera* subgroup have this enlarged scale but lack tibiotarsal spurs. Arias *et al.* (2011a,b) found concordance in these characters among their samples (species with spurs lack the enlarged scale), however we did not. Among the 12 specimens at hand, only one (AMNH 36375 from Bahia, Brazil) has the enlarged scale, however, this male specimen has well-developed tibiotarsal spurs. On the other hand, five specimens from Mato Grosso (3 males, 2 females) lack both tibiotarsal spurs and the enlarged temporal scale. Some of the specimens from Mato Grosso have an unusually large fourth subocular; possibly, the fourth subocular and enlarged temporal have fused in this population. A specimen from Bolivia, the specimen from

Bahia, and five specimens from Paraguay have tibiotarsal spurs, yet they lack other characters of the *A. littoralis* subgroups (i.e., they have fewer than 21 femoral pores, long entire first supraciliaries, 27–31 transverse rows of ventrals, 8 longitudinal ventral rows).

FIGURE 62. *Aspidoscelis burti stictogrammus* from Catalina State Park, Pima County, Arizona, USA (A, photo by J. Mays); juvenile *A. deppei* from Reserva Natural Heloderma, Motagua Valley, Guatemala (B, photo by T. Schrei); *A. gularis* from Cooks Slough, Uvalde County, Texas, USA (C, photo by T. L. Hibbits); *A. marmorata* from Winkler County, Texas, USA (D, photo by T. L. Hibbits); *A. motaguae* from Reserva Natural Heloderma, Motagua Valley, Guatemala (E, photo by T. Schrei) and from Ocozocuautla, Chiapas, Mexico (F, photo by R. Pencino); *A. sexlineata sexlineata* from Hobe Sound National Wildlife Refuge, Florida, USA (G, photo by G. N. Ugueto); *A. tigris tigris* from Gila Box Conservation Riparian Area, Graham County, Arizona, USA (H, photo by T. L. Hibbits).

The "subgroups" of Arias *et al.* (2011a,b) may be natural. Some characters of coloration such a light vertebral stripe (present in the *Ameivula littoralis* subgroup, absent in the *A. ocellifera* subgroup) and a blue tail (present in the *A. littoralis* subgroup, absent in the *A. ocellifera* subgroup) also appear to support recognition of these groups. Nevertheless, some of the characters used to define these groups such as tibiotarsal spurs and enlarged temporals are more variable than originally thought. Color characters are unknown for juveniles of some species. The divided first supraciliary in the *Ameivula littoralis* subgroup would appear to ally its members (*A. abaetensis*, *A. cyanura*, *A. littoralis*, and *A. venetacauda)* with *Ameiva*. These four species should be assessed for additional characters to test whether they should be retained in *Ameivula*, transferred to *Ameiva*, or placed in a third, unnamed genus. Although we formally define species groups of *Ameiva* and *Cnemidophorus* in this publication, we are hesitant to formally recognize these subgroups until contradictory character evidence can be investigated.

***Aspidoscelis* Fitzinger**

Figure 62

Aspidoscelis Fitzinger 1843: 20. Type species *Lacerta sexlineata* Linnaeus by monotypy.
Verticaria Cope 1869b: 158. Type species *Cnemidophorus hyperythrus* Cope by original designation.

Diagnosis.—We know of no single unique diagnostic character of *Aspidoscelis*. However, *Aspidoscelis* and *Holcosus* are the only teiids with postanal plates in males. As in *Holcosus*, most *Aspidoscelis* have a wide scale (2–3X as wide as long) at the heel flanked postaxially by another wide scale (1.5–2X as wide as long). Unlike *Holcosus* (characters in parentheses), *Aspidoscelis* has homogeneous subdigital lamellae of the hand (subarticular lamellae enlarged; note, however, basal lamellae enlarged in some *Aspidoscelis*) and the nostril positioned in front of the nasal suture (nasal suture passing through nostril). *Aspidoscelis* lacks a serrated row of supracaudals (present). The tongue of *Aspidoscelis* is not retractile into a lingual sheath, whereas a lingual sheath is present in all species of *Holcosus*.

Compared to other Teiinae, *Aspidoscelis* is further characterized by the following characters: nasal in contact with prefrontal, parietals three, nostril usually oval (round in *A. angusticeps*), first supraciliary usually short, and preanal spurs and auricular flap absent.

Remarks.—Our study focused primarily on Neotropical teiids, and, a priori, we accepted *Aspidoscelis* monophyly as established by Reeder *et al.* (2002). For this reason, we included only four species (Table 8) of this large genus in our phylogenetic analysis and scored eleven others (Appendix) for characters in the diagnosis. Thus, we do not include a complete "account" for the genus here.

***Aurivela* New Genus**

Figure 63

Type Species.—Type species *Ameiva longicauda* Bell by original designation.

Diagnosis.—*Aurivela* is the only teiid genus with a subtriangular auricular flap partially covering the external auditory meatus, 2–3 suboculars, the first and second chinshields in medial contact, a single subtriangular preanal plate larger than the scale in front of it, and a single row of 3–4 poorly developed tibiotarsal spurs consisting of large triangular scales with raised and pointed distal ends.

Content.—*Aurivela longicauda* (Bell), *Aurivela tergolaevigata* (Cabrera).

Definition.—Small lizards reaching 62 mm SVL; tail about 2.6X as long as body (Table 8); posterior maxillary and dentary teeth longitudinally compressed, tricuspid; pupil reniform.

Prefrontal in contact with nasal, separated from first supraciliary; frontal entire, lacking longitudinal ridge, its posterior suture contacting third supraocular; scales of frontoparietal region smooth, outwardly convex to flat (key-hole shaped depression absent); frontoparietals paired; parietals consisting of three regular scales; interparietal entire, smaller than flanking parietals; medial pair of enlarged occipitals absent; occipitals 10–14, usually larger than first row of dorsals; supratemporals slightly to moderately enlarged, separated from parietals by one or more scales.

TABLE 8. Selected meristic and morphological data of some Teiinae from North and South America examined by us. Means ± standard deviation follow ranges.

	Ameivula ocellifera (*n* = 10)	*Aurivela longicauda* (*n = 1)*	*Aurivela tergolaevigata* (*n* = 7)	*Aspidoscelis sexlineata* (*n* = 7)	*Aspidoscelis gularis* (*n* = 1)	*Aspidoscelis marmorata* (*n* = 5)	*Aspidoscelis tigris* (*n* = 5)
Occipitals	13–18 (15 ± 2)	10	12–14 (13 ± 1)	11–16 (14 ± 2)	11	17–20 (18 ± 1)	14–17 (15 ± 1)
Lateral Supraocular Granules	26–56 (37 ± 11)	28	29–42 (37 ± 6)	23–64 (42 ± 14)	38	36–66 (54 ± 11)	28–59 (43 ± 13)
Circumorbitals	21–31 (27 ± 4)	25	18–25 (22 ± 2)	6–10 (7 ± 2)	6	15–27 (21 ± 5)	10–16 (12 ± 2)
Supraciliaris	10–12 (11 ± 1)	12	14–19 (16 ± 2)	11–13 (12 ± 1)	14	14–16 (15 ± 1)	14–15 (14 ± 0)
Supralabials	10–14 (12 ± 1)	14	12–14 (13 ± 1)	12–13 (12 ± 0)	12	12	12
Infralabials	10–11 (10 ± 0)	14	12–16 (14 ± 1)	10–13 (12 ± 1)	13	13–15 (14 ± 1)	12–16 (14 ± 1)
Anterior Gulars	14–22 (19 ± 3)	15	18–28 (24 ± 3)	17–22 (20 ± 2)	18	22–26 (24 ± 2)	20–24 (22 ± 2)
Posterior Gulars	9–14 (12 ± 2)	14	11–16 (14 ± 2)	10–16 (12 ± 2)	9	15–19 (17 ± 2)	12–18 (14 ± 2)
Transverse Ventral Rows	27–31 (28 ± 1)	32	30–35 (33 ± 2)	33–34 (33 ± 1)	34	29–32 (31 ± 1)	28–31 (29 ± 1)
Longitudinal Ventral Rows	8	10	10	8	8	8	8
Preanals	4	4	4–5 (4 ± 0)	5–7 (6 ± 1)	4	5–6 (6 ± 0)	5–6 (5 ± 0)
Lamellae Under Fourth Finger	15–19 (16 ± 1)	17	16–19 (17 ± 1)	13–15 (14 ± 1)	12	18	16–17 (17 ± 1)
Prefemorals	4–5 (4 ± 0)	5	5–8 (6 ± 1)	6–7 (7 ± 1)	8	6–8 (7 ± 1)	7–8 (7 ± 0)
Femoral and Abdominal Pores	14–20 (17 ± 2)	30	25–33 (29 ± 2)	30–34 (33 ± 2)	32	42–48 (45 ± 2)	38–44 (42 ± 3)
Scales Separating Pore Rows	1–2 (2 ± 0)	2	2–3 (2 ± 0)	2–5 (4 ± 1)	4	2–4 (3 ± 1)	3–5 (4 ± 1)
Lamellae Under Fourth Toe	25–30 (27 ± 2)	30	28–31 (29 ± 2)	26–28 (27 ± 1)	29	31–37 (35 ± 3)	29–33 (31 ± 2)
Tail Length/ SVL	2.1–2.3 (2.2 ± 0.1, *n* = 3)	Not Available	2.6 (*n* = 1)	2.3–2.5 (2.4 ± 0.1, *n* = 4)	Not Available	2.5–2.7 (*n* = 2)	2.6–2.8 (*n* = 2)

Rostral groove present; nostril oval and oriented anteroventrally, in front of suture and not touching it; loreal single; supraoculars eight; first supraocular entire, subequal to or smaller than fourth supraocular, partially separated from second supraocular; circumorbital semicircles consisting of 18–25 small scales, extending to posterior border of first supraocular; supraciliaries 12–19, separated from supraoculars by 1–1.5 rows of 28–42 granular scales; supraciliaries subequal (*Aurivela tergolaevigata*) or first supraciliary long (*A. longicauda*); angulate keel extending from first subocular to elongate subocular below eye; suboculars two (*A. longicauda*) or three (*A. tergolaevigata*); first subocular entire, contacting or separated from first supraciliary, contacting supralabials; scales in front of auditory meatus not enlarged; subtriangular auricular flap covered in granular scales, projecting posteriorly and ventrally from anterodorsal edge of external auditory meatus; preauricular fold absent.

Supralabials 12–14; first supralabial smaller than second, its ventral margin "toothy"; infralabials 12–16; first pair of chinshields broadly contacting infralabials or partially to completely separated from them by small granular scales; first and second pairs of chinshields in broad medial contact; interangular sulcus absent; anterior gulars 15–28; gular patch absent; posterior gulars 11–16; intertympanic sulcus absent; larger anterior gulars undergoing sharp transition to smaller posterior gulars at intertympanic crease; mesoptychials not to slightly enlarged; larger scales of mesoptychium forming serrated edge along gular fold.

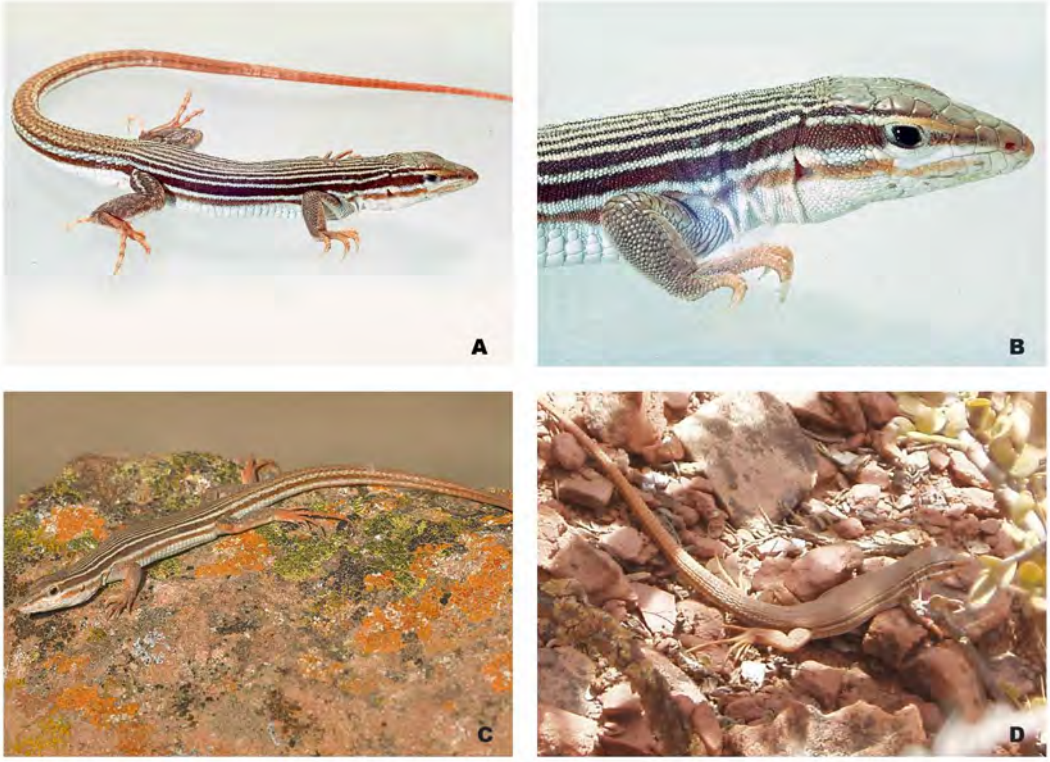

FIGURE 63. *Aurivela longicauda* from Neuquén, Argentina (A, B, photos by R. D. Sage) and General Roca, Rio Negro, Argentina (C, photo by J. Prieto); *A. tergolaevigata* from Cuesta de Miranda, La Rioja, Argentina (D, photo by N. R. Chimento).

Dorsals smooth; scales on flank subequal to middorsals, not projecting laterally, supported by small apical granules; scales on rump much smaller than proximal subcaudals; scales of chest large and flat; pectoral sulcus absent; ventrals smooth, in 30–35 transverse and ten longitudinal rows; lateral-most ventrals flanked by small scales (i.e., ventrals not gradually decreasing in size on flanks); preanals 4–5; preanal plate present, bordered by subtriangular scales; preanal scale single, subtriangular, larger than scale in front of it; preanal spurs, postcloacal buttons, and postanal plates absent; scales on dorsolateral edge of tail like those on top and sides, denticulate edge and dorsolateral crests absent; caudal annuli complete; proximal subcaudals smooth.

Enlarged scales of brachium connected by continuous band of enlarged subtriangular plates on dorsal surface of arm; preaxial brachial scales 1–2X as wide as long, extending to or beyond center of arm; postaxial brachials 1–2X as wide as long, restricted to patch at elbow; antebrachial scales enlarged and smooth, broadly separated from preaxial brachial scales by gap of small scales; postaxial antebrachial scales slightly enlarged; subdigital lamellae of hand homogeneous in size, 16–19 under fourth finger.

Prefemorals 5–8; femoral and abdominal pores 25–33 in continuous row on each side (abdominal pores not separated from femoral pores by gap); each compound pore-bearing scale consisting of partially fused prefemoral or abdominal scale and 2–6 granular scales; 2–3 scales separating right and left pore rows; scales at heel relatively small and numerous; tibiotarsal spurs consisting of 3–4 large triangular scales with thickened, elevated, and pointed distal ends; tibiotarsal shields absent; lamellae under fourth toe 28–31; distal lamellae of fourth toe smooth; continuous low, serrate row of keeled scales along postaxial edge separating digital lamellae of toes 2–4; noticeably enlarged postaxial scales between fourth and fifth toe absent; fifth toe well-developed, base of its claw extending beyond level of skin between third and fourth toes when adpressed.

β-keratin containing layers of dorsal scales folded into macrohoneycomb; dorsal and caudal scales with one subterminal lenticular scale organ; ventrals lacking scale organs; generation glands absent.

Snout same color as dorsal head scales. In juveniles, light vertebral and paravertebral stripes solid and straight (*Aurivela longicauda*) or absent (*A. tergolaevigata*); dark dorsolateral field solid; dorsolateral light stripe solid and extending to tail; dark lateral field solid; in juveniles, upper lateral light stripes solid and extending to groin; lower lateral light stripe absent; thigh and flanks lacking light spots. In adult males, turquoise ventrolateral spots absent; venter immaculate, lacking melanic areas; juvenile dorsal color pattern present in adult males with only slight modification.

Morphology of hemipenis unknown.

Etymology.—*Aurivela* is a feminine Latin noun in the nominative singular derived from the Latin words *auris* meaning ear and *velatus* meaning covered or concealed. The new name alludes to the auricular flap diagnostic of this genus.

Distribution.—Endemic to the Monte Desert region of western Argentina (Cabrera 2004; Cabrera & Etheridge 2006; Frutos *et al.* 2005; Yoke *et al.* 2006).

***Cnemidophorus* Wagler**

Figures 64–65

Cnemidophorus Wagler 1830: 154. Type species *Seps murinus* Laurenti subsequently designated by Fitzinger (1834).

Diagnosis.—*Cnemidophorus* is the only genus of Teiidae with a single pair of preanal spurs in males and proximal hemipenial laminae ornamented in short papillae. Female *Cnemidophorus* can be distinguished from all other teiids by the combination of long first supraciliaries, long first supralabials with straight ventral margins, subtriangular to subcircular nostrils, five regular parietals, smooth ventrals, and a continuous postaxial row of keeled, serrate scales separating the digital lamellae of all five toes.

Content.—Sixteen species, each assigned herein to one of four species groups.

Definition.—Small to medium lizards reaching 159 (*Cnemidophorus murinus*) mm SVL (Tables 9–11); posterior maxillary and dentary teeth longitudinally compressed, tricuspid; pupil reniform.

Prefrontal usually separated from nasal (except in *Cnemidophorus arenivagus*), separated from or in contact with first supraciliary; frontal entire, lacking longitudinal ridge, its posterior suture contacting third supraocular; scales of frontoparietal region smooth, outwardly convex to flat (key-hole shaped depression absent); frontoparietals paired; parietals consisting of five regular scales; interparietal entire, its relative size varying among species; medial pair of enlarged occipitals present in some species, absent in others; occipitals 11–24; supratemporals slightly to moderately enlarged, separated from parietals by one or more scales.

Rostral groove usually absent; nostril usually subtriangular to subcircular, centered or slightly to mostly anterior to nasal suture; loreal single; supraoculars eight (rarely 9–11); first supraocular entire, variable in size, usually broadly contacting second supraocular; circumorbital semicircles consisting of 4–17 small scales; supraciliaries 8–13, separated from supraoculars by 1–3 rows of 21–96 granular scales; first supraciliary long, greater than one-half as long as second; angulate keel extending from first subocular to elongate subocular below eye; suboculars four (rarely 3 or 5); first subocular usually entire, usually contacting first supraciliary, usually contacting supralabials (most species) or usually separated from supralabials by anterior expansion of second subocular (*Cnemidophorus ruthveni*, *C. vanzoi*, and many *C. murinus* and *C. arubensis*); patch of slightly to distinctly enlarged scales in front of auditory meatus; auricular flap and preauricular fold absent.

FIGURE 64. Adult males of *Cnemidophorus arenivagus* from La Vela de Coro, Falcón, Venezuela (A, photo by Y. Surget-Groba) and Fundo San Francisco, Península de Paraguaná, Falcón, Venezuela (B, photo by G. van Buurt); adult male *C. arubensis* from Aruba (C, photo by G. van Buurt); male (top) and female (bottom) *C. flavissimus* from Isla Real, Los Frailes Archipelago, Venezuela (D, photo by O. Lasso); adult male *C. gramivagus* from Módulos Fernando Corrales, UNELLEZ, 80 km WNW Mantecal, Apure, Venezuela (E, photo by J. E. García Pérez); adult male *C. lemniscatus espeuti* from San Andrés Island, Colombia (F, photo by P. Jürgen Jaskolka); adult male *C. l. lemniscatus* from La Unión, Miranda, Venezuela (G, photo by G. N. Ugueto); adult male *C. l. gaigei* from Tayrona National Park, Magdalena, Colombia (H, photo by D. Smyth).

FIGURE 65. Adult male *Cnemidophorus lemniscatus gaigei* from Las Brisas, Macao, Antioquia, Colombia (A, photo by M. Rivera, courtesy of MHUA); adult male *C. l. splendidus* from Fundo San Francisco, Península de Paraguaná, Falcón, Venezuela (B, photo by G. van Buurt); adult male *C. murinus* from Curaçao (C, photo by G. van Buurt); adult male *C. nigricolor* from Sebastopol, Los Roques Archipelago, Venezuela (D, photo by G. Rivas); adult male *C. leucopsammus* from Isla La Blanquilla, Venezuela (E, photo by G. Rivas); adult male *C. ruthveni* from Bonaire (F, photo by G. van Buurt); adult male *C. senectus* from Playa Guacuco, Isla de Margarita, Nueva Esparta, Venezuela (G, photo by G. N. Ugueto); adult male *C. vanzoi* from Maria Major, St. Lucia (H, J. P. Burgess).

TABLE 9. Selected characters useful in the recognition of species groups within the genus *Cnemidophorus*.

Characters	*C. lemniscatus* Group	*C. murinus* Group	*C. nigricolor* Group	*C. vanzoi* Group
Maximum SVL	127 mm	159 mm	101 mm	121 mm
Interparietal	Usually Entire	Usually partially or completely divided	Entire or irregularly broken	Partially or completely divided
Median occipitals	Small or large	Small	Usually large	Small
First subocular	Usually Entire and contacting supralabials	Usually separated from supralabials	Usually Entire and contacting supralabials	Separated from supralabials
Rows of Lateral Supraocular Granules	Single, partially or completely doubled	Partially or completely tripled	Single; rarely partially doubled	Single
Mesoptychials	Moderately enlarged (small in *C. arubensis)*	Small	Small	Small
Transverse rows of ventrals	26–33	35–40	30–35	32–38
Longitudinal rows of ventrals	8	10–12	8	10
Proximal subcaudals	Keeled	Smooth	Smooth	Keeled
Scales on dorsum of arm	Subtriangular	Granular	Granular, slightly larger towards elbow	Granular
Preaxial Brachials	Moderately (only in *C. arubensis*) or distinctly enlarged	Barely enlarged and restricted to patch near distal edge of brachium	Slightly enlarged and restricted to patch near distal edge of brachium or moderately enlarged	Moderately enlarged and extending beyond center of arm
Postbrachials	Moderately to distinctly enlarged; restricted to patch near elbow in some *C. arubensis*	Barely enlarged and restricted to patch near elbow	Moderately enlarged	Barely enlarged and in patch near elbow
Separation of Brachials and Antebrachials	Narrow	Large gap of distinctly smaller scales	Narrow	Large gap of distinctly smaller scales
Femoral pores (combining counts for both legs)	32–65 (32–57 excluding *C. arubensis*)	57–86	45–58	49–58
Tibio-tarsal shields	Present and wide	Absent	Present	Present
Striped pattern in juveniles	Stripes present and complete or only minimally broken	Stripes absent or very faint	Stripes present but profusely broken into spots	Stripes present and complete
Flank spots in adult males	Small	Large	Small	Small
Throat in adult male	Pale, never black	Not black but dark gray	Black	Not black or black posteriorly
Chest in adult male	Pale, never black	Gray	Black	Black
Abdomen in adult male	Pale, never black or bright yellow	Grayish-blue, never black or yellow	Black	Bright yellow

TABLE 10. Meristic data of species of the *Cnemidophorus lemniscatus* group examined by us. Means ± standard deviation follow ranges.

	C. arenivagus (*n* = 4)	*C. arubensis* (*n* = 12)	*C. flavissimus* (*n* = 9)	*C. l. gaigei* (*n* = 11)	*C. gramivagus* (*n* = 15)	*C. l. lemniscatus* (n = 36)	*C. senectus* (*n = 31)*	*C. l. splendidus* (*n* = 2)
Occipitals	16–18 (17 ± 1)	16–21 (19 ± 1)	13–20 (16 ± 2)	15–17 (16 ± 1)	14–22 (18 ± 2)	11–21 (15 ± 2)	12–18 (14 ± 2)	15
Lateral Supraocular Granules	39–56 (49 ± 8)	47–72 (56 ± 7)	26–33 (28 ± 3)	22–36 (26 ± 4)	23–46 (31 ± 7)	35–69 (52 ± 8)	31–57 (39 ± 6)	21–39
Circumorbitals	10–13 (12 ± 2)	7–12 (9 ± 2)	5–11 (8 ± 2)	8–13 (10 ± 2)	7–15 (11 ± 3)	8–17 (12 ± 4)	8–14 (11 ± 2)	12–13
Supraciliaris	10–11 (11 ± 1)	10–12 (11 ± 1)	10–11 (10 ± 0)	10–11 (10 ± 0)	10–11 (10 ± 0)	8–12 (10 ± 2)	10–12 (10 ± 0)	10–13
Supralabials	11–12 (12 ± 1)	12–14 (13 ± 1)	12–14 (12 ± 1)	12	12–14 (12 ± 1)	11–15 (13 ± 1)	12–14 (12 ± 1)	13–14
Infralabials	10–12 (12 ± 1)	11–15 (13 ± 1)	10–14 (11 ± 2)	10–14 (12 ± 1)	10–12 (11 ± 1)	10–16 (13 ± 1)	10–13 (11 ± 1)	12
Anterior Gulars	18–20 (19 ± 1)	22–26 (23 ± 1)	15–23 (18 ± 3)	17–26 (20 ± 3)	16–25 (20 ± 3)	18–27 (22 ± 2)	15–23 (19 ± 2)	18
Posterior Gulars	12–14 (13 ± 1)	13–17 (15 ± 1)	12–17 (15 ± 2)	11–14 (12 ± 1)	11–16 (13 ± 1)	12–20 (16 ± 2)	11–17 (14 ± 2)	12–13
Transverse Ventral Rows	32–33 (31 ± 1)	30–33 (32 ± 1)	29–33 (31 ± 1)	28–32 (30 ± 1)	30–34 (32 ± 1)	28–31 (30 ± 1)	29–33 (30 ± 1)	30–31
Longitudinal Ventral Rows	8	8	8	8	8	8	8	8
Preanals	4–5 (5 ± 1)	4–5 (5 ± 0)	5	4–5 (4 ± 0)	4–5 (4 ± 0)	4–6 (5 ± 1)	4–5 (5 ± 0)	4
Lamellae Under Fourth Finger	16 (*n* = 1)	17–21 (19 ± 2)	17–18 (18 ± 1)	16–18 (17 ± 1)	16–19 (17 ± 1)	14–19 (17 ± 1)	15–18 (16 ± 1)	14–15
Prefemorals	6–7 (7 ± 1)	6–8 (7 ± 1)	6–7 (7 ± 1)	6–7 (7 ± 1)	5–7 (6 ± 1)	5–8 (7 ± 1)	5–7 (6 ± 0)	5–6
Femoral and Abdominal Pores	44–47 (45 ± 2)	57–66 (6 ± 3)	43–49 (46 ± 2)	34–46 (40 ± 2)	38–48 (43 ± 3)	41–57 (48 ± 4)	23–51 (46 ± 5)	46–47
Scales Separating Pore Rows	2–4 (3 ± 1)	3–4 (4 ± 1)	2–3 (2 ± 0)	2–4 (3 ± 1)	1–2 (2 ± 0)	1–4 (2 ± 1)	2–3 (2 ± 0)	2
Lamellae Under Fourth Toe	33–36 (34 ± 2)	36–42 (39 ± 2)	31–37 (34 ± 2)	30–34 (32 ± 1)	26–34 (30 ± 2)	29–35 (33 ± 2)	28–35 (31 ± 1)	28–31

Supralabials 11–15 (usually 12); first supralabial subequal to or larger than second, its ventral margin straight (rarely curved); infralabials 10–15; first pair of chinshields broadly contacting infralabials and forming a medial suture greater than or equal to half their length; interangular sulcus absent; anterior gulars 15–37; gular patch absent; posterior gulars 11–22; intertympanic sulcus absent; larger anterior gulars undergoing sharp transition to smaller posterior gulars at intertympanic crease; mesoptychials not or moderately enlarged; gular fold lacking serrated edge.

Dorsals smooth; scales on flank subequal to middorsals, supported by small apical granules, not projecting laterally; scales on rump much smaller than proximal subcaudals; scales of chest large and flat; pectoral sulcus absent; ventrals smooth, in 28–40 transverse and 8–12 longitudinal rows; lateral-most ventrals flanked by small scales (i.e., ventrals not gradually decreasing in size on flanks); preanals 4–7; preanal plate present, bordered by subtriangular scales; preanals one-half as large to larger than scale anterior to them; in males, preanal spurs 1/1; postcloacal buttons and postanal plates absent; scales on dorsolateral edge of tail like those on top and sides, denticulate edge and dorsolateral crests absent; caudal annuli complete; proximal subcaudals smooth (*Cnemidophorus murinus* and *C. nigricolor* groups) or keeled (*C. lemniscatus* and *C. vanzoi* groups).

TABLE 11. Meristic data of the *Cnemidophorus murinus*, *C. nigricolor*, and *C. vanzoi* groups examined by us. Means ± standard deviation follow ranges.

	Cnemidophorus leucopsammus (*n* = 3)	*Cnemidophorus nigricolor* (*n* = 29)	*Cnemidophorus rostralis* (*n* = 11)	*Cnemidophorus murinus* (*n* = 17)	*Cnemidophorus ruthveni* (*n* = 10)	*Cnemidophorus vanzoi* (*n* = 5)
Occipitals	11–17	14–19 (16 ± 1)	12–15 (13 ± 1)	15–24 (20 ± 3)	17–24 (21 ± 2)	13–17 (15 ± 2)
Lateral Supraocular Granules	25–28	30–32 (26 ± 3)	25–38 (32 ± 5)	60–92 (72 ± 9)	51–96 (73 ± 12)	31–37 (34 ± 3)
Circumorbitals	4–6	4–13 (7 ± 2)	4–8 (7 ± 1)	8–14 (10 ± 2)	8–12 (10 ± 1)	6–9 (8 ± 1)
Supraciliaris	10	10–12 (10 ± 0)	10–12 (11 ± 1)	10–12 (11 ± 1)	10–12 (12 ± 1)	9–12 (11 ± 1)
Supralabials	14	12–14 (13 ± 1)	12–14 (12 ± 1)	12–13 (12 ± 0)	11–13 (12 ± 0)	12
Infralabials	14	10–14 (12 ± 1)	10–14 (13 ± 1)	10–14 (11 ± 1)	10–12 (11 ± 1)	11–13 (12 ± 1)
Anterior Gulars	20–24	23–30 (26 ± 2)	19–24 (21 ± 2)	21–28 (24 ± 2)	25–37 (30 ± 5)	30–36 (33 ± 3)
Posterior Gulars	15–18	13–22 (17 ± 2)	14–19 (16 ± 2)	12–19 (16 ± 2)	16–19 (18 ± 1)	17–20 (19 ± 1)
Transverse Ventral Rows	33–35	30–33 (32 ± 1)	30–32 (31 ± 1)	35–39 (37 ± 1)	35–40 (38 ± 2)	32–37 (34 ± 2)
Longitudinal Ventral Rows	8	8	8	10–12 (10 ± 0)	10–12 (11 ± 1)	10
Preanals	6	4–6 (5 ± 0)	5–6 (5 ± 1)	5–7 (6 ± 0)	6–7 (7 ± 1)	4–6 (5 ± 1)
Lamellae Under Fourth Finger	19–22	17–28 (19 ± 2)	18–20 (19 ± 1)	20–24 (21 ± 1)	20–22 (21 ± 1)	19–22 (20 ± 1)
Prefemorals	6–8	7–9 (8 ± 1)	6–8 (7 ± 1)	7–9 (8 ± 1)	8–10 (9 ± 1)	7–8 (7 ± 1)
Femoral and Abdominal Pores	51–57 (54 ± 3)	45–58 (55 ± 3)	48–57 (51 ± 3)	57–67 (63 ± 3)	65–86 (78 ± 7)	52–58 (55 ± 2)
Scales Separating Pore Rows	2	2–4 (3 ± 1)	2	2–5 (3 ± 1)	2–4 (2 ± 1)	5–6 (5 ± 0)
Lamellae Under Fourth Toe	36–39	31–38 (35 ± 2)	35–39 (37 ± 1)	40–46 (43 ± 2)	39–44 (42 ± 2)	40–46 (43 ± 2)

Enlarged scales of brachium connected by granular (*Cnemidophorus murinus, nigricolor,* and *vanzoi* Groups) or small to large subtriangular plates (*C. lemniscatus* Group) on dorsal surface of arm; size and proximal extent of preaxial and postaxial brachial scales varying among species; antebrachial scales enlarged and smooth, widely (*C. murinus* and *C. vanzoi* Groups) or narrowly (*C. lemniscatus* and *C. nigricolor* Groups) separated from preaxial brachial scales; postaxial antebrachial scales granular; subdigital lamellae of hand homogeneous in size, mostly divided at phalangeal articulations, 14–28 under fourth finger.

Prefemorals 5–10; femoral and abdominal pores 23–86 in continuous row on each side (abdominal pores not separated from femoral pores by gap); each compound pore-bearing scale consisting of partially fused prefemoral or abdominal scale and 2–6 granular scales; 1–6 scales separating right and left pore rows; scales at heel relatively small and numerous; tibiotarsal shields present (*Cnemidophorus lemniscatus, C. nigricolor,* and *C. vanzoi* Groups) or absent (*C. murinus* Groups); tibiotarsal spurs absent; lamellae under fourth toe 26–46; distal lamellae of fourth toe smooth; continuous row of low serrate keeled scales completely separating digital lamellae along postaxial edge of all toes; noticeably enlarged postaxial scales between fourth and fifth toe absent; fifth toe well-developed, base of its claw extending beyond level of skin between third and fourth toes when adpressed.

β-keratin containing layers of dorsal scales folded into macrohoneycomb; dorsal and caudal scales with one subterminal lenticular scale organ; ventrals lacking scale organs; generation glands present, usually unpigmented (pigmented in *Cnemidophorus murinus* Group).

Snout same color as dorsal head scales; specimens of *Cnemidophorus leucopsammus* and *C. rostralis* sometimes with tan cast but lacking decidedly red snout. In juveniles, light vertebral stripe present, usually solid and straight (most species), split and straight (*C. l. espeuti, C. l. lemniscatus, C. vanzoi*), breaking into very few or numerous spots (*C. flavissimus, C. nigricolor*), or very faded, almost absent (*C. gramivagus, C. leucopsammus, C. murinus, C.* cf. *nigricolor, C. rostralis, C. ruthveni*); light paravertebral stripes present and straight (most species) or faded and/or broken into spots (*C. leucopsammus, C. nigricolor, C.* cf. *nigricolor, C. rostralis*); paravertebral stripes usually broken at some point along their length in juvenile *C. flavissimus* (coded as continuous in phylogenetic analysis, because most of stripe remains solid); paravertebral stripes of *C. murinus* and *C. ruthveni* very inconspicuous, faded and often difficult to discern but nonetheless present and straight; dark dorsolateral field solid in all species (present but very faint and sometimes difficult to observe or only distinct posteriorly in *C. arubensis, C. leucopsammus, C. murinus, C. nigricolor, C.* cf. *nigricolor, C. rostralis, C. ruthveni*); dorsolateral light stripe solid and extending to tail (most species) or broken into spots (*C. leucopsammus, C. nigricolor, C.* cf. *nigricolor, C. rostralis*); dorsolateral light stripe of *C. murinus* and *C. ruthveni* very inconspicuous, faded and often difficult to discern but nonetheless present and extending to tail; dark lateral field usually solid and distinct at least posteriorly (most species) or absent (*C. leucopsammus, C. nigricolor, C.* cf. *nigricolor, C. rostralis*); upper lateral light stripe solid and extending to groin (most species), broken into spots not always coinciding with stripes (*C. arubensis, C. leucopsammus, C. nigricolor, C.* cf. *nigricolor, C. rostralis*), or absent (*C. murinus, C. ruthveni*); lower lateral light stripe solid and extending to groin (*C. arenivagus, C. flavissimus, C. lemniscatus gaigei, C. l. splendidus, C.* cf. *lemniscatus, C. senectus*), broken into spots not always coinciding with stripes (*C. arubensis, C. l. espeuti, C. gramivagus, C. l. lemniscatus, C. leucopsammus, C. nigricolor, C.* cf. *nigricolor, C. rostralis, C. vanzoi*), or absent and instead replaced by large spots (*C. murinus, C. ruthveni*); thigh with light spots. Adult males with small (most species) or large (*C. murinus, C. ruthveni*) light spots on flanks; turquoise ventrolateral spots always absent (some specimens of predominantly blue species may have blue flank spots invading ventrolateral areas but these are not homologous to turquoise spots present in other teiids); venter immaculate (pale or black in melanic species); juvenile of all species undergoing considerable ontogenetic changes in coloration, less conspicuously so in *C. murinus* and *C. ruthveni* and most distinct in *C. flavissimus*.

Hemipenis with pair of taβ-like and smooth apical awns; apical papillae and apical basin absent; asulcate expansion pleat well-developed, interrupting about 14–23 distal laminae; discontinuous distal laminae absent; 5–13 laminae proximal to expansion pleat; proximal laminae ornamented with short papillae.

Interspecific Relationships and Biogeography.—We identified suites of morphological characters to define four species groups (Table 9) within *Cnemidophorus*. In our phylogenetic analysis, each of the four groups was monophyletic (Fig. 66). *Cnemidophorus vanzoi* is sister to the *C. murinus* Group. Together, these large insular and vegetarian species are the closest relatives of the *C. nigricolor* Group in the ordered analysis, whereas the *C. nigricolor* Group is sister to the *C. lemniscatus* Group in the unordered trees. Within the *C. nigricolor* Group, the recently described species *C. leucopsammus* and *C. rostralis* are each other's closest relatives.

Recent analyses of molecular characters (Giugliano 2009; Giugliano *et al.* 2006; Reeder *et al.* 2002) included only five of the taxa studied here (Fig. 66). Each of these studies included *C. lemniscatus*, *C. arenivagus*, and *C. gramivagus*. Reeder *et al.* (2002) also included *C. l. splendidus*, whereas Giugliano (2009) also included *C. vanzoi*. Although these analyses agreed with our results in excluding *Cnemidophorus vanzoi* from an otherwise monophyletic *C. lemniscatus* Group, interspecific relationships within the *C. lemniscatus* Group differ from our results. Reeder *et al.* (2002, p. 18) called attention to the close relationship between *C. l. splendidus* and *C. arenivagus* and suggested, "that the specific status of '*C.*' *lemniscatus splendidus* merits reevaluation." *Cnemidophorus l. gaigei* and *C. l. splendidus* are very similar morphologically. Their distributions are contiguous in western Venezuela (G. N. Ugueto, unpublished data) and, perhaps not surprisingly, appear to be sister species. Reeder *et al.* (2002) did not include molecular data for *C. l. gaigei* or *C. l. espeuti* in their analyses. Morphological evidence suggests that *C. lemniscatus* is monophyletic with three subspecies (*C. l. gaigei*, *C. l. lemniscatus*, and *C. l. splendidus*) if the insular taxon *C. l. espeuti* is excluded. However, we only examined a few specimens of *C. l. gaigei*, *C. l. espeuti*, and *C. l. splendidus*. There are differences in some scale counts (some of which were not scored in this study) among these taxa, and at least some of them may be distinct species. Additionally, the taxonomic situation of *Cnemidophorus* in northern South America, particularly in western Venezuela, is still unclear (G. N. Ugueto, unpublished data). The authors are currently reviewing *C. l. espeuti* and populations of *C. lemniscatus* in northwestern Venezuela, Colombia and Central America.

Most species of *Cnemidophorus* occur on islands of the southern Caribbean (Ugueto & Harvey 2010), with only a few species of the *C. lemniscatus* Group occurring on the mainland. Interestingly, the most basal member of this group (*C. arubensis*) is also an insular species. Consequently, we can now conclude with relative certainty that *Cnemidophorus* evolved in the southern Caribbean. Moreover, the most parsimonious interpretation of our data is that *C. lemniscatus*, *C. gramivagus*, and *C. arenivagus* represent independent invasions of the mainland from an insular point of origin. The other mainland species of *Cnemidophorus*, *C. cryptus* and *C. pseudolemniscatus*, are parthenogens that arose from hybridization events involving *C. lemniscatus* and *C. gramivagus* (Cole & Dessauer 1993; Reeder *et al.* 2002).

Remarks.—Reeder *et al.* (2002) partially resolved polyphyly of *Cnemidophorus* when they revalidated *Aspidoscelis*. As redefined here, *Cnemidophorus* is a morphologically and geographically cohesive group defined by a suite of synapomorphies. Other species left in the genus by Reeder *et al.* (2002) are here transferred to *Ameiva*, *Ameivula*, *Aurivela*, and *Contomastix*.

Cnemidophorus lemniscatus Group

Definition.—The following combination of characters distinguishes the *Cnemidophorus lemniscatus* Group (Table 9) from other groups of *Cnemidophorus*: small to medium lizards reaching 127 mm SVL; interparietal entire (very rarely partially longitudinally divided along midline, only completely divided in one specimen of *C. l. lemniscatus*, n = 36); most species usually with noticeably enlarged median pair of occipital plates flanked by smaller scales (*C. flavissimus*, *C. lemniscatus gaigei*, *C. l. lemniscatus*, *C. l. splendidus*, *C. senectus*), or median occipitals small and always subequal to adjacent scales (*C. arenivagus*, *C. arubensis*, *C. gramivagus*); first subocular usually entire and in contact with supralabials, occasionally subocular separated from supralabials by anterior expansion of second subocular in some specimens of *C. arenivagus* and *C. arubensis*; single to partially or completely doubled row of granules between supraocular and supraciliaries; mesoptychials moderately enlarged (only barely to slightly enlarged in *C. arubensis*); ventral scales in 26–33 transverse and 8 longitudinal rows; proximal subcaudals keeled; preaxial and postaxial brachial scales separated by small triangular scales or connected by enlarged subtriangular plates; preaxial brachial scales from moderately (1–1.5 times as wide as long) to distinctly enlarged (1.5–2+ times wider than long) and extending beyond center of arm; postbrachials distinctly enlarged (except in few specimens of *C. arubensis* in which they are moderately enlarged) and extending beyond center of arm (except in few *C. arubensis* in which these scales are only discernable near elbow); enlarged antebrachials in continuous row or narrowly separated from enlarged preaxial brachials; combined femoral and abdominal pores 41–65; tibiotarsal shields transversely enlarged and wide; juveniles with distinct striped pattern with continuous or only slightly discontinuous stripes (latter only in *C. flavissimus*); spots on flanks of adult males small (slightly larger in *C. arubensis* and *C. gramivagus* than in other species); throat, chest or abdomen in adult males never melanic; abdomen of adult males never bright yellow.

Distribution.—Mainland Central and northern South America, Trinidad, Tobago, Aruba, continental southern Caribbean Islands, Isla San Andres, Isla Santa Catalina, and Isla de Providencia.

Content.—*Cnemidophorus arenivagus* Markezich *et al.*, *Cnemidophorus arubensis* (Lidth de Jeude), *Cnemidophorus cryptus* Cole and Dessauer, *Cnemidophorus flavissimus* Ugueto *et al.*, *Cnemidophorus gramivagus* McCrystal and Dixon, *Cnemidophorus lemniscatus espeuti* Boulenger, *Cnemidophorus lemniscatus gaigei* Ruthven, *Cnemidophorus lemniscatus lemniscatus* (Linnaeus), *Cnemidophorus lemniscatus splendidus* Markezich *et al.*, *Cnemidophorus pseudolemniscatus* Cole and Dessauer, *Cnemidophorus senectus* Ugueto *et al.*, *Cnemidophorus* sp. B.

Remarks.—Among species in the *Cnemidophorus lemniscatus* Group, *C. arubensis* is the most divergent and is included within this group with some reservation. Unlike other species in the group, *C. arubensis* has only moderately enlarged brachials, small mesoptychials, and many more femoral pores (57–65 in *C. arubensis* vs. 32–57 in the remaining species). Additionally, the scales on the dorsal aspect of the arm are smaller and the proximal subcaudals are more weakly keeled than in the remaining species of the group. We include *C. arubensis* in the *C. lemniscatus* Group rather than one of the other insular groups, because it has 8 longitudinal rows of ventrals, broad tibiotarsal shields, brachials and antebrachials continuous, adult males with pale ventral surfaces, and striped juveniles.

***Cnemidophorus murinus* Group**

Definition.—The following combination of characters distinguishes the *Cnemidophorus murinus* Group (Tables 9, 11) from other groups of *Cnemidophorus*: medium lizards reaching 159 mm SVL; interparietal frequently partially or completely longitudinally divided along midline [only 30% of *C. ruthveni* (n = 10) and 47% of *C. murinus* (n = 17) have completely entire interparietals]; median pair of occipitals small and flanked by subequal scales; first subocular usually separated from supralabials by anterior expansion of second subocular, occasionally subocular entire and contacting supralabials; partially or completely tripled row of granules between supraocular and supraciliaries (doubled in only one specimen of *C. murinus*); mesoptychials not or only slightly enlarged; ventral scales in 35–40 transverse and 10 or 12 longitudinal rows; smooth proximal subcaudals; preaxial and postaxial brachial scales separated by granular scales; preaxial brachial scales barely enlarged and forming small patch near distal end of brachium; postbrachials not or only barely enlarged and, if discernible, restricted to small patch near elbow; enlarged antebrachials broadly separated from enlarged preaxial brachials by large gap of granules or distinctly smaller scales; combined femoral and abdominal pores 57–86; tibiotarsal shields absent; stripes absent or very inconspicuous (only slightly visible on posterior dorsum) in juveniles; spots on flanks of adult males very large; throat not melanic although very dark in some adult males; chest not black but often dark, often darker than the abdomen, pale bluish or grayish in adult males, never bright yellow.

Content.—*Cnemidophorus murinus* (Laurenti) and *Cnemidophorus ruthveni* (Ruthven).

Distribution.—Curaçao, Klein Curaçao, Bonaire and Klein Bonaire.

Remarks.—The *Cnemidophorus murinus* Group is the most divergent morphologically. The two species in this group attain much larger SVLs than congeners and are unique in having a partially or completely tripled row of granules between the supraoculars and supraciliaries. Additionally, species in the *C. murinus* Group are the only *Cnemidophorus* with large flank spots in adult males and juveniles with no or very inconspicuous light stripes. Species of the *C. murinus* and *C. vanzoi* Groups have longitudinally divided interparietals and more transverse ventrals than congeners. The longer abdomen in the highly herbivorous species of the *C. murinus* Group may have evolved to accommodate unusually long intestines required to process plant matter (Dearing 1993). We were surprised to find longitudinally divided interparietals in the three species of the *C. murinus* and *C. vanzoi* Groups. In other teiids, this trait occurs only in the geographically proximate species of the *Ameiva erythrocephala* Group.

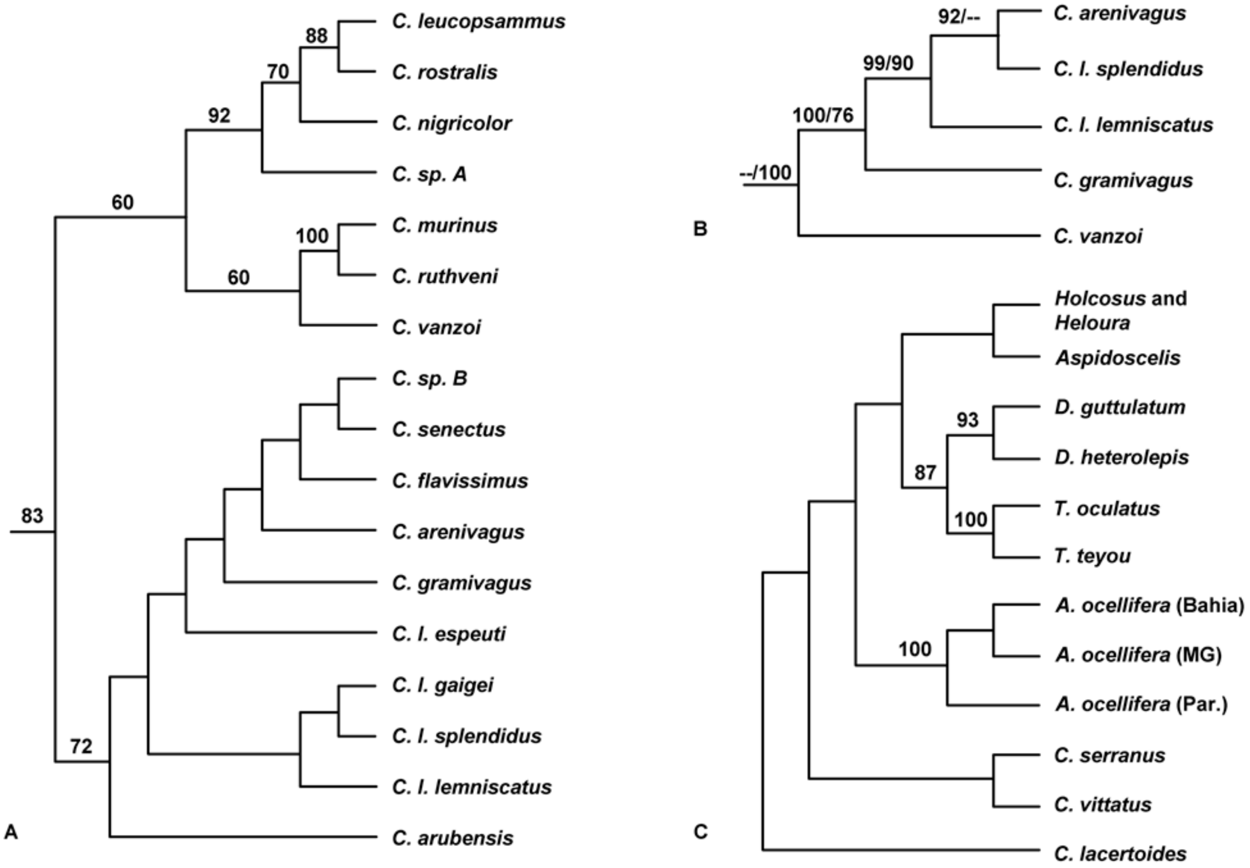

FIGURE 66. Phylogeny of *Cnemidophorus* based on morphology (A, this study, all characters ordered) compared to phylogeny based on allozymes and mtDNA (B, Reeder *et al.* 2002) or mtDNA c-mos nuclear DNA (Giugliano 2009). Morphology based phylogeny depicting interspecific relationships among species of *Dicrodon*, *Teius*, *Ameivula*, and *Contomastix* (C, this study). In all trees, numbers indicate bootstrap support. For the molecular tree (B), a solidus sepates bootstrap values appearing in figure 3 of Reeder *et al.* (2002) from values in figure 20A of Giugliano (2009).

Cnemidophorus nigricolor Group

Definition.—The following combination of characters distinguishes the *Cnemidophorus nigricolor* Group (Tables 9, 11) from other groups of *Cnemidophorus*: small lizards reaching 101 mm SVL; interparietal entire or broken into smaller scales (particularly anteriorly or laterally) but never longitudinally divided along midline; usually with noticeably enlarged median pair of occipitals flanked by smaller scales (somewhat variable in *C. nigricolor*, less often so in *C. rostralis*); first subocular entire and in contact with supralabials (rarely subocular contacting supralabials but longitudinally divided in *C. rostralis*); granules between supraocular and supraciliaries in single row (partially doubled only rarely in *C. rostralis*); mesoptychials not or only slightly enlarged; ventral scales in 30–35 transverse and 8 longitudinal rows; proximal subcaudals smooth; preaxial and postaxial brachial scales separated by granular scales, slightly larger towards elbow; preaxial brachial scales from barely to moderately (1–1.5 times as wide as long) enlarged and forming patch near distal end of brachium or extending beyond center of arm; postbrachials moderately enlarged (1–1.5 times as wide as long) and extending beyond center of arm; enlarged antebrachials in continuous row or narrowly separated from enlarged preaxial brachials; combined femoral and abdominal pores 45–58; tibiotarsal shields distinct (conspicuously enlarged transversely in *C. rostralis*), although individual shields of frequently divided; juveniles with dorsal striped pattern present but stripes broken into longitudinal series of spots and rather inconspicuous in *C. leucopsammus* and *C. rostralis*; flank spots of adult males small, often completely lost or obscured in old specimens; adult males usually completely melanic, with throat, chest and abdomen uniformly black.

Content.—*Cnemidophorus leucopsammus* Ugueto and Harvey, *Cnemidophorus nigricolor* (Peters), *Cnemidophorus rostralis* Ugueto and Harvey, *Cnemidophorus* sp. A.

Distribution.—Venezuelan Antilles (Las Aves Archipelago, Los Roques Archipelago, La Orchila, La Blanquilla and Los Hermanos Archipelago) and the island of La Tortuga (Venezuela).

***Cnemidophorus vanzoi* Group**

Definition.—The following combination of characters distinguishes the *Cnemidophorus vanzoi* Group (Tables 9, 11) from other groups of *Cnemidophorus*: medium lizards reaching 121 mm SVL; interparietal partially or completely divided longitudinally along midline; median pair of occipitals small and flanked by subequal scales; first subocular separated from supralabials by anterior expansion of second subocular; single row of granules between supraocular and supraciliaries; mesoptychials not or only slightly enlarged; ventral scales in 32–37 (33–38 according to Schwartz & Henderson 1991) transverse and 10 longitudinal rows; proximal subcaudals keeled; preaxial and postaxial brachial scales separated by granular scales; preaxial brachial scales moderately (1–1.5 times as wide as long) enlarged and extending beyond center of arm; postbrachials only barely to slightly enlarged (1–1.5 times as wide as long) and forming small patch near elbow; enlarged antebrachials broadly separated from enlarged preaxial brachials by large gap of distinctly smaller scales; femoral pores 52–58 (49–58 according to Schwartz & Henderson 1991); tibiotarsal shields moderately distinct, although individual shields of frequently divided; juveniles with distinct striped pattern (usually only vertebral, paravertebral and dorsolateral stripes visible); spots on sides of adult males small; throat in adult males not melanic or only slightly so posteriorly (terminal posterior gulars and mesoptychium); chest in adult males black; abdomen in adult males bright yellow.

Content.—*Cnemidophorus vanzoi* (Baskin & Williams).

Distribution.—Southernmost of 2 Maria Islands off southeastern end of St. Lucia.

Remarks.—This species shares some characteristics with each of the remaining three groups of *Cnemidophorus*. Like the *C. murinus* Group, it has 10 longitudinal rows of ventrals, a longitudinally divided or semidivided interparietal, very small scales separating brachials and postbrachials along the dorsal aspect of the arm, and antebrachials conspicuously separated from brachials by a large gap of small scales. It shares with the *C. nigricolor* Group moderately sized brachial scales that extend beyond the center of the arm, melanic chest and posterior portion of throat, and small spots on flanks of adult males. It is also similar to species of the *C. lemniscatus* Group in having striped juveniles, small spots on the flanks of males, and keeled proximal subcaudals. However, *C. vanzoi* is unique in that adult males have a bright yellow abdomen, which contrast with the black chest and dark gray chin and throat.

***Contomastix* New Genus**

Figure 67

Type Species.—*Cnemidophorus vittatus* Boulenger by original designation.

Diagnosis.—We know of no single unique character that distinguishes *Contomastix* from all other teiids. The tail of species in this genus is shorter than that of other Teiinae. These small teiids are most likely to be confused with *Ameivula*. Unlike species in that genus (characters in parentheses), *Contomastix* has a short tail (long), three parietals (five), a straight to curved ventral margin of the first supralabial (toothy), the first supralabial subequal to the second (much smaller than second), three relatively large scales at the heel (scales small and numerous), and a well-developed fifth toe (fifth toe reduced).

Contomastix was previously confused with *Cnemidophorus*. Unlike the species in this genus, male *Contomastix* lack preanal spurs (spurs present) and the species in this genus have the nasal and prefrontal in contact (separate), three parietals (five), homogeneous subdigital lamellae of the hand (subarticular lamellae of hand divided), and lamellae in contact along the postaxial sides of the toes (serrate row of keeled scales completely separating digital lamellae of toes).

Content.—*Contomastix charrua* (Cabrera & Carreira), *Contomastix lacertoides* (Duméril & Bibron), *Contomastix leachei* (Peracca), *Contomastix serrana* (Cei & Martori), *Contomastix vacariensis* (Feltrim & Lema), *Contomastix vittata* (Boulenger).

FIGURE 67. *Contomastix lacertoides* from nearby Cacapava do Sul, Rio Grande do Sul, Brazil (A, photo by A. Kwet); *C. vittatus* from Cerro Cota, 1.5 Km NE Vinto Chico, Cochabamba, Bolivia (B and C, photos by M. B. Harvey); *C. vacariensis* from Vacaria, Rio Grande do Sul, Brazil (D, photo by A. Kwet).

Definition.—Small lizards reaching 76 (*Contomastix vittata*) mm SVL; tail 1.6–2.1X (Table 12) as long as body; posterior maxillary and dentary teeth longitudinally compressed, tricuspid; pupil reniform.

Prefrontal in contact with nasal, usually separated from first supraciliary; frontal entire (except some *Contomastix vittata*), lacking longitudinal ridge, its posterior suture contacting second (most *C. lacertoides*) or third (*C. serrana*, *C. vittata*) supraocular; scales of frontoparietal region smooth, outwardly convex to flat (key-hole shaped depression absent); frontoparietals paired; parietals consisting of three (rarely five) regular scales; interparietal entire, smaller to larger than flanking parietals; medial pair of enlarged occipitals absent; occipitals 9–17, larger than or subequal to first row of dorsals; supratemporals slightly to moderately enlarged, separated from parietals by one or more scales.

Rostral groove present; nostril oval (*Contomastix serrana*, *C. vittata*) to subcircular (*C. lacertoides*), oriented anteroventrally, anterior to nasal suture, touching suture (*C. vittata*) or not (*C. lacertoides*, *C. serrana*); loreal single; supraoculars six (rarely eight); first supraocular entire, larger than fourth (when present) supraocular, and broadly contacting or partly separated from (rarely completely separated from) second supraocular; circumorbital semicircles consisting of 4–8 small scales, usually extending anterior to point medial to third supraocular (rarely behind third supraocular); supraciliaries 10–15, separated from supraoculars by 1–1.5 rows of 18–38 granular scales; first supraciliary long, greater than one-half as long as second; angulate keel extending from first subocular to elongate subocular below eye; suboculars 4–6 (usually 4); first subocular contacting or separated from first supraciliary, contacting supralabials, entire (except in some *C. vittata*); patch of distinctly enlarged scales in front of auditory meatus; auricular flap and preauricular fold absent.

Supralabials 12–14; first supralabial smaller than (*Contomastix serrana*) to subequal to (*C. lacertoides*, *C. vittata*) second, its ventral margin curved; infralabials 10–13; first pair of chinshields broadly contacting infralabials or partially (rarely completely) separated from infralabials by row of granular scales; chinshields medially separated from one another or forming a suture of variable length; interangular sulcus absent; anterior gulars 13–20; gular patch absent; posterior gulars 9–15; intertympanic sulcus absent; larger anterior gulars undergoing sharp transition to smaller posterior gulars at intertympanic crease; mesoptychials moderately enlarged; gular fold lacking serrated edge.

TABLE 12. Selected meristic and morphological data of some Teiinae from South America examined by us. Means ± standard deviation follow ranges.

	Contomastix vittatus (*n* = 9)	*Contomastix lacertoides* (*n* = 15)	*Contomastix serranus* (*n* = 4)	*Teius teyou* (*n* = 9)	*Teius oculatus* (*n* = 5)	*Dicrodon guttulatum* (*n* = 10)	*Dicrodon heterolepis* (*n* = 9)
Occipitals	12–16 (14 ± 2)	9–17 (13 ± 3)	13–15 (14 ± 1)	Not Applicable	13–15 (14 ± 1)	10–16 (13 ± 2)	10–13 (11 ± 1)
Lateral Supraocular Granules	21–38 (29 ± 6)	18–38 (23 ± 5)	23–26 (25 ± 1)	68–100 (80 ± 11)	44–73 (62 ± 11)	44–84 (62 ± 13)	43–59 (47 ± 5)
Circumorbitals	4–7 (5 ± 1)	3–8 (6 ± 1)	4–7 (6 ± 1)	26–35 (31 ± 3)	26–31 (28 ± 2)	21–30 (26 ± 3)	21–27 (24 ± 2)
Supraciliaris	10–15 (12 ± 2)	10–13 (11 ± 1)	10–11 (11 ± 1)	11–14 (12 ± 1)	12	11–14 (13 ± 1)	11–15 (13 ± 1)
Supralabials	12–14 (13 ± 1)	12–13 (12 ± 0)	12–13 (12 ± 1)	13–17 (14 ± 1)	13–15 (14 ± 1)	12–14 (12 ± 1)	12–14 (13 ± 1)
Infralabials	10–13 (12 ± 1)	10–12 (10 ± 1)	Not Available	12–15 (13 ± 1)	12–14 (13 ± 1)	10–13 (12 ± 1)	10–12 (11 ± 1)
Anterior Gulars	14–20 (17 ± 2)	13–20 (15 ± 2)	15–17 (16 ± 1)	23–34 (29 ± 4)	19–22 (20 ± 1)	15–26 (18 ± 3)	17–26 (21 ± 3)
Posterior Gulars	12–15 (13 ± 1)	9–11 (10 ± 1)	13–15 (14 ± 1)	12–18 (16 ± 2)	8–14 (11 ± 2)	7–15 (12 ± 2)	12–20 (15 ± 2)
Transverse Ventral Rows	30–33 (32 ± 1)	30–36 (33 ± 2)	32–33 (33 ± 1)	32–35 (33 ± 1)	33–35 (34 ± 1)	30–34 (32 ± 1)	28–32 (30 ± 1)
Longitudinal Ventral Rows	10	10	10	8	10	8	8–10
Preanals	4–5 (5 ± 0)	4–5 (5 ± 0)	5	4–5 (5 ± 0)	6–7 (7 ± 1)	5	4–5 (4 ± 0)
Lamellae Under Fourth Finger	13–15 (14 ± 1)	12–16 (14 ± 1)	14–15 (14 ± 1)	15–17 (16 ± 1)	13–15 (14 ± 1)	17–21 (18 ± 1)	15–17 (16 ± 1)
Prefemorals	5–7 (6 ± 1)	6–7 (6 ± 0)	7–8 (7 ± 1)	8–11 (9 ± 1)	6–8 (7 ± 1)	7–9 (8 ± 1)	9–11 (10 ± 1)
Femoral and Abdominal Pores	20–25 (22 ± 2)	16–24 (20 ± 3)	24–26 (25 ± 1)	35–48 (42 ± 4)	30–41 (33 ± 5)	37–44 (40 ± 2)	26–38 (31 ± 4)
Scales Separating Pore Rows	3–4 (4 ± 0)	6–9 (7 ± 1)	3–4 (4 ± 1)	2–4 (3 ± 1)	3–4 (3 ± 1)	4–5 (4 ± 0)	3–6 (4 ± 1)
Lamellae Under Fourth Toe	24–28 (25 ± 1)	19–30 (23 ± 3)	25–28 (26 ± 1)	32–40 (36 ± 2)	27–34 (29 ± 3)	33–41 (37 ± 2)	29–34 (31 ± 2)
Tail Length/ SVL	1.6–2.1 (1.8 ± 0.2, *n* = 6)	1.5–1.9 (1.7 ± 0.2, *n* = 7)	1.9 (*n* = 3)	2.2–2.4 (2.3 ± 0.1, *n* = 3)	Not Available	2.2–2.8 (2.4 ± 0.2, *n* = 5)	2.4–2.6 (2.5 ± 0.1, *n* = 3)

Dorsals smooth; scales on flank subequal to middorsals, not projecting laterally, supported by small apical granules; scales on rump much smaller than proximal subcaudals; scales of chest large and flat; pectoral sulcus absent; ventrals smooth, in 30–36 transverse and ten longitudinal rows; lateral-most ventrals flanked by small scales (i.e., ventrals not gradually decreasing in size on flanks); preanals 4–5; preanal plate present, bordered by subtriangular scales; preanals one-half as large to larger than scale anterior to them; preanal spurs, postcloacal buttons, and postanal plates absent; scales on dorsolateral edge of tail like those on top and sides, denticulate edge and dorsolateral crests absent; caudal annuli complete; proximal subcaudals smooth (*Contomastix vittata*) or keeled (*C. lacertoides*, and *C. serrana*).

Enlarged scales of brachium connected by continuous band of enlarged subtriangular plates on dorsal surface of arm; preaxial brachial scales 1.5–2X as wide as long, extending proximally to or beyond center of arm; postaxial brachial scales restricted to small patch near elbow, usually 1–1.5X as wide as long (frequently longer than wide in *Contomastix vittata*); antebrachial scales enlarged and smooth, narrowly separated from or in continuous row with preaxial brachial scales; postaxial antebrachial scales slightly enlarged; lamellae under fourth finger 12–16; subdigital lamellae of hand homogeneous.

Prefemorals 5–8; femoral and abdominal pores 16–26, in continuous row on each side (abdominal pores not separated from femoral pores by gap); each compound pore-bearing scale consisting of partially fused prefemoral or abdominal scale and 2–6 granular scales; 3–4 (*Contomastix serrana*, *C. vittata*) or 6–9 (*C. lacertoides*) scales separating right and left pore rows; three relatively large, subequal scales at heel; tibiotarsal shields and spurs absent; lamellae under fourth toe 19–30; distal lamellae of fourth toe smooth; scales between subdigital and supradigital lamellae of toes small and mostly restricted to phalangeal articulations; noticeably enlarged postaxial scales between fourth and fifth toe absent; fifth toe well-developed, base of its claw extending beyond level of skin between third and fourth toes when adpressed.

β-keratin containing layers of dorsal scales folded into macrohoneycomb; dorsal and caudal scales with one subterminal lenticular scale organ; ventrals lacking scale organs; generation glands absent.

Snout same color as dorsal head scales. In juveniles, light vertebral stripe absent; light paravertebral stripes present and broken (*Contomastix vittata*) or absent (*C. lacertoides*, *C. serrana*, *C. vacariensis*); dark dorsolateral field completely broken into blotches (*C. lacertoides*, *C. vacariensis*) or solid anteriorly and broken into blotches posteriorly (*C. serrana*, *C. vittata*); dorsolateral light stripe solid and extending to tail (most species) or broken into spots (*C. vacariensis*; may be broken at some point along length in some specimens of *C. lacertoides* but most of stripe solid); dark lateral field solid (*C. serrana*) or completely broken into dark blotches (*C. lacertoides*, *C. vacariensis*, *C. vittata*); upper and lower lateral light stripes broken and extending to groin (*C. lacertoides*, *C. vacariensis*) or upper stripe solid and lower fading toward groin (*C. serrana*, *C. vittata*); thigh with light spots (*C. vacariensis*) or marked by light stripes (*C. lacertoides*, *C. serrana*, *C. vittata*). Adult males without light spots or ocelli on flanks; turquoise ventrolateral spots absent; venter immaculate, lacking melanic areas; juvenile dorsal color pattern present in adult males with only slight modification.

Hemipenis (based on *Contomastix vittata*) with pair of taβ-like and smooth apical awns; apical papillae and apical basin absent; asulcate expansion pleat well-developed, interrupting 18–19 distal laminae; discontinuous distal laminae absent; 14–15 laminae proximal to expansion pleat; basal papillae absent.

Etymology.—*Contomastix* is a feminine noun in the nominative singular derived from the Greek adjective *kontos*, meaning short, and noun *mastix*, meaning whip. The name alludes to the relatively short tails of *Contomastix* compared to other whiptail lizards.

Distribution.—The six species of *Contomastix* occur in Argentina, Uruguay, southeastern Brazil, and the Andes of Bolivia. Reports of "*Cnemidophorus lacertoides*" from eastern Bolivia in the Serranía de Santiago (Dirksen & De la Riva 1999) were based on misidentified specimens of *Teius teyou* and *Ameiva ameiva* in the FMNH. Known only from Cabo Polonio, Uruguay, *C. charrua* is thought to be extinct (Cabrera & Carreira 2009).

Interspecific Relationships.—In our phylogenetic analysis, *Contomastix* is not monophyletic. *Contomastix lacertoides* is placed outside of a clade containing *C. serrana* and *C. vittata*. *Contomastix lacertoides* differs considerably from these congeners. Unlike them (character in parentheses), *C. lacertoides* has a subcircular nostril (oval), frontal suture contacting the second supraocular (third), 6–9 scales separating the left from the right femoral pore rows (3–4), dark dorsolateral fields completely broken into blotches (solid anteriorly), and lower lateral stripe broken to groin (solid and fading). We have not seen the hemipenis of *C. lacertoides*, however Böhme (1988) mentions apical papillae in this species, whereas these structures are clearly absent from the hemipenis of *C. vittata*.

Recent authors (Cabrera & Carreira 2009; Cei & Martori 1991; Cei & Scrocchi 1991; Feltrim & Lema 2000) have generally thought that *Contomastix charrua*, *C. lacertoides*, *C. leachei*, and *C. vacariensis* are closely related. Additional research is required to determine if the distinctive characters of *C. lacertoides* exclude it from *Contomastix*. We prefer to retain this species in *Contomastix* for the time being.

Dicrodon Duméril and Bibron

Figure 68

Dicrodon Duméril and Bibron 1839: 137. Type species *Dicrodon guttulatum* Duméril and Bibron by monotypy.

Diagnosis.—*Dicrodon* and *Teius* are the only teiids with transversely oriented, bicuspid teeth. Unlike *Teius* (characters in parentheses), *Dicrodon* lacks an apical basin on its hemipenis (basin present) and has fused frontoparietals (paired), a fifth toe with four phalanges (fifth toe vestigial, reduced to small nub), and sharply keeled distal digital lamellae under the fourth toe (weakly keeled or smooth). In addition, the first supraocular usually broadly contacts the second supraocular (separated by complete row of granular scales) in *Dicrodon*, although this character shows some regional variation (Fugler 1973).

Content.—*Dicrodon guttulatum guttulatum* Duméril and Bibron, *Dicrodon guttulatum holmbergi* Schmidt, *Dicrodon heterolepis* (Tschudi).

Definition.—Medium lizards reaching 163 (*Dicrodon guttulatum*) mm SVL; tail 2.2–2.8X (Table 12) as long as body; posterior maxillary and dentary teeth transversely compressed, bicuspid; pupil reniform.

Prefrontal usually in contact with nasal, separated from or in contact with first supraciliary; frontal entire, with longitudinal ridge in center of scale, its posterior suture contacting third supraocular; scales of frontoparietal region smooth, outwardly convex to flat (*Dicrodon heterolepis*) or with weak key-hole shaped depression (*D. guttulatum*); frontoparietals fused; parietals arrayed in oblique rows; interparietal entire; medial pair of enlarged occipitals absent; occipitals 10–16, usually subequal to first row of dorsals; supratemporals slightly to moderately enlarged, separated from parietals by one or more scales.

FIGURE 68. *Dicrodon guttulatum* from Olmos, Lambayeque, Peru (A, photo by P. Venegas) and from Piura, Peru (B, photo by A. Catenazzi); *D. heterolepis* from Piura, Peru (C, photo by A. Catenazzi) and from Puerto Morín, Libertad, Peru (D, photo by P. Venegas).

Rostral groove present; nostril oval and oriented anteroventrally, positioned anterior to and not touching nasal suture; loreal single; supraoculars eight; first supraocular entire, usually larger than fourth supraocular, usually broadly contacting second supraocular; circumorbital semicircles consisting of 21–30 small scales, extending to posterior margin of first supraocular or point medial to second supraocular; supraciliaries subequal, 11–15, separated from supraoculars by 1.5–3 rows of 43–84 granular scales; first supraciliary contacting or separated from first subocular; angulate keel extending from first subocular to elongate subocular below eye; suboculars four; first subocular separated from supralabials by scale inserted between suboculars and loreal or, less frequently, by anterior expansion of second subocular; patch of distinctly enlarged scales in front of auditory meatus; auricular flap and preauricular fold absent.

Supralabials 12–14; first supralabial smaller than second, its ventral margin curved to "toothy"; infralabials 10–13; first pair of chinshields broadly contacting or partially (rarely completely) separated from infralabials, forming medial suture greater than or equal to half their length; interangular sulcus absent; anterior gulars 16–26; gular patch absent; posterior gulars 7–20; intertympanic sulcus absent; larger anterior gulars undergoing sharp transition to smaller posterior gulars at intertympanic crease; mesoptychials moderately enlarged; gular fold lacking serrated edge.

Dorsals smooth (*Dicrodon guttulatum*) or keeled (*D. heterolepis*); scales on flank subequal to (*D. guttulatum*) or much smaller than (*D. heterolepis*) middorsals, not projecting laterally, supported by small apical granules; scales on rump much smaller (*D. guttulatum*) to slightly smaller (*D. heterolepis*) than proximal subcaudals; scales of chest large and flat; pectoral sulcus absent; ventrals smooth, in 29–34 transverse and 8–10 longitudinal rows; lateral-most ventrals flanked by small scales (i.e., ventrals not gradually decreasing in size on flanks); preanals 4–5; preanal plate present, bordered by subtriangular scales; preanals one-half as large to larger than scale anterior to them; preanal spurs, postcloacal buttons, and postanal plates absent; scales on dorsolateral edge of tail like those on top and sides, denticulate edge and dorsolateral crests absent; caudal annuli complete; proximal subcaudals smooth.

Enlarged scales of brachium connected by continuous band of enlarged subtriangular plates on dorsal surface of arm; preaxial brachial scales 1–2X as wide as long, extending to or beyond center of arm; postaxial brachial scales 1–2X as wide as long (not enlarged in some *Dicrodon guttulatum*), restricted to patch near elbow; antebrachial scales enlarged and smooth, narrowly (*D. guttulatum*) or broadly (*D. heterolepis*) separated from preaxial brachial scales; postaxial antebrachial scales slightly enlarged (*D. guttulatum*) to granular (*D. heterolepis*); subdigital lamellae of hand homogeneous in size, 15–21 under fourth finger.

Prefemorals 7–11; femoral and abdominal pores 26–44, in continuous row on each side (abdominal pores not separated from femoral pores by gap); each compound pore-bearing scale consisting of partially fused prefemoral or abdominal scale and 2–6 granular scales; 3–6 scales separating right and left pore rows; scales at heel small and numerous; tibiotarsal shields and spurs absent; lamellae under fourth toe 29–41; distal lamellae of fourth toe sharply keeled; continuous low serrate row of scales separating subdigital and supradigital lamellae of toes 2–4 (*Dicrodon guttulatum*) or 2–5 (*D. heterolepis*); noticeably enlarged postaxial scales between fourth and fifth toe absent; fifth toe reduced, base of its claw not passing level of skin between third and fourth toes when adpressed.

β-keratin containing layers of dorsal scales folded into macrohoneycomb; dorsal and caudal scales with one subterminal lenticular scale organ; ventrals lacking scale organs; generation glands present.

Snout same color as dorsal head scales; adult male *Dicrodon heterolepis* often with sides of head, chin and sometimes throat pink or whitish but color not restricted to snout. In juveniles, light vertebral stripe absent (*D. guttulatum*) or present and solid, although often breaking posteriorly (*D. heterolepis*); light paravertebral stripes absent (*D. guttulatum*) or present and solid, although fading towards head (*D. heterolepis*); dark dorsolateral field absent or only faintly indicated; dorsolateral light stripe solid, extending to tail; dark lateral field solid (*D. heterolepis*) or with light spots within it (*D. guttulatum*); upper lateral light stripes mostly solid, extending to groin (*D. heterolepis*) or broken, especially anteriorly (*D. guttulatum*); lower lateral light stripe absent in *D. guttulatum* (condition in *D. heterolepis* could not be observed); thigh lacking light spots. In adult males, flanks with light spots; presence or absence of turquoise ventrolateral spots could not be observed; venter immaculate, lacking melanic areas; juvenile dorsal color pattern present in adult males with moderate modification.

Hemipenis with pair of taβ-like and smooth apical awns; apical papillae and apical basin absent; asulcate expansion pleat well-developed, interrupting about 17 distal laminae; discontinuous distal laminae absent; zero (*Dicrodon guttulatum*) or about six (*D. heterolepis*) laminae proximal to expansion pleat; basal papillae absent.

Etymology.—*Dicrodon* is a masculine noun in the nominative singular derived from the Greek prefix *di* and noun *odontos*. The name refers to the bifid posterior teeth characteristic of this genus.

Distribution.—The two species of *Dicrodon* occur west of the Andes in arid environments of Ecuador and Peru.

Holcosus Cope
Figure 69

Holcosus Cope 1862: 60. Type species *Ameiva septemlineata* Duméril designated herein (see remarks).

Diagnosis.—Holcosus could only be confused with species of *Ameiva* and *Aspidoscelis*. Unlike *Ameiva* (characters in parentheses), species of *Holcosus* have a denticulate dorsolateral row of caudals (dorsolateral caudals like adjacent scales, laterally projecting mucrons absent), subarticular lamellae of hands distinctly enlarged and swollen (homogeneous), two or three large scales at the heel (scales at heel small and numerous), ventrals abruptly transitioning to scales on flanks (gradually decreasing in size in most species), and scales on flank "bristly" due to presence of large apical granules or outwardly projecting scales (not "bristly," apical granules small). The species of *Holcosus* also usually have six supraoculars (eight).

Unlike *Aspidoscelis*, *Holcosus* has a tongue retractile into a basal sheath (sheath absent), heterogeneous subdigital lamellae (homogeneous, although basal lamellae are enlarged in some species), denticulate dorsolateral row of caudals (dorsolateral caudals like adjacent scales, laterally projecting mucrons absent), and the nasal suture passing through the nostril (nostril anterior to but in contact with nasal suture).

Content.—Holcosus anomalus (Echternacht) **new combination**, *Holcosus bridgesii* Cope, *Holcosus chaitzami* (Stuart) **new combination**, *Holcosus festivus* (Lichtenstein & Von Martens) **new combination**, *Holcosus leptophrys* (Cope) **new combination**, *Holcosus niceforoi* (Dunn) **new combination**, *Holcosus orcesi* (Peters) **new combination**, *Holcosus quadrilineatus* (Hallowell) **new combination**, *Holcosus septemlineatus* (Duméril & Duméril), *Holcosus undulatus* (Wiegmann) **new combination**.

Definition.—Small to medium lizards reaching 88 (*Holcosus quadrilineatus*) to 135 (*H. septemlineatus*) mm SVL; tail about 2.0–2.4X (Table 13) as long as body; posterior maxillary and dentary teeth longitudinally compressed, tricuspid; pupil reniform.

Prefrontal separated or in contact with nasal and first supraciliary; frontal entire (*Holcosus undulatus* Group) or replaced by three or more irregularly keeled scales (*Holcosus orcesi* and *H. septemlineatus* Groups), lacking longitudinal ridge; when entire, posterior suture of frontal contacting second or third supraocular or suture between them; scales of frontoparietal region smooth, outwardly convex to flat (*H. undulatus* and *H. orcesi* Groups) or frontoparietals, parietals, and occipitals heavily fractured into irregular keeled scales (small irregular interparietal present in some specimens); key-hole shaped depression absent (*H. undulatus* and *H. orcesi* Groups) or well-developed, its margins formed by aligned high keels of adjacent scales (*H. septemlineatus* Group); in the *H. undulatus* and *H. orcesi* Groups frontoparietals paired and parietals consisting of three (infrequently five) regular scales (small scales separating parietals in *H. leptophrys*); in *H. undulatus* Group interparietal entire (with deep longitudinal furrow in *H. chaitzami* and *H. undulatus*), larger than (infrequently subequal to) flanking parietals; medial pair of enlarged occipitals absent; occipitals 10–16 (*H. undulatus* and *H. orcesi* Groups, character not applicable to *H. septemlineatus* Group), usually subequal to first row of dorsals; supratemporals slightly to moderately enlarged, separated from parietals by one or more scales.

Rostral groove absent (except in *Holcosus niceforoi*); nostril oval and oriented anteroventrally, its position relative to nasal suture varying among species; loreal single; supraoculars six (rarely eight); first supraocular entire (*H. undulatus* and *H. orcesi* Groups) or heavily fractured into irregular keeled scales (*H. septemlineatus* Group), larger than fourth (when present) supraocular, usually broadly contacting second supraocular (*H. undulatus* Group) or separated from them by complete row of scales (*H. orcesi* and *H. septemlineatus* Groups); circumorbital semicircles consisting of 4–30 small scales, extending anteriorly to point medial to third supraocular or beyond suture between second and third supraoculars; supraciliaries 9–15, separated from supraoculars by 0.5–2.5 rows of 19–84 (43–111 in *H. septemlineatus* Group) granular scales; first supraciliary small; second supraciliary greatly elongate (*H. chaitzami, H. festivus, H. orcesi, H. undulatus*, and *H. septemlineatus* Group) or second supraciliary small and third enlarged (most *A. leptophrys, A. niceforoi, A. quadrilineatus*); angulate keel extending from first subocular to elongate subocular below eye; suboculars 4–6 (usually 4 or 5); first subocular entire, usually separated from first supraciliary by small granular scales; first subocular contacting supralabials (*H. septemlineatus*, most *H. festivus, H. niceforoi*, and *H. orcesi*) or separated from supralabials by scale inserted between suboculars and loreal or anterior expansion of second supralabial (most *H. anomalus, H. bridgesii, H. chaitzami, H. leptophrys, H. quadrilineatus*, and *H. undulatus*); patch of slightly enlarged scales in front of auditory meatus (most species) or scales in front of meatus granular (*H. anomalus* and *H. bridgesii*); auricular flap and preauricular fold absent.

FIGURE 69. *Holcosus festivus* from El Valle, Chocó, Colombia (A, photo by M. B. Harvey); *H. leptophrys* from Carara National Park, Costa Rica (B, photo by C. L. Barrio-Amorós); *H. nicefori* from Municipio de Puerto Berrio, Antioquia, Colombia (C and D, photo by J. P. Hurtado); *H quadrilineatus* from Manzanillo, Costa Rica (E, photo by M. Berroneau); *H. septemlineatus* from Parque Nacional Machililla, Manabí, Ecuador (F, photo by M. B. Harvey) and from Parque Nacional Cerros de Amotape, Tumbes, Peru (G, photo by P. Venegas); *H. undulatus* from Reserva Natural Heloderma, Motagua Valley, Guatemala (E, photo by T. Schrei).

TABLE 13. Selected meristic and morphological data of *Holcosus* examined by us. Means ± standard deviation follow ranges.

	Holcosus orcesi (*n* = 1)	*Holcosus festivus* (*n* = 16)	*Holcosus niceforoi* (*n* = 3)	*Holcosus undulatus* (*n* = 5)	*Holcosus leptophrys* (*n* = 11)	*Holcosus quadrilineatus* (*n* = 11)	*Holcosus septemlineatus* (*n* = 10)	*Holcosus anomalus* (*n* = 10)	*Holcosus bridgesii* (*n* = 6)
Occipitals	16	10–16 (13 ± 2)	10–16 (13 ± 4)	12–14 (14 ± 1)	10–15 (13 ± 2)	12–16 (14 ± 1)	Not Applicable	Not Applicable	Not Applicable
Lateral Supraocular Granules	31	36–84 (54 ± 14)	29–40 (33 ± 6)	31–42 (38 ± 5)	19–67 (50 ± 14)	31–75 (57 ± 11)	43–67 (52 ± 8)	63–91 (78 ± 10)	80–111 (95 ± 11)
Circumorbitals	9	13–28 (19 ± 4)	13–19 (15 ± 3)	4–7 (6 ± 1)	10–17 (15 ± 2)	8–30 (20 ± 6)	14–24 (18 ± 4)	20–27 (24 ± 3)	20–29 (23 ± 4)
Supraciliaris	12	10–13 (11 ± 1)	10–12 (11 ± 1)	10	10–14 (12 ± 1)	10–13 (12 ± 1)	10–12 (11 ± 1)	9–12 (10 ± 1)	10
Supralabials	12	12–15 (13 ± 1)	12–13 (12 ± 1)	12–13 (12 ± 0)	12	12–14 (12 ± 1)	12–14 (12 ± 1)	12–14 (13 ± 1)	12
Infralabials	10	10–13 (11 ± 1)	10	10	10–12 (11 ± 1)	10–12 (10 ± 1)	10–12 (10 ± 1)	10–12 (10 ± 1)	10
Anterior Gulars	25	20–24 (23 ± 2)	20–25 (22 ± 3)	22–28 (25 ± 2)	20–27 (24 ± 3)	24–34 (28 ± 3)	24–44 (33 ± 5)	43–60 (50 ± 5)	42–51 (47 ± 4)
Posterior Gulars	8	10–15 (12 ± 2)	11–13 (12 ± 1)	7–10 (9 ± 1)	8–13 (11 ± 2)	13–18 (16 ± 1)	9–14 (11 ± 2)	13–21 (16 ± 3)	12–22 (15 ± 4)
Transverse Ventral Rows	29	26–30 (28 ± 1)	28–29 (29 ± 1)	29–32 (30 ± 1)	28–29 (29 ± 0)	29–31 (30 ± 1)	26–28 (27 ± 1)	Not Applicable	25–26 (26 ± 1)
Longitudinal Ventral Rows	8	8	8	8	8	8	6	6	6
Preanals	7	5–8 (7 ± 1)	5–7 (6 ± 1)	6–7 (6 ± 0)	7–11 (9 ± 1)	6–9 (7 ± 1)	6–10 (8 ± 1)	10–18 (14 ± 3)	9–13 (11 ± 2)
Lamellae Under Fourth Finger	17	14–17 (16 ± 1)	15–17 (16 ± 1)	16–17 (17 ± 1)	15–17 (16 ± 1)	15–19 (17 ± 1)	13–17 (15 ± 1)	12–15 (13 ± 1)	13–15 (14 ± 1)
Prefemorals	10	5–7 (5 ± 1)	5–6 (5 ± 1)	7	7–8 (8 ± 1)	5–6 (5 ± 0)	5–7 (6 ± 1)	10–14 (12 ± 2)	9–12 (10 ± 1)
Femoral and Abdominal Pores	40	36–44 (40 ± 3)	29–35 (31 ± 3)	33–37 (35 ± 2)	42–50 (46 ± 2)	30–36 (33 ± 2)	37–46 (41 ± 3)	45–56 (51 ± 3)	43–53 (48 ± 3)
Scales Separating Pore Rows	8	6–10 (8 ± 1)	9–11 (10 ± 1)	9–11 (10 ± 1)	8–13 (10 ± 2)	13–21 (16 ± 2)	6–8 (7 ± 1)	5–12 (9 ± 3)	4–7 (6 ± 1)
Lamellae Under Fourth Toe	28	25–32 (29 ± 2)	26–29 (28 ± 2)	30–34 (32 ± 2)	24–30 (27 ± 2)	29–33 (31 ± 1)	23–28 (25 ± 2)	21–24 (23 ± 1)	21–25 (23 ± 1)
Tail Length/ SVL	Not Available	2.1–2.4 (2.3 ± 0.1, *n* = 4)	Not Available	2–2.2 (2.1 ± 0.1, *n* = 3)	2.1–2.2 (2.2 ± 0.1, *n* = 3)	2.3 (*n* = 1)	2.3–2.5 (2.4 ± 0.1, *n* = 4)	2.1–2.6 (2.3 ± 0.2, *n* = 5)	2.4 (*n* = 1)

Supralabials 12–15; first supralabial smaller than or subequal to second, its ventral margin straight to curved; infralabials 10–13; first pair of chinshields broadly contacting infralabials and forming a medial suture of variable length (infrequently partially separated from infralabials by row of small granular scales in some specimens of *Holcosus septemlineatus* Group); interangular sulcus absent; anterior gulars 18–30 (24–60 in *H. septemlineatus*

Group); gular patch present (most Central American species) or absent (*Holcosus orcesi*, *H. septemlineatus* Group, and some *H. quadrilineatus*); posterior gulars 7–22; intertympanic sulcus absent; larger anterior gulars undergoing sharp transition to smaller posterior gulars at intertympanic crease (*H. orcesi* and *H. undulatus* Groups) or gulars uniform in size with no evident transition to smaller posterior gulars at intertympanic crease (*H. septemlineatus* Group); in most species mesoptychials greatly to moderately enlarged, forming differentiated transverse row (not to slightly enlarged in *H. anomalus* and *H. bridgesii*); when present, gular fold lacking serrated edge.

Dorsals smooth (*Holcosus orcesi* and *H. undulatus* Groups) or keeled (*H. septemlineatus* Group); scales on flank subequal to middorsals, projecting laterally and supported by large apical granules (*H. undulatus* Group) or subpyramidal (*H. septemlineata* Group); scales on rump much smaller than proximal subcaudals; scales of chest large and flat (small, granular, and weakly keeled in *H. anomalus*); pectoral sulcus absent; ventrals smooth, in 25–32 transverse and six (*H. septemlineatus* Group) or eight (*H. undulatus* and *H. orcesi* Groups) longitudinal rows; lateral-most ventrals flanked by small scales (i.e., ventrals not gradually decreasing in size on flanks); preanals 5–17; preanal plate present, bordered by small granular (larger subtriangular scales in *Holcosus chaitzami* and *H. undulatus*) scales; preanals paired and small, less than one-half as large as scale anterior to them (except *H. chaitzami, H. undulatus,* and female *H. quadrilineatus*); preanal spurs and postcloacal buttons absent; postanal plates present in males; dorsolateral row of caudals with laterally projecting mucrons forming denticulate edge; dorsolateral crests absent; caudal annuli complete; proximal subcaudals smooth (most species) or keeled (*H. anomalus* and *H. bridgesii*).

Enlarged scales of brachium separated by small granular scales on dorsal surface of arm; preaxial brachial scales 1–2X as wide as long, extending proximally beyond middle of arm (most species) or relatively small, longer than wide, and restricted to patch near distal end of brachium (*Holcosus anomalus* and *H. bridgesii*; postaxial brachial scales 1–2X as wide as long (most species) or small and mostly longer than wide (*H. anomalus*); postaxial brachials forming patch near elbow (*H. anomalus, H. bridgesii, H. leptophrys, H. orcesi, H. quadrilineatus*) or extending beyond center of arm (remaining species); antebrachial scales enlarged and smooth, narrowly separated from or in continuous row with preaxial brachial scales; postaxial antebrachial scales granular (*H. anomalus, H. bridgesii,* and *H. quadrilineatus*), slightly enlarged (*H. festivus, H. leptophrys, H. niceforoi, H. septemlineatus,* and *H. orcesi*), or distinctly enlarged (*H. chaitzami, H. undulatus*); lamellae under fourth finger 12–19; subarticular lamellae of hand distinctly enlarged and swollen.

Prefemorals 5–10 (9–14 in *Holcosus anomalus* and *H. bridgesii*); femoral and abdominal pores 29–56, in continuous row on each side (abdominal pores not separated from femoral pores by gap, not reaching abdomen in *H. septemlineatus* Group); each compound pore-bearing scale consisting of partially fused prefemoral or abdominal scale and 2–6 granular scales; 4–21 scales separating right and left pore rows; two wide (*H. septemlineata* Group, *H. festivus, H. niceforoi,* and most *H. leptophrys*) or 3–4 large (*H. chaitzami, H. orcesi, H. quadrilineatus, H. undulatus*) scales at heel; tibiotarsal shields and spurs absent; lamellae under fourth toe 21–34; distal lamellae of fourth toe sharply keeled (except *H. orcesi*); scales between subdigital and supradigital lamellae of toes small and mostly restricted to phalangeal articulations; noticeably enlarged postaxial scales between fourth and fifth toe absent; fifth toe well-developed (*H. festivus, H. niceforoi, H. orcesi, H. quadrilineatus,* and *H. septemlineatus* Group) or shortened (*H. chaitzami, H. leptophrys,* and *H. undulatus*) so that base of claw not extending to level of skin between third and fourth toes when adpressed.

β-keratin containing layers of dorsal scales folded into macrohoneycomb (*Holcosus orcesi* and *H. undulatus* Group) or short macroridges (*H. septemlineatus* Group); dorsal and caudal scales with one subterminal lenticular scale organ; ventrals lacking scale organs; generation glands absent.

Snout same color as dorsal head scales; adult male *Holcosus festivus, H. quadrilineatus* and *H. undulatus* (at least in some populations) with sides of head, chin and throat red or orange (at least during breeding season) but color not restricted to or most conspicuous on snout. In juveniles, light vertebral stripe solid and straight (*H. festivus* and *H. septemlineatus* Group), solid anteriorly and breaking into blotches posteriorly (*H. chaitzami, H. niceforoi*) or absent (*H. leptophrys, H. quadrilineatus, H. undulatus*); light paravertebral stripes absent; dark dorsolateral field broken into blotches (condition in *H. anomalus* and *H. bridgesii* unknown); dorsolateral light stripe solid and extending to tail (*H. anomalus, H. chaitzami, H. niceforoi, H. quadrilineatus*) or broken (*H. bridgesii, H. festivus, H. leptophrys, H. septemlineatus, H. undulatus*); dark lateral field solid; upper lateral light stripe solid (*H. anomalus* and *H. quadrilineatus*) or broken and extending to groin (*H. bridgesii, H. chaitzami, H.*

festivus, H. leptophrys, H. niceforoi, H. septemlineatus H. undulatus); lower lateral light stripe absent (*H. leptophrys, H. undulatus*) or broken and extending to groin (*H. chaitzami, H. festivus, H. niceforoi, H. quadrilineatus*, and *H. septemlineatus* Group); thigh lacking light spots. In adult males, flanks lacking light spots or ocelli (adult males of *H. undulatus* have very conspicuous, wide, transverse bands on flanks); turquoise ventrolateral spots present (*H. undulatus*) or absent (*H. festivus, H. leptophrys, H. quadrilineatus, H. septemlineatus*, condition unknown in other species); venter immaculate, lacking melanic areas; juvenile dorsal color pattern present in adult males with only slight (*H. leptophrys*) to conspicuous (*H. festivus, H. H. quadrilineatus, H. septemlineatus, H. undulatus*) modification (condition of other species unclear).

Hemipenis with pair of taβ-like and smooth apical awns; apical papillae and apical basin absent; asulcate expansion pleat well-developed, interrupting 10–11 (14–26 in *Holcosus septemlineatus* Group) distal laminae; discontinuous distal laminae absent (Central American species) or 5–7 (*H. septemlineatus* Group) on asulcate side; 2–50 laminae proximal to expansion pleat; basal papillae absent.

Etymology.—Cope (1862) did not discuss the derivation of *Holcosus*. He may have been inspired by the masculine Latin noun *holcos* (from Greek *holkos*), meaning a kind of grain. The name may be a reference to the many cephalic shields that have fragmented into numerous small and, therefore, grain-like keeled scales in the type species *H. septemlineatus*. *Holcosus* is a masculine noun in the nominative singular.

Distribution.—The species of *Holcosus* extend from Mexico to trans-Andean Colombia and Ecuador.

Interspecific Relationships.—Most species of *Holcosus* have not been included in recent phylogenetic analyses of teiids. Echternacht (1971) assigned *H. festivus* and *H. leptophrys* to his Group II, characterized by relatively high numbers of femoral pores and a tendency for scales in the frontoparietal region to exhibit irregular patterns. He assigned *H. quadrilineatus, H. chaitzami,* and *H. undulatus* to his Group III characterized by nasal-prefrontal contact, a normal pattern of scales in the frontoparietal region, a color pattern that emphasizes stripes rather than spots, and a broad vertebral field lacking a vertebral stripe. Furthermore, he hypothesized that *H. undulatus* and *H. chaitzami* are more closely related to each other than either is to *H. quadrilineatus*. Finally, he appreciated that *Ameiva praesignis* (his Group I) is "farther removed phylogenetically from Groups II and III than these are from each other."

In the ordered phylogenetic analyses, *Holcosus* is a well-supported clade sister to *Aspidoscelis* (Fig. 70). The Ecuadorian endemic *H. orcesi* is the sister species of all other congeners in the ordered analysis and sister to the Central American species in the unordered analysis. Herein, we assign this species to its own species group.

Holcosus anomalus, H. bridgesii, and *H. septemlineatus* form a well-supported clade, which we refer to as the *Holcosus septemlineatus* Group. These three distinctive species share a suite of characters not present in any other *Holcosus*. Echternacht (1977) realized that *H. anomalus* is most closely related to *H. bridgesii* and *H. septemlineatus*, but he did not speculate about which of the two might be its sister species. There can be little doubt that *H. anomalus* and *H. bridgesii* are each other's closest relatives. Unlike *H. septemlineatus* (characters in parentheses), these two species share the first subocular usually separated from the supralabials by anterior expansion of the second subocular (first subocular in contact with supralabials), granular scales in front of the auditory meatus (slightly enlarged scales), not to slightly enlarged mesoptychials (greatly enlarged and forming transverse row), small preaxial brachials (enlarged), both preaxial and postaxial brachials restricted to small patch near distal end of brachium (extending to center of arm), granular postaxial antebrachials (slightly enlarged), and 9–14 prefemorals (5–7).

The three species of the *Holcosus septemlineatus* Group are restricted to humid forests of the lowlands and piedmont of western Colombia and Ecuador. Interestingly, the group bears special resemblance to *Kentropyx*. The *H. septemlineatus* Group and *Kentropyx* are the only teiids with β-keratin containing layers of the epidermis folded into macroridges. Unlike *H. orcesi* and the Central American species, the *H. septemlineatus* Group and *Kentropyx* also share keeled dorsals and a well-developed keyhole shaped depression in the parietal region.

When all characters were included in the ordered phylogenetic analysis, the *Holcosus septemlineatus* Group was deeply nested within *Holcosus* as the sister group to *H. festivus* (Fig. 70). This placement seems counterintuitive, because extreme morphological divergence of the group suggests great age. *Holcosus festivus* and the *H. septemlineatus* Group are the only congeners with a narrow light vertebral stripe in juveniles, and this character seems to be largely responsible for the surprising placement of the *H. septemlineatus* Group. When color characters were excluded from the analysis, the Central American species formed a clade sister to the *H.*

septemlineatus Group, whereas the Central American species formed a clade sister to *H. orcesi* in the unordered analysis (Fig. 70). Both hypotheses make more sense on biogeographic grounds and better account for the extreme morphological divergence of the *H. septemlineatus* Group. For these reasons, we accept monophyly of the Central American species and *H. niceforoi* as the most likely phylogeny of the group and assign these species to the *H. undulatus* Group.

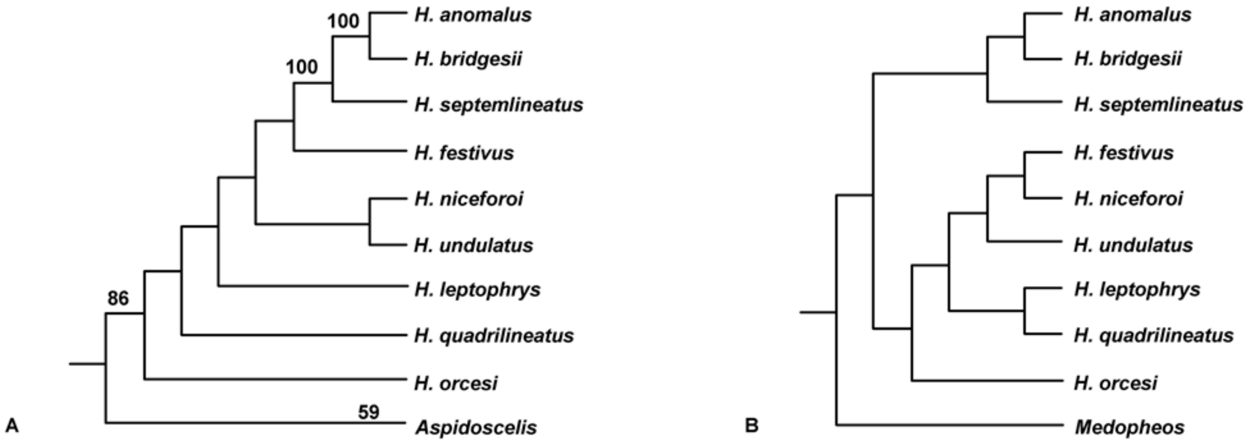

FIGURE 70. Phylogeny of *Holcosus* when all morphological characters were orderd (A) and unordered (B). Numbers above internodes are bootstrap support.

Complete absence of *Holcosus* from cis-Andean South America and their recovered phylogeny clearly point to a trans-Andean or Central American origin for the genus. The *H. septemlineatus* and *H. orcesi* Groups are old lineages that evolved in northern South America. The *H. undulatus* Group likely diversified in lower Mesoamerica with *H. festivus* and *H. niceforoi* only recently reaching the continent, perhaps after formation of the Panamanian Portal.

Holcosus niceforoi has been compared to *Holcosus festivus* (e. g., Echternacht 1970). We recovered these species as sister taxa in the unordered analysis, but found *H. niceforoi* to be closely related to *H. undulatus* in all ordered analyses. We did not examine *H. chaitzami* and did not include it in the phylogenetic analysis. Nonetheless, we examined photographs of the holotype of this species on the UMMZ website. Echternacht (1971, p. 64) remarked that, "*Ameiva chaitzami* is very closely related to *undulata*," and we suspect that he is correct. As we noted in the synopsis of characters, these species share partially divided interparietals and we did not observe this trait in congeners.

Remarks.—Peters and Donoso-Barros (1970) attribute Cope (1869a) as the author of *Holcosus* and list *H. bridgesii* as the type species. However selection of *H. bridgesii* as type species is not valid, because Cope (1869a) described it after he (1862) erected *Holcosus* to accommodate *Ameiva septemlineata* Duméril and Duméril and *A. sex-scutata* Günther (= *Holcosus septemlineatus actuorum*). Accordingly, we here designate *Ameiva septemlineata* Duméril and Duméril 1851, as type species of *Holcosus* Cope 1862.

Holcosus orcesi Group

Diagnosis.—The single species of this group ordinarily has eight longitudinal ventral rows at midbody. A fourth supraocular is normally absent, and the first supraocular is entire. Irregular, keeled scales replace the frontal, however the frontoparietals and parietals are normal. A keyhole shaped depression is absent. Large anterior gulars undergo a sharp transition at the intertympanic crease. Dorsals are smooth and covered in macrohoneycomb. Discontinuous distal laminae are absent.

Content.—*Holcosus orcesi*.

Distribution.—*Holcosus orcesi* is endemic to western Ecuador.

Holcosus septemlineatus **Group**

Diagnosis.—Species of the *Holcosus septemlineatus* Group normally have six longitudinal rows of ventrals at midbody, reducing to two large plates in front of the preanals. A fourth supraocular is normally absent, and the first supraocular is fractured into three or more keeled scales (similar fracturing only occurs in *Callopistes*), leaving 2/2 discrete supraoculars. The frontal, frontoparietals, parietals, and occipitals are all heavily fragmented into keeled scales. Keels of the frontoparietal region form a distinct keyhole shaped depression. Anterior and posterior gulars are similar in size and an intertympanic crease is absent. Dorsals are keeled and covered in aligned macroridges. The hemipenis has 5–7 discontinuous distal laminae.

Content.—*Holcosus anomalus*, *Holcosus bridgesii*, and *Holcosus septemlineatus*.

Distribution.—The three species of the *Holcosus septemlineatus* Group occur in the lowlands and piedmont of western Colombia and Ecuador.

Holcosus undulatus **Group**

Diagnosis.—Species of the *Holcosus undulatus* Group have eight longitudinal rows of ventrals at midbody. A fourth supraocular is usually absent, however the first supraocular is discrete. The dorsal head plates are not heavily fragmented, although small scales may separate some of the parietals in *H. leptophrys*. A keyhole shaped depression is absent. Larger anterior gulars undergo a sharp transition to smaller posterior gulars at the intertympanic crease. The dorsals are smooth and covered in macrohoneycomb. The hemipenis lacks discontinuous distal laminae.

Content.—*Holcosus chaitzami*, *Holcosus festivus*, *Holcosus leptophrys*, *Holcosus niceforoi*, *Holcosus quadrilineatus*, and *Holcosus undulatus*.

Distribution.—Species of the *Holcosus undulatus* Group extend from Central Mexico to Colombia.

Kentropyx **Spix**

Figure 71

Kentropyx Spix 1825: 21. Type species *Kentropyx calcaratus* Spix by monotypy.
Pseudameiva Fitzinger 1826: 21. Type species *Lacerta striata* Daudin by monotypy.
Trachygaster Wagler 1830: 154. Type species *Kentropyx calcaratus* Spix.
Acanthopyga Gray 1838:278. Type species *Lacerta striata* Daudin by monotypy.

Diagnosis.—*Kentropyx* is the only genus of teiids with scales between the digital lamellae continuing as a row of enlarged scales between the fourth and fifth toe and relatively long, apical papillae on the lobes of the hemipenis. Unlike all other Teiidae, *Kentropyx* apparently lacks visible subterminal lenticular scale organs on its dorsals and caudals. No other Teiinae has keeled ventrals (also in *Dracaena*) or relatively small, keeled antebrachials (small antebrachials that are either keeled or smooth occur in *Callopistes* and the various genera of Tupinambinae). Unlike other Teiinae, *Kentropyx* lacks a subocular keel or has a weak keel restricted to the first and second subocular, but not extending to the long subocular below the eye.

Content.—*Kentropyx altamazonica* Cope, *Kentropyx borkiana* Peters, *Kentropyx calcarata* Spix, *Kentropyx lagartija* Gallardo, *Kentropyx paulensis* Boettger, *Kentropyx pelviceps* Cope, *Kentropyx striata* (Daudin), *Kentropyx vanzoi* Gallagher and Dixon, *Kentropyx viridistriga* Boulenger.

Definition.—Small to medium lizards reaching 127 (*Kentropyx striata*) mm SVL; tail 2.0–2.5X (Table 14) as long as body; posterior maxillary and dentary teeth longitudinally compressed, tricuspid; pupil reniform.

Prefrontal separated from nasal, usually separated from first supraciliary; frontal entire, lacking longitudinal ridge, its posterior suture contacting second supraocular; scales of frontoparietal region smooth, with well-developed key-hole shaped depression absent; frontoparietals paired; parietals consisting of three regular scales; interparietal entire; medial pair of enlarged occipitals usually present; occipitals 10–20, usually larger than first row of dorsals; supratemporals slightly to moderately enlarged, separated from parietals by one or more scales.

TABLE 14. Meristic data of *Kentropyx* examined by us. Means ± standard deviation follow ranges.

	Kentropyx pelviceps (*n* = 11)	*Kentropyx calcarata* (*n* = 2)	*Kentropyx altamazonica* (*n* = 13)	*Kentropyx viridistriga* (*n* = 3)	*Kentropyx lagartija* (*n* = 10)	*Kentropyx vanzoi* (*n* = 2)	*Kentropyx borkiana* (*n* = 10)	*Kentropyx striata* (*n* = 8)
Occipitals	12–15 (14 ± 1)	16	12–20 (15 ± 2)	11–13	10–12 (12 ± 1)	12–14	10–12 (11 ± 1)	10–13 (11 ± 1)
Lateral Supraocular Granules	25–52 (34 ± 8)	26–33	15–39 (22 ± 6)	31–48	23–39 (29 ± 6)	39–56	31–41 (36 ± 3)	12–20 (16 ± 3)
Circumorbitals	0–6 (4 ± 2)	2–4	4–7 (6 ± 1)	4	4	4–6	4–5 (4 ± 0)	4–6 (4 ± 1)
Supraciliaris	8–10 (10 ± 1)	10	8–10 (10 ± 1	10	10	10–11	8–10 (9 ± 1)	8
Supralabials	12	12–13	12–14 (12 ± 1)	12–14	12–13 (12 ± 0)	12	12	12
Infralabials	10–12 (11 ± 1)	12	10–14 (12 ± 1)	10–12 (11 ± 1)	10–12 (11 ± 1)	12	11–13 (12 ± 0)	10
Anterior Gulars	22–30 (25 ± 3)	23–28	25–35 (31 ± 3)	22–23	18–25 (23 ± 2)	25	21–27 (23 ± 2)	19–26 (23 ± 2)
Posterior Gulars	6–12 (10 ± 2)	11–13	10–16 (12 ± 2)	7–9	8–11 (9 ± 1)	7–10	9–12 (10 ± 1)	7–10 (9 ± 1)
Transverse Ventral Rows	31–32 (31 ± 1)	32	31–35 (33 ± 1)	32–34 (33 ± 1)	34–41 (38 ± 2)	33	30–33 (32 ± 1)	31–34 (33 ± 1)
Longitudinal Ventral Rows	14	14	14	14	14	12–14	14–16 (16 ± 1)	14–16 (14 ± 1)
Preanals	4–6 (5 ± 0)	5	4–6 (5 ± 1)	4–5	5–6 (5 ± 0)	4–5	4–5 (5 ± 0)	4–5 (4 ± 0)
Lamellae Under Fourth Finger	17–18 (18 ± 0)	16–17	17–19 (18 ± 1)	14–16	14–17 (16 ± 1)	14–16	17–19 (18 ± 1)	15–18 (17 ± 1)
Prefemorals	13–18 (15 ± 1)	18–19	14–17 (15 ± 1)	10	10–13 (12 ± 1)	11–12	12–14 (13 ± 1)	8–10 (9 ± 1)
Femoral and Abdominal Pores	36–43 (40 ± 3)	38–40	28–36 (32 ± 2)	18–19	22–28 (25 ± 2)	19–21	24–27 (26 ± 1)	12
Scales Separating Pore Rows	2–5 (4 ± 1)	4	4–7 (5 ± 1)	4	3–5 (4 ± 1)	4	4–5 (4 ± 0)	4–5 (4 ± 1)
Lamellae Under Fourth Toe	24–27 (26 ± 1)	26–28	25–29 (27 ± 2)	21–22	23–26 (25 ± 1)	23–24	25–28 (26 ± 1)	23–28 (26 ± 2)

Rostral groove absent; nostril oval and oriented anteroventrally, its position relative to nasal suture varying among species; loreal single; supraoculars six (rarely eight); first supraocular entire, usually broadly contacting second supraocular (*Kentropyx altamazonica*, *K. borkiana*, *K. calcarata*, *K. pelviceps*, *K. striata*) or frequently partially to completely separated from second supraocular (*K. lagartija*, *K. vanzoi*, *K. viridistriga*); circumorbital semicircles consisting of 0–7 (usually 4) small scales, extending to posterior border of third supraocular or slightly in front of its posterior border; supraciliaries 8–11, separated from supraoculars by 1–2 rows of 12–56 granular scales; first supraciliary long, greater than one-half as long as second; subocular keel absent (most species) or weak and restricted to suboculars 1 and 2 (*K. striata*); suboculars four (rarely 5); first subocular entire, contacting first supraciliary, contacting supralabials or separated from them by anterior expansion of second supralabial (rarely separated from supralabials by scale inserted between suboculars and loreal); patch of slightly to distinctly enlarged scales in front of auditory meatus; auricular flap and preauricular fold absent.

FIGURE 71. Adult *Kentropyx altamazonica* from Iquitos, Peru (A, photo by W. Lamar) and from Parque Nacional Cordillera Azul, San Martín, Peru (B, photo by P. Venegas); *K. calcarata* from Para, Brazil (C, photo by P. Bernardo); *K. paulensis* from Brazil (D, photo by C. Medolago); *K. pelviceps* from Zona Reservada Gueppi, Loreto, Peru (E, photo by P. Venegas); *K. striata* from Apure, Venezuela (F, photo by C. L. Barrio-Amorós). Note particularly prominent keyhole-shaped depressions in parietal regions of specimens in figures E and F.

Supralabials 12–14; first supralabial usually subequal to second, its ventral margin straight; infralabials 10–14; first pair of chinshields broadly contacting infralabials, forming medial suture of variable length, separated medially by small granular scales in *Kentropyx lagartija* and many *K. pelviceps* and *K. viridistriga*; interangular sulcus absent; anterior gulars 18–35; gular patch present (*K. borkiana, K. striata*) or absent (all other species); posterior gulars 6–16; intertympanic sulcus absent; anterior and posterior gulars subequal, not undergoing transition at intertympanic crease; mesoptychials distinctly (*K. striata*) to moderately (all other species) enlarged, not forming differentiated transverse row; gular fold lacking serrated edge.

Dorsals keeled; not projecting laterally, supported by small apical granules; scales on flank much smaller than (*Kentropyx borkiana, K. striata*) or subequal to (all other species) middorsals; scales on rump much smaller (*K. altamazonica, K. calcarata, K. pelviceps*) or slightly smaller (*K. borkiana, K. lagartija, K. striata, K. vanzoi, K. viridistriga*) than proximal subcaudals; scales of chest large, keeled; pectoral sulcus absent; ventrals keeled, mucronate, in 31–41 transverse and 12–16 (usually 14) longitudinal rows; lateral-most ventrals flanked by small scales (i.e., ventrals not gradually decreasing in size on flanks); preanals 4–6 (usually 4 or 5); preanal plate present, consisting of keeled scales similar to ventrals; preanal spurs 2/2, each narrow and attenuate, extending next to body, separated from preanal plate by large (i.e., as long as base length of spur) scales; small vestigial spur usually present, positioned above and behind larger spurs; postcloacal buttons and postanal plates absent; scales on dorsolateral edge of tail like those on top and sides, denticulate edge and dorsolateral crests absent; caudal annuli complete; proximal subcaudals keeled.

Dorsal surface of arm covered by enlarged, subtriangular, keeled scales; preaxial and postaxial brachial scales longer than wide; preaxial antebrachial scales relatively small, subtriangular, keeled; postaxial antebrachial scales granular (*Kentropyx altamazonica*) to slightly enlarged (all other species); subdigital lamellae of hand homogeneous (*K. altamazonica*, *K. striata*), heterogeneous with noticeably larger subarticular lamellae (*K. borkiana, K. calcarata, K. pelviceps*), or with mostly divided subarticular lamellae (*K. lagartija, K. vanzoi, K. viridistriga*), 14–19 under fourth finger.

Prefemorals 8–19; femoral and abdominal pores 12–43 in continuous row on each side (abdominal pores not separated from femoral pores by gap); each compound pore-bearing scale consisting of partially fused prefemoral or abdominal scale and 2–6 granular scales; 2–7 scales separating right and left pore rows; scales at heel small and numerous; tibiotarsal shields and spurs absent; lamellae under fourth toe 21–29; distal lamellae of fourth toe smooth (*Kentropyx lagartija*, *K. viridistriga*) or keeled (all other species); scales between subdigital and supradigital lamellae of toes serrate (*K. lagartija*, *K. viridistriga*, *K. vanzoi*) or denticulate (*K. altamazonica*, *K. borkiana*, *K. calcarata*, *K. pelviceps, K. striata*), continuing as row of noticeably enlarged postaxial scales between fourth and fifth toe; fifth toe well-developed, base of its claw extending beyond level of skin between third and fourth toes when adpressed.

β-keratin containing layers of dorsal scales folded into short macroridges; dorsal, ventral, and caudal scales lacking apparent subterminal lenticular scale organ (although lenticular scale organs present on scales of head and neck); generation glands absent.

Snout same color as dorsal head scales, some specimens of *Kentropyx calcarata* with red heads but color not restricted to snout. In juveniles, light vertebral stripe solid and straight (*Kentropyx altamazonica*, *K. calcarata*, *K. vanzoi*), widening substantially on posterior body (*K. lagartija, K. pelviceps, K. viridistriga*), or absent (*K. striata*); light paravertebral stripes absent; dark dorsolateral field solid (*K. vanzoi*, *K. viridistriga*), solid anteriorly and breaking into blotches posteriorly (*K. pelviceps, K. striata*), or absent (*K. altamazonica*); dorsolateral light stripe solid and extending to tail (*K. altamazonica*), fading towards head or sacrum (*K. lagartija*, *K. vanzoi*, *K. viridistriga*), or absent (*K. calcarata, K. pelviceps, K. striata*); dark lateral field solid (most species) or absent (*K. pelviceps*); upper lateral light stripe extending above leg (most species) or solid and extending to groin (*K. altamazonica*); lower lateral light stripe solid to groin (*K. lagartija, K. striata, K. vanzoi, K. viridistriga*), broken and extending to groin (*K. calcarata*), or absent (*K. altamazonica*, *K. pelviceps*); thigh lacking light spots. In adult males, light spots on flanks absent (most species) or small and numbering around 17 (*K. calcarata*), 35 (*K. pelviceps*) or 36 (*K. striata*); turquoise ventrolateral spots absent; venter immaculate, lacking melanic areas; juvenile dorsal color pattern present in adult males with only slight to moderate modification (*K. altamazonica*, *K. pelviceps*, *K. striata*, *K. vanzoi*) or completely absent (*K. calcarata*, *K. lagartija*, and *K. viridistriga*).

Hemipenis lacking apical awns and circular apical basin; relatively long apical papillae present, densest between lobes where they interrupt sulcus; asulcate expansion pleat absent; about 26–35 (based on two species) laminae encircling body of organ, interrupted; basal papillae absent.

Etymology.—Kentropyx is a feminine noun in the nominative singular derived from the Greek words *kentron* meaning spur and *pyxos* meaning box. The name is likely an allusion to the preanal spurs in species of this genus.

Distribution.—Cis-Andean South America, Barbados, and Trinidad.

Interspecific Relationships.—Gallagher and Dixon (1980, 1992) recognized three species groups within *Kentropyx*. In our survey of morphological characters, we identified additional characters that strengthen the diagnoses of these groups. These characters proved useful in species identification and will likely aid in the diagnosis of undescribed species of this genus.

The phylogeny of *Kentropyx* (Fig. 72) has been investigated using morphology (this study; Werneck *et al.* 2008), mtDNA (Werneck *et al.* 2008), and combined mtDNA and allozymes (Reeder *et al.* 2002). Each analysis recovered the species groups proposed by Gallagher and Dixon (1980; 1992). However, the phylogenies differ in both the relationships among and within groups. Interestingly, three previous hypotheses have strong bootstrap support for all branches (Fig. 72), even though the topologies are considerably different from one another.

Remarks.—Herein, we make one correction to the synonymy of *Kentropyx:* Gray proposed the junior synonym *Acanthopyga* in 1838 rather than in his later *Catalogue* (Gray 1845) as thought by Peters and Donoso-Barros (1970).

Kentropyx calcarata Group

Definition.—The following list of characters distinguishes the *Kentropyx calcarata* Group from other *Kentropyx*: scales on flanks gradually increasing in size middorsally where they are relatively small (no sharp transition to large middorsal scales); scales on rump much smaller than proximal caudals; prefemorals 13–19; femoral and abdominal pores (both sides combined) 27–43 (20–49 in samples of Werneck *et al.* 2008); subarticular lamellae of hands usually entire; scales between pedal lamellae large and denticulate; lower lateral stripe broken or absent.

Content.—Kentropyx altamazonica Cope, *Kentropyx calcarata* Spix, *Kentropyx pelviceps* Cope.

Distribution.—The *Kentropyx calcarata* Group occurs primarily in forested habitats of Amazonia, the Guianas, and the Atlantic Forests of Brazil.

Remarks.—For many years, Neotropical herpetologists have struggled to distinguish *Kentropyx altamazonica* from *K. calcarata*. In their key, Gallagher and Dixon (1992) used striping pattern to distinguish these species, however the stripes often completely fade in older specimens and may not be visible in badly preserved material. As mentioned in our synopsis of characters, Avila-Pires (1995) included differences in subdigital lamellae and development of the pedal fringe in her key. To these characters, we would add that the first subocular contacts the supralabials in *K. altamazonica*, whereas it appears to be separated from the supralabials by anterior expansion of the second subocular in *K. calcarata*. Nonetheless, our sample of *K. calcarata* is small and this character may be more variable than we realize.

Kentropyx paulensis Group

Definition.—The following list of characters distinguishes the *Kentropyx paulensis* Group from other *Kentropyx*: scales on flanks gradually increasing in size middorsally where they are relatively small (no sharp transition to large middorsal scales); scales on rump slightly smaller than proximal caudals; prefemorals 10–13; femoral and abdominal pores 18–28 (6–28 in samples examined by Werneck *et al.* 2008); subarticular lamellae of hands usually divided; scales between pedal lamellae moderate and serrate; lower lateral stripe solid to groin.

Content.—Kentropyx paulensis Boettger, *Kentropyx vanzoi* Gallagher and Dixon, *Kentropyx viridistriga* Boulenger (including *Kentropyx lagartija* Gallardo). In addition to these species Werneck *et al.* (2009) have apparently identified a still undescribed species of the *K. paulensis* Group.

Distribution.—Species of the *Kentropyx paulensis* Group occur in open formations of Argentina, Bolivia, Brazil, and Paraguay.

Remarks.—Gallagher and Dixon (1992) considered *Kentropyx lagartija* to be a synonym of *K. viridistriga*, and their action was followed by Werneck *et al.* (2008). Although we treated these species as separate taxa in this analysis, we found few characters to separate them (Table 14). Our three specimens of *K. viridistriga* have more lateral supraoculars and fewer femoral pores and fourth toe lamellae than the 10 *K. lagartija* we examined, but the differences are slight and may disappear with larger sample sizes. Ranges of lateral supraoculars are broader for some species than the combined ranges of lateral supraoculars in *K. viridistriga* and *K. lagartija*.

Kentropyx striata Group

Definition.—The following combination of characters distinguishes the *Kentropyx striata* Group from other *Kentropyx*: at midbody, scales on flanks much smaller and strongly differentiated from enlarged middorsal scales; scales on rump slightly smaller than proximal caudals; prefemorals 8–10; femoral and abdominal pores 18–28 (10–16 in samples examined by Werneck *et al.* 2008); subarticular lamellae of hands homogeneous, usually entire; scales between pedal lamellae large and denticulate; lower lateral stripe solid to groin.

Content.—Kentropyx striata (Daudin)

Remarks.—Gallagher and Dixon (1980, 1992) included *Kentropyx borkiana* in the *K. striata* Group, because like *K. striata* this species has enlarged middorsal scales sharply differentiated from scales on the flanks. *Kentropyx borkiana* is a parthenogenetic species likely resulting from hybridization between *K. calcarata* and *K. striata* (Cole *et al.* 1995; Reeder *et al.* 2002). Not surprisingly, this species is morphologically intermediate between these species. Like *K. striata*, *K. borkiana* has large differentiated middorsals, however like *K. calcarata* the subarticular lamellae of the hands of *K. borkiana* are swollen. Counts of prefemorals and femoral pores in *K. borkiana* are intermediate between those of *K. calcarata* and *K. striata* (Table 14).

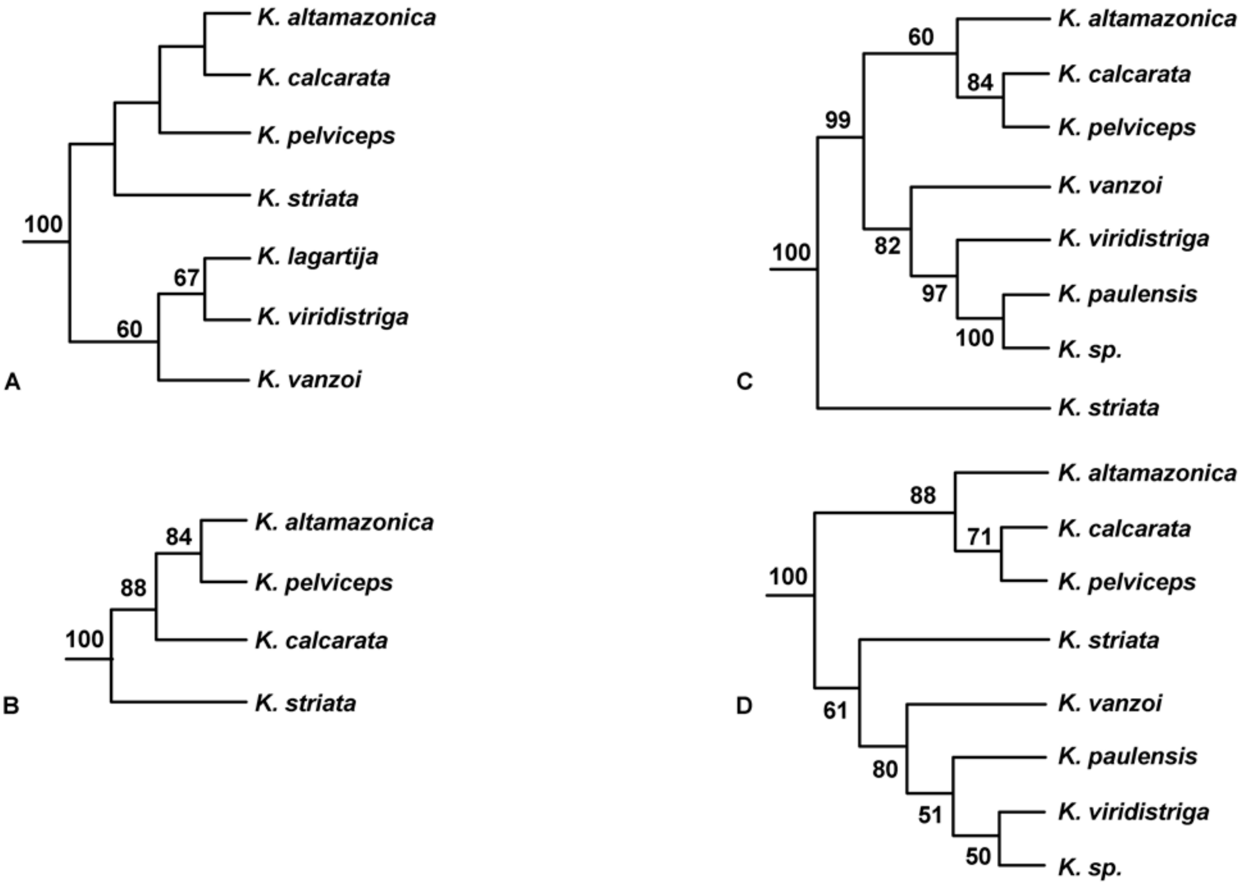

FIGURE 72. Phylogeny of *Kentropyx* based on morphology in our study (A, all characters ordered) and that of Werneck *et al.* (D, 2008, their figure 2A) compared to phylogenies based primarily on allozymes and mtDNA (B, Reeder *et al.* 2002, their figure 3) or just mtDNA (C, Werneck *et al.* 2008, their figure 3A). In all trees, numbers indicate bootstrap support.

Medopheos New Genus

Figure 73

Type Species.—*Ameiva edracantha* Bocourt by monotypy.

Diagnosis.—*Medopheos* differs from all other Teiidae in having a cluster of 5–6 preanal spurs on either side of the vent in males. Unlike mainland *Ameiva* (characters in parentheses), *Medopheos* has ventrals in 8 longitudinal rows at midbody (10), large triangular scales on the dorsal surface of the brachium (granular), and three relatively large subequal scales at the heel (scales at heel small and numerous). Unlike *Holcosus*, *Medopheos* also has five parietals (three, except in the *H. septemlineatus* Group where the parietals are heavily and irregularly fractured), a rostral groove (absent except in *H. niceforoi*), homogeneous subdigital lamellae on the hands (subarticular lamellae swollen), and smooth distal lamellae of the fourth toe (sharply keeled). *Medopheos* lacks postanal plates and a dorsolateral row of serrated caudals (both present in *Holcosus*).

Content.—*Medopheos edracanthus* (Bocourt).

Definition.—Small lizards reaching 94 mm SVL; tail about 2.2X as long as body; posterior maxillary and dentary teeth longitudinally compressed, tricuspid; pupil reniform.

Prefrontal separated from nasal, in contact with first supraciliary; frontal entire, lacking longitudinal ridge, its posterior suture contacting second or third supraocular or suture between them; scales of frontoparietal region smooth, outwardly convex to flat; frontoparietals fused (70% *n* = 10) or paired (30%); parietals consisting of five regular scales; interparietal entire, smaller to larger than flanking parietals; medial pair of enlarged occipitals absent; occipitals 13–17, usually (90%, *n* = 10) larger than first row of dorsals; supratemporals slightly to moderately enlarged, in contact with or separated from parietals by one or more scales.

FIGURE 73. Adult male *Medopheos edracanthus* from Parque Nacional Machililla, Manabí, Ecuador (A, photo by M. B. Harvey) and adult female from Olmos, Lambayeque, Peru (B, photo by P. Venegas) , illustrating marked sexual dichromatism in this species.

Rostral groove present; nostril oval and oriented anteroventrally, usually (70%, *n* = 10) mostly anterior to but in contact with nasal suture, less frequently centered in (20%) or somewhat posterior to suture (10%); loreal single; supraoculars 6 (60%, *n* = 10) or 8 (40%); first supraocular entire, larger than fourth supraocular, and broadly contacting second supraocular; circumorbital semicircles consisting of 2–7 small scales, extending anteriorly to position medial to third supraocular, usually slightly beyond suture between third and fourth supraoculars; supraciliaries 12–15, separated from supraoculars by single row of 19–32 granular scales; first and second supraciliaries small, third (infrequently fourth) elongate; angulate keel extending from first subocular to elongate subocular below eye; suboculars four (rarely 5); first subocular entire, usually (70%, *n* = 10) contacting first supraciliary, contacting supralabials (50%, *n* = 10) or separated from supralabials by anterior expansion of second subocular; patch of distinctly enlarged scales in front of auditory meatus; auricular flap and preauricular fold absent.

Supralabials 14; first supralabial smaller than second, its ventral margin curved; infralabials 12 (rarely 13); first pair of chinshields broadly contacting infralabials and forming medial suture greater than or equal to half their length; interangular sulcus absent; anterior gulars 13–21; gular patch absent; posterior gulars 10–12; intertympanic sulcus absent; larger anterior gulars undergoing sharp transition to smaller posterior gulars at intertympanic crease; mesoptychials moderately enlarged; gular fold lacking serrated edge.

Dorsals smooth; scales on flank subequal to middorsals, not projecting laterally, supported by small apical granules; scales on rump much smaller than proximal subcaudals; scales of chest large and flat; pectoral sulcus absent; ventrals smooth, in 27–31 transverse and eight longitudinal rows; lateral-most ventrals flanked by small scales (i.e., ventrals not gradually decreasing in size on flanks); preanals 3–5 (usually 4); preanal plate present, bordered by subtriangular scales; preanals one-half as large to larger than scale anterior to them; preanal spurs 5–6, each distinctly large at base and short, projecting away from body; three (rarely four) longitudinal rows of small scales separating spurs from preanal plate; postcloacal buttons and postanal plates absent; scales on dorsolateral edge of tail like those on top and sides, serrated edge and dorsolateral crests absent; caudal annuli complete; proximal subcaudals smooth.

Enlarged scales of brachium connected by continuous band of enlarged subtriangular plates on dorsal surface of arm; preaxial and postaxial brachial scales 1.5–2X as wide as long; preaxial scales extending to or beyond center of arm; postaxial scales extending to center of arm or restricted to patch at elbow; antebrachial scales enlarged and smooth, narrowly separated from or in continuous row with preaxial brachial scales; postaxial antebrachial scales slightly enlarged; subdigital lamellae of hand homogeneous in size, 14–17 under fourth finger.

Prefemorals 5–7; femoral and abdominal pores 24–26 in continuous row on each side (abdominal pores not separated from femoral pores by gap); each compound pore-bearing scale consisting of partially fused prefemoral or abdominal scale and 2–6 granular scales; 2–4 scales separating right and left pore rows; three relatively large, subequal scales at heel; tibiotarsal shields and spurs absent; lamellae under fourth toe 24–29; distal lamellae of fourth toe smooth; scales between subdigital and supradigital lamellae of toes small and mostly restricted to phalangeal articulations; noticeably enlarged postaxial scales between fourth and fifth toe absent; fifth toe well-developed, base of its claw extending beyond level of skin between third and fourth toes when adpressed.

β-keratin containing layers of dorsal scales folded into macrohoneycomb; dorsal and caudal scales with one subterminal lenticular scale organ; ventrals lacking scale organs; generation glands absent.

Snout same color as dorsal head scales. In juveniles, light vertebral stripe solid and straight; light paravertebral stripes broken into blotches (sometimes rather inconspicuous); dark dorsolateral field absent; dorsolateral light stripe solid and extending to tail; dark lateral field solid (adult males often with bright green spots within lateral field); upper and lower lateral light stripes broken and extending to groin, sometimes upper stripe mostly solid but always broken at some points along length; thigh lacking light spots. In adult males, flanks lacking light spots or ocelli; turquoise ventrolateral spots absent; venter immaculate, lacking melanic areas; juvenile dorsal color pattern present in adult males with only slight modification.

Hemipenis with pair of taβ-like and smooth apical awns; apical papillae and apical basin absent; asulcate expansion pleat well-developed, interrupting about 14 distal laminae; discontinuous distal laminae absent; about 2 laminae proximal to expansion pleat; basal papillae absent.

Etymology.—Medopheos is a masculine noun in the nominative singular derived from the Greek noun *medea* meaning genitalia and *pheos*, a term used to refer to certain spiny plants. The name alludes to the distinctive cluster of 5–6 preanal spurs on either side of the vent of males.

Distribution.—Medopheos edracanthus occurs west of the Andes in Ecuador and Peru.

***Teius* Merrem**
Figure 74

Teius Merrem 1820: 60. Type species *Teius viridis* Merrem (= *Teius teyou*) subsequently designated by Burt and Burt (1933). [Genus spelled *Tejus* in German text and *Teius* in parallel Latin text of same publication]
Acrantus Wagler 1830: 154. Type species *Lacerta teyou* Daudin.

Diagnosis.—Teius is the only genus of Teiidae with a vestigial fifth toe and a high-walled, circular basin positioned between the hemipenial awns. *Dicrodon* and *Teius* are the only other extant Teiidae with bicuspid, transversely oriented teeth on the posterior maxilla and mandible.

Content.—Teius oculatus (d'Orbignyi & Bibron), *Teius suquiensis* Avila and Martori, and *Teius teyou* (Daudin).

FIGURE 74. Adult male *Teius oculatus* from Rivera, Uruguay (A) and adult female from Bagé, Rio Grande do Sul, Brazil (B, both photos by A. Kwet).

Definition.—Medium lizards reaching 144 mm SVL; tail about 2.2–2.4X as long as body (Table 12); posterior maxillary and dentary teeth transversely compressed, bicuspid; pupil reniform.

Prefrontal in contact with nasal, usually separated from first supraciliary; frontal usually entire, with longitudinal ridge, its posterior suture contacting third supraocular or, rarely, suture between second and third supraoculars; scales of frontoparietal region smooth, outwardly convex to flat (key-hole shaped depression absent);

frontoparietals paired; parietals short, arrayed in oblique rows and separated by small scales (*Teius teyou*) or consisting of three regular scales (*T. oculatus*); interparietal entire; medial pair of enlarged occipitals absent; occipitals 13–15 (*T. oculatus*; character not applicable to *T. teyou*), usually larger than first row of dorsals; supratemporals slightly to moderately enlarged, separated from parietals by several rows of small granular scales.

Rostral groove absent (faint indication of groove in some *Teius teyou*); nostril oval and oriented anteroventrally, positioned anterior to and not touching nasal suture; loreal single; supraoculars usually eight; first supraocular entire, larger than fourth supraocular, separated from second by complete row of small scales; circumorbital semicircles consisting of 26–35 small scales, extending to posterior border of first supraocular; supraciliaries 12–14, subequal in size, separated from supraoculars by 1.5–2.5 rows of 44–100 granular scales; first supraciliary separated from (*T. teyou*) or usually in contact with (*T. oculatus*) first supraocular; angulate keel extending from first subocular to elongate subocular below eye; suboculars four; first subocular usually separated from supralabials by scale inserted between suboculars and loreal; patch of slightly to distinctly enlarged scales in front of auditory meatus; auricular flap and preauricular fold absent.

Supralabials 13–17; first supralabial smaller than (*Teius teyou*) or subequal to (*T. oculatus*) second, its ventral margin curved to "toothy"; infralabials 12–15; first pair of chinshields broadly contacting infralabials, forming medial suture of variable length; interangular sulcus absent; anterior gulars 19–34; gular patch absent; posterior gulars 8–18; intertympanic sulcus absent; larger anterior gulars undergoing sharp transition to smaller posterior gulars at intertympanic crease; mesoptychials moderately enlarged; gular fold lacking serrated edge.

Dorsals smooth; scales on flank subequal to middorsals, supported by moderate apical granules; scales on rump much smaller than proximal subcaudals; scales of chest large and flat; pectoral sulcus absent; ventrals smooth, in 32–35 transverse and eight (*T. teyou*) or ten (*T. oculatus*) longitudinal rows; lateral-most ventrals flanked by small scales (i.e., ventrals not gradually decreasing in size on flanks); preanals 4–5; preanal plate present, bordered by subtriangular scales; preanals one-half as large to larger than scale anterior to them; preanal spurs, postcloacal buttons, and postanal plates absent; scales on dorsolateral edge of tail like those on top and sides, denticulate edge and dorsolateral crests absent; caudal annuli complete; proximal subcaudals keeled (*T. teyou*) or smooth (*T. oculatus*).

Enlarged scales of brachium connected by continuous band of small subtriangular scales on dorsal surface of arm; preaxial brachial scales usually 1.5–2X as wide as long, extending proximally to or beyond center of arm; postaxial brachial scales 1–1.5X as wide as long, restricted to small patch near elbow; antebrachial scales enlarged and smooth, narrowly separated from or in continuous row with preaxial brachial scales; postaxial antebrachial scales granular; subdigital lamellae of hand homogeneous in size, 13–17 under fourth finger.

Prefemorals 6–11; femoral and abdominal pores 30–48, in continuous row on each side (abdominal pores not separated from femoral pores by gap); each compound pore-bearing scale consisting of partially fused prefemoral or abdominal scale and 2–6 granular scales; 2–4 scales separating right and left pore rows; scales at heel relatively small and numerous; tibiotarsal shields and spurs absent; lamellae under fourth toe 27–40; distal lamellae of fourth toe smooth; continuous low serrate row of scales separating subdigital and supradigital lamellae along postaxial edge of each toe; noticeably enlarged postaxial scales between fourth and fifth toe absent; fifth toe vestigial, reduced to small nub.

β-keratin containing layers of dorsal scales folded into macrohoneycomb; dorsal and caudal scales with one subterminal lenticular scale organ; ventrals lacking scale organs; generation glands present.

Snout same color as dorsal head scales. In juveniles, light vertebral stripe absent; light paravertebral stripes absent (*Teius oculatus*, *T. suquiensis*) or present and solid, although tending to fade anteriorly (*T. teyou*); dark dorsolateral field completely broken into blotches, although partially solid in some specimens of *T. teyou*; dorsolateral light stripe solid, extending to tail; dark lateral field completely broken into blotches; upper lateral light stripes mostly solid (usually breaking into spots near insertion of forelimb), extending to groin; lower lateral light stripe absent; thigh lacking light spots. In adult males, flanks lacking light spots (*T. oculatus*), or with light blotches (*T. teyou*); turquoise ventrolateral spots present; venter immaculate, lacking melanic areas; juvenile dorsal color pattern present in adult males with only slight (*T. oculatus*, *T. suquiensis*) to moderate (*T. teyou)* modification. Hemipenis with pair of taβ-like and smooth apical awns; apical papillae absent; circular apical basin located between awns; asulcate expansion pleat well-developed, interrupting about 13 distal laminae; discontinuous distal laminae absent; no laminae proximal to expansion pleat; basal papillae absent.

Remarks.—In many collections, specimens of *Teius oculatus* are frequently misidentified. Recent keys (e.g., Cei 1993; Peters & Donoso-Barros 1970) and reviews (e.g., Avila & Martori 1991) are not very helpful for identifying these lizards. Available descriptions of the unisexual species *T. suquiensis* are so incomplete, that we had little option but to ignore this species in our generic account. Nonetheless, the bisexual species are remarkably different from one another. Unlike *T. oculatus* (characters in parentheses), *T. teyou* has parietals arrayed in oblique rows and separated by small scales (three regular parietals), ten longitudinal ventral rows (eight), and keeled proximal subcaudals (smooth). The habitus of these species is strikingly different. *Teius oculatus* is much shorter and more robust than *T. teyou*. The rostral frequently contacts the prefrontal in *T. oculatus*; we have not observed this trait in *T. teyou*.

Tupinambinae Estes, de Queiroz, and Gauthier

Tupinambinae Estes, de Queiroz, and Gauthier 1988: 215.

Type Genus.—*Tupinambis* Daudin, designated herein.

Diagnosis.—Of characters we examined, the Tupinambinae are the only living teiids with complete caudal annuli alternating with annuli divided dorsally and a gap of granular scales separating femoral from abdominal pores. They lack circumorbital scales or have 1–3/1–3 circumorbitals restricted to the posterior border of the fourth supraocular. Other characters likely to be diagnostic of the Tupinambinae but assessed for relatively few Teiinae include synapomorphies identified by Presch (1974a) and Sullivan and Estes (1997): short interclavicular median process, second ceratobranchial absent, and postfrontal not in contact with jugal.

Content.—*Crocodilurus* Spix, *Dracaena* Daudin, *Salvator* Duméril and Bibron, and *Tupinambis* Daudin.

Remarks.—The subfamily names Tupinambinae and Teiinae are attributed to Estes *et al.* (1988) who elevated Teiini Presch and Tupinambini Presch to subfamiliar rank when defining Teiidae. These authors did not designate a type genus of the subfamily. Accordingly, we here designate *Tupinambis* as the type genus of Tupinambinae Estes, de Queiroz, and Gauthier.

Crocodilurus Spix
Figure 75

Crocodilurus Spix 1825: 19. Type species *Crocodilurus amazonicus* Spix by subsequent designation (Massary & Hoogmoed 2001).

Diagnosis.—*Crocodilurus* possesses several characters found in no other Teiidae. These include (1) an elongate fifth toe extending beyond the proximal free phalangeal articulation of Toe IV, (2) apical granules on the flanks that point upward and anteriorly from a fold of skin behind each dorsal so that each granule's pointed apex contacts the apex of the preceding dorsal, and (3) long, styloid apical awns on the hemipenis, each separated from an exceptionally pronounced catchment fold by a deep groove.

FIGURE 75. Adult captive *Crocodilurus amazonicus* at Reptilandia, Costa Rica (A) and juvenile from Amazonas, Venezuela (B, both photos by C. L. Barrio-Amorós).

Content.—*Crocodilurus amazonicus* Spix.

Definition.—Large lizards reaching 222 mm SVL; tail about twice as long as body (Table 15); posterior maxillary and dentary teeth longitudinally compressed, tricuspid; pupil reniform.

TABLE 15. Selected meristic and morphological data of Callopistinae and Tupinambinae examined by us. Means ± standard deviation follow ranges.

	Callopistes maculatus (*n* = 5)	*Callopistes flavipunctatus* (*n* = 5)	*Dracaena guianensis* (*n* = 6)	*Salvator merianae* (*n* = 10)	*Salvator rufescens* (*n* = 2)	*Tupinambis teguixin* (*n* = 6)	*Tupinambis paulustris* (*n* = 1)	*Crocodilurus amazonicus* (*n* = 3)
Occipitals	11–14 (12 ± 1)	Not Applicable	10–12 (11 ± 1)	8–14 (10 ± 2)	10–13	7–9 (8 ± 1)	10	2–9 (5 ± 2)
Lateral Supraocular Granules	38–45 (41 ± 3)	Not Applicable	15–22 (17 ± 3)	16–23 (19 ± 2)	18–26	0	0	0
Circumorbitals	16–21 (18 ± 2)	23–27 (25 ± 2)	0–6 (1 ± 2)	2	2–8	2	0	0
Supraciliaris	24–28 (27 ± 2)	28–33 (30 ± 2)	23–28 (26 ± 2)	25–29 (26 ± 1)	26–28	14–19 (17 ± 2)	16	14–18 (16 ± 2)
Supralabials	19–24 (21 ± 2)	22–24 (23 ± 1)	16–18 (17 ± 1)	14–16 (15 ± 1)	16–18	13–16 (14 ± 1)	13	12–13 (13 ± 1)
Infralabials	19–22 (21 ± 2)	20–22 (21 ± 1)	20–24 (21 ± 1)	14–16 (16 ± 1)	19–20	13–16 (15 ± 1)	13	10–13 (12 ± 2)
Anterior Gulars	23–26 (24 ± 1)	34–41 (38 ± 3)	19–25 (21 ± 2)	24–32 (27 ± 2)	32–34	19–25 (21 ± 2)	22	21–22 (21 ± 1)
Posterior Gulars	15–17 (16 ± 1)	20–26 (23 ± 2)	6–9 (7 ± 1)	9–16 (13 ± 2)	11–13	8–10 (9 ± 1)	12	8
Transverse Ventral Rows	42–45 (43 ± 1)	56–66 (61 ± 4)	29–33 (32 ± 2)	36–39 (38 ± 1)	40–41	31–36 (34 ± 2)	34	35–38 (37 ± 2)
Longitudinal Ventral Rows	25–27 (26 ± 1)	48–56 (52 ± 3)	32–39 (36 ± 3)	30–39 (35 ± 3)	35–38	21–28 (25 ± 2)	22	20–21 (20 ± 1)
Preanals	7–8 (8 ± 1)	8–10 (9 ± 1)	4–6 (5 ± 1)	9–11 (10 ± 1)	12–14	5–8 (7 ± 1)	8	4–5 (4 ± 1)
Lamellae Under Fourth Finger	18–19 (18 ± 0)	22–23 (22 ± 1)	22–26 (25 ± 2)	14–17 (15 ± 1)	16–19	14–18 (16 ± 1)	18	20–21 (21 ± 1)
Prefemorals	13–16 (15 ± 1)	Not Applicable	Not Applicable	22–29 (25 ± 3)	27	18	18	15–19 (17 ± 2)
Femoral and Abdominal Pores	0	0	8–11 (9 ± 1)	41–51 (46 ± 3)	21–26	20–33 (26 ± 6)	30	21–28 (24 ± 4)
Scales Separating Pore Rows	Not Applicable	Not Applicalbe	3–5 (4 ± 1)	2–5 (3 ± 1)	7	2–3 (3 ± 0)	4	4–6 (5 ± 1)
Lamellae Under Fourth Toe	32–34 (33 ± 1)	33–35 (34 ± 1)	35–38 (36 ± 1)	24–31 (28 ± 2)	27–29	33–38 (34 ± 2)	36	28–30 (29 ± 1)
Tail Length/ SVL	Not Available	2.3 (*n* = 1)	1.6–1.7 (1.7 ± 0, *n* = 3)	1.7–2.2 (1.9 ± 0.2, *n* = 4)	1.8 (*n* = 1)	1.7–2.1 (1.9 ± 0.2, *n* = 3)	2.1	2.0 (*n* = 2)

Prefrontal separated from nasal, contacting first supraciliary; frontal entire, lacking longitudinal ridge; posterior suture of frontal contacting second or third supraocular; scales of frontoparietal region smooth; key-hole shaped depression well-developed; frontoparietals paired; parietals consisting of three regular scales; interparietal entire, variable in size; medial pair of enlarged occipitals present; occipitals 2–9, larger than scales in first row of dorsals; supratemporals forming distinctive row of large, angulate scales behind supraciliaries; supratemporals broadly contacting parietals.

Rostral groove absent; nostril subcircular to subtriangular, centered in nasal suture; loreal single; supraoculars eight; first supraocular entire, smaller than fourth supraocular, in contact with second supraocular; circumorbital semicircles absent; supraciliaries subequal, 14–18, in contact with supraoculars (i.e., lateral supraocular granules absent); subocular keel absent; suboculars 4–6; suboculars below eye contacting supralabials; first subocular contacting or separated from first supraciliary, contacting supralabials or separated from supralabials by anterior expansion of second subocular; scales in front of auditory meatus slightly enlarged; auricular flap and preauricular fold absent.

Supralabials 12–13; first supralabial subequal to or longer than second, its ventral margin straight; infralabials 10–13; first pair of chinshields in contact with infralabials or partially separated from them by granular scales; first pair of chinshields in medial contact; interangular sulcus absent; anterior gulars 21–22; gular patch absent; posterior gulars 8; intertympanic sulcus filled with small granular scales, complete medially; larger anterior gulars not undergoing transition to smaller posterior gulars at intertympanic sulcus; mesoptychials moderately enlarged, not forming differentiated transverse row or serrated edge of gular fold.

Dorsals convex to keeled; scales on flank subequal to middorsals; apical granule pointed, curving upward and anterior from fold of skin posterior to each dorsal, its pointed apex touching apex of preceding dorsal; scales on rump slightly smaller than proximal subcaudals; scales of chest large and flat; pectoral sulcus absent; ventrals smooth, in 35–38 transverse and 20–21 longitudinal rows; subrectangular scales lateral to ventrals gradually decreasing in size on flanks, bordering transverse folds of skin; preanals 4–5; preanal plate present; preanal spurs and postanal plates absent; postcloacal buttons present in males; tail flattened; dorsolateral crests on tail consisting of enlarged heavily keeled scales projecting at about 45° to tail; accessory crests at base of tail consisting of four rows of enlarged heavily keeled scales between dorsolateral crests and second pair positioned laterally; medial rows of accessory crests separated by 9–10 rows of flat, elongate, and keeled scales, others by 1–2 rows of scales; complete caudal annuli alternating with annuli complete ventrally but divided on sides and dorsum of tail; proximal subcaudals smooth.

Preaxial brachials 1–2 X as wide as long, differentiated from large flat scales covering rest of brachium (scales largest on preaxial and dorsal brachium and antebrachium, grading to granular scales postaxially); antebrachium covered in scales longer than wide; scales on proximal, ventral surface of antebrachium slightly enlarged; subdigital lamellae of hand homogeneous in size, mostly divided, 20–21 under fourth finger.

Prefemorals 15–19; femoral and abdominal pores 21–28; each compound pore-bearing scale consisting of partially fused prefemoral or abdominal scale and 2 or more granular scales; 4–6 scales separating abdominal pore series medially; distal-most femoral pores not separated from others; gap of about 4 granular scales separating femoral from abdominal pores; scales at heel relatively small and numerous; tibiotarsal spurs and shields absent; lamellae under fourth toe 28–30; distal lamellae of fourth toe smooth; scales between subdigital and supradigital lamellae along postaxial side of toes serrate; noticeably enlarged postaxial scales between fourth and fifth toe absent; fifth toe well-developed, base of its claw surpassing proximal free phalangeal articulation of fourth toe.

β-keratin containing layers of dorsal trunk scales lacking macrohoneycomb, instead uniformly covered in simple lamellae; long aligned macroridges covering supracaudal scales; single subterminal lenticular scale organ positioned atop keel on dorsals and proximal supracaudals; ventrals lacking scale organs; generation glands absent. Snout same color as dorsal head scales. In juveniles, light vertebral, paravertebral, dorsolateral, upper and lower lateral stripes absent; dark dorsolateral and lateral fields absent; thigh lacking light spots. Adult males lacking flank spots but with conspicuous light ocelli; turquoise ventrolateral spots absent; venter with large melanic; juvenile dorsal color pattern present in adult males with only slight modification.

Hemipenis with pair of long, styloid apical awns, each separated by deep groove from exceptionally pronounced sulcate catchment fold extending distally from organ as triangular flap; apical papillae and apical basin absent; asulcate expansion pleat well-developed, interrupting about 44 distal laminae; discontinuous distal laminae absent; about 29 laminae proximal to expansion pleat; basal papillae absent.

Etymology.—Spix (1825) did not discuss the etymology of *Crocodilurus*. The name is likely derived from the Greek nouns *krokodeilos* originally meaning lizard and *oura* meaning tail. In his generic description, Spix (1825) emphasized characteristics of the tail, which resembles that of crocodilians.

Distribution.—Crocodilurus occurs along the Amazon and Orinoco Rivers and their tributaries in Brazil, Colombia, Peru, and Venezuela. This species is known from a few localities in coastal French Guiana and Pará, Brazil. Bertoni (1926) reported a specimen from Paraguay where locals apparently refer to this species as "yakarerâ." Since all other known localities are above about 5°S latitude, Bertoni's report is surprising and should be confirmed.

Dracaena **Daudin**

Figure 76

Dracaena Daudin 1801: 421. Type species *Dracaena guianensis* Daudin by monotypy.
Ada Gray 1825: 200. Type species *Teius crocodilinus* Merrem (=*Dracaena guianensis*).
Thorictis Wagler 1830: 153. Type species *Dracaena guianensis* Daudin.

Diagnosis.—Dracaena is the only genus of Teiidae with subterminal lenticular scale organs positioned atop the prominently keeled ventrals and a complete interangular sulcus containing small granular scales. The combination of two loreals, a laterally compressed tail, and heterogeneous dorsals consisting of large keeled scales surrounded by smaller scales immediately distinguishes *Dracaena* from all other Teiidae.

Content.—Dracaena guianensis Daudin and *Dracaena paraguayensis* Amaral.

Definition.— Large lizards reaching 450 mm SVL (*Dracaena paraguayensis*); tail 1.6–1.7X as long as body; posterior maxillary and dentary teeth molariform; pupil round.

FIGURE 76. Adult captive *Dracaena guianensis* at Reptilandia, Costa Rica (A, photo by C. L. Barrio-Amorós) and *D. paraguayensis* from Fazenda Barranco Alto, Pantanal, Brazil (B, photo by L. Leuzinger).

Prefrontals irregularly divided; frontal entire, lacking longitudinal ridge; posterior suture of frontal contacting second supraocular; scales of frontoparietal region smooth, outwardly convex to flat; key-hole shaped depression absent; frontoparietals paired; parietals consisting of three regular scales; interparietal entire, larger than flanking parietals; medial pair of enlarged occipitals absent; occipitals 10–12, larger than or subequal to scales in first row of dorsals; supratemporals slightly to moderately enlarged, separated from parietals by one or more scales.

Rostral groove absent; nostril subcircular to subtriangular, positioned slightly anterior to nasal suture; loreals two; supraoculars 8–11; first supraocular entire, smaller than fourth supraocular, in contact with or partially to completely separated from second supraocular by granular scales; circumorbital semicircles consisting of 0–6 small scales, restricted (when present) to posterior border of fourth supraocular; supraciliaries subequal, 23–28, separated from supraoculars by one row of 15–22 granular scales; first supraciliary in contact with first subocular or separated from it by small granular scales; suboculars 8–9, heavily fractured; first subocular separated from supralabials by scale inserted between suboculars and loreal; scales in front of auditory meatus distinctly enlarged; auricular flap and preauricular fold absent.

Supralabials 16–18; first supralabial smaller than second, its ventral margin straight; infralabials more numerous than supralabials, 20–24; first pair of chinshields completely separated from infralabials by small granular scales; first and second pairs of chinshields in medial contact; interangular sulcus complete, consisting of small granular scales; anterior gulars 19–25; gular patch absent; posterior gulars 6–9; intertympanic sulcus incomplete medially, with small granular scales on sides of gular region; larger anterior gulars not undergoing transition to smaller posterior gulars; mesoptychials not to slightly enlarged, not forming differentiated transverse row or serrated edge of gular fold.

Dorsals heterogeneous, large convex scales separated by smaller scales; dorsals keeled; large scales on flanks supported posteriorly by transverse fold of skin covered in tiny granular scales (i.e., instead of single apical granules); scales of chest large and flat; pectoral sulcus absent; ventrals keeled, in 29–33 transverse and 32–39 longitudinal rows; subrectangular scales lateral to ventrals gradually decreasing in size on flanks, bordering transverse folds of skin; preanals 4–6; preanal plate, preanal spurs, and postanal plates absent; postcloacal buttons present in males; tail with pair of dorsolateral crests; enlarged scales of crest heavily keeled and projecting away from tail at about 45°; accessory crests disposed in irregular rows at base of tail; complete caudal annuli alternating with annuli complete ventrally but divided on sides and dorsum of tail; proximal subcaudals keeled.

Preaxial, dorsal, and postaxial sides of brachium and antebrachium covered in scales longer than wide, noticeably enlarged series absent from arm (scales largest on preaxial and dorsal brachium and antebrachium, grading to granular scales postaxially); scales on proximal, ventral surface of antebrachium slightly enlarged; subdigital lamellae entire and sharply keeled distally, divided under penultimate phalanx, divided and separated by one or more small scales under more proximal phalanges, completely fractured into 7–8 small rounded scales arrayed in transverse rows under basal phalanx; 22–26 subdigital lamellae (including rows of fractured scales) under fourth finger.

Prefemorals not differentiated; femoral and abdominal pores 8–11 (1-2/1-2 femoral and 2–4/2–4 abdominal), each pore opening in center of single oval scale; 3–5 scales separating abdominal pore series medially; gap of about five granular scales separating femoral from abdominal pores; scales at heel relatively small and numerous; tibiotarsal spurs and shields absent; lamellae under fourth toe 35–38; distal lamellae of fourth toe sharply keeled; small granular scales separating digital lamellae along postaxial edge of each toe; noticeably enlarged postaxial scales between fourth and fifth toe absent; fifth toe well-developed, base of its claw extending beyond level of skin between third and fourth toes when adpressed, but not surpassing proximal free phalangeal articulation of fourth toe.

β-keratin containing layers folded into macrohoneycomb on all body surfaces (including ventrals); lenticular scale organs well developed, single, positioned subterminally atop keel of large dorsal scale on trunk and tail; scale organs present on ventrals; generation glands apparently absent.

Snout same color as dorsal head scales, head of adult *Dracaena guianensis* often bright reddish but this color not restricted to snout. In juveniles, light vertebral, paravertebral, dorsolateral, upper and lower lateral stripes absent; dark dorsolateral and lateral fields absent (*D. paraguayensis* with large black or dark brown blotch side of neck in same position as lateral field); thigh lacking light spots (some adult specimens of *D. paraguayensis* with large pale blotches on flanks but lacking light spots or ocelli). In adult males, turquoise ventrolateral spots absent; venter immaculate or with brownish blotches, lacking large melanic areas or blotches in adult males; juvenile dorsal color pattern present in adult males with no or only minimum modification.

According to Cope (1896), hemipenis laminate and with asulcate expansion pleat (referred to as a “welt” opposite the sulcus by him, p. 465).

Etymology.—The generic name *Dracaena* is the Latin noun *Dracaena* meaning dragon or, less commonly, lizard. As discussed recently by Massary *et al.* (2000), Daudin (1801) based his description on the figure titled “La dragonne” and description of *Lacerta dracæna* by La Cepède (1788). *Lacerta Dracaena* also appears in Gmelin’s (1789) list along with a brief Latin description. Gmelin’s name would appear to be an available senior synonym of *D. guianensis*, albeit one that should be suppressed since it has not been used since the late 1700s.

Distribution.—Amazon Basin and Pantanal Region of Bolivia, Brazil, Colombia, Ecuador, French Guiana, Paraguay, and Peru.

Salvator Duméril and Bibron
Figure 77

Salvator Duméril and Bibron 1839: 78. Type species *Salvator merianae* by subsequent designation (Peters & Donoso-Barros 1970).

Diagnosis.—*Salvator* is the only genus of Teiidae with the combination of two loreals, smooth ventrals, and a subcylindrical tail with two divided caudal annuli alternating with complete annuli. Unlike the superficially similar genus *Tupinambis* (characters in parentheses), *Salvator* also has a round pupil (reniform), complete row of lateral supraocular granules (absent), an incomplete or absent intertympanic sulcus (complete), and keeled proximal subcaudals (smooth).

Content.—Salvator duseni (Lönnberg) **new combination**, *Salvator merianae* Duméril & Bibron, and *Salvator rufescens* (Günther) **new combination**.

Definition.—Large lizards reaching 614 mm SVL (*Salvator rufescens*); tail 1.7–2.2X as long as body; posterior maxillary and dentary teeth longitudinally compressed, tricuspid in juveniles, becoming molariform in adults; pupil round.

Prefrontal separated from nasal, contacting first supraciliary; frontal entire, lacking longitudinal ridge; posterior suture of frontal usually contacting second supraocular; scales of frontoparietal region smooth, outwardly convex to flat; key-hole shaped depression absent; frontoparietals paired; parietals consisting of three regular scales; interparietal entire, smaller than flanking parietals; medial pair of enlarged occipitals absent; occipitals 8–14, larger than scales in first row of dorsals; supratemporals slightly to moderately enlarged, separated from parietals by one or more scales.

Rostral groove absent; nostril subcircular to subtriangular, positioned posterior (*Salvator rufescens*) or somewhat posterior (*S. merianae*) to nasal suture; loreals two; supraoculars eight; first supraocular entire, smaller than fourth supraocular, in contact or partially separated from second supraocular; circumorbital semicircles consisting of 2–8 small scales, restricted to posterior border of fourth supraocular or extending slightly anterior to its suture with third; supraciliaries subequal, 25–29, separated from supraoculars by one row of 16–26 granular scales; angulate keel extending from first subocular to suboculars below eye; suboculars 6–8; suboculars below eye contacting supralabials; first subocular contacting first supraciliary, separated from supralabials by scale inserted between suboculars and loreal; scales in front of auditory meatus not enlarged; auricular flap and preauricular fold absent.

Supralabials 14–18; first supralabial usually subequal to second, its ventral margin straight; infralabials 14–20; first pair of chinshields usually completely separated from infralabials by small granular scales; first pair of chinshields in medial contact; interangular sulcus absent; anterior gulars 24–34; gular patch absent; posterior gulars 9–16; intertympanic sulcus absent; larger anterior gulars not undergoing transition to smaller posterior gulars; mesoptychials not to slightly enlarged, not forming serrated edge of gular fold.

Dorsals round and flat, smooth on anterior trunk, keeled on posterior body and rump; scales on flank subequal to middorsals, not supported by small apical granules; scales on rump slightly smaller than proximal subcaudals; scales of chest large and flat; pectoral sulcus absent; ventrals smooth, in 36–41 transverse and 30–39 longitudinal rows; subrectangular scales lateral to ventrals gradually decreasing in size on flanks, bordering transverse folds of skin; preanals 9–14; preanal plate absent; preanal spurs and postanal plates absent; postcloacal buttons present in males; scales on dorsolateral edge of tail like those on top and sides, denticulate edge and dorsolateral crests absent; complete caudal annuli alternating with annuli complete ventrally but divided on sides and dorsum of tail; proximal subcaudals keeled.

Preaxial, dorsal, and postaxial sides of brachium and antebrachium covered in scales longer than wide (scales largest on preaxial and dorsal brachium and antebrachium, grading to granular scales postaxially), noticeably widened series absent from arm; scales on proximal, ventral surface of antebrachium slightly enlarged; subdigital lamellae of hand homogeneous in size, mostly divided, 14–19 under fourth finger.

Prefemorals 22–29; femoral and abdominal pores 21–51; each compound pore-bearing scale consisting of partially fused prefemoral or abdominal scale and 2–6 granular scales; 2–7 scales separating abdominal pore series medially; distal-most 1–2 femoral pores usually separated from others by 1–3 scales (*Salvator merianae*) or not separated (*S. rufescens*); gap of 2–7 granular scales separating femoral from abdominal pores; scales at heel relatively small and numerous; tibiotarsal spurs and shields absent; lamellae under fourth toe 24–31; distal lamellae of fourth toe smooth; continuous row of small granular scales separating digital lamellae along postaxial edge of each toe; noticeably enlarged postaxial scales between fourth and fifth toe absent; fifth toe well-developed, base of its claw extending beyond level of skin between third and fourth toes when adpressed, but not surpassing proximal free phalangeal articulation of fourth toe.

FIGURE 77. Adult *Salvator merianae* from Sao Martinho, Santa Catarina (A, photo by A. Kwet) and São Paulo, Brazil (B, photo by P. Bernardo); adult *S. rufescens* from north of General Roca, Río Negro, Argentina (C and D, photos by I. Hernández).

β-keratin containing layers of granular dorsal scales folded into macrohoneycomb; large flat dorsals lacking macrohoneycomb, instead uniformly covered in simple lamellae; large dorsal trunk scales usually lacking scale organs or with one subterminal lenticular scale organ (positioned atop keel on posterior trunk); caudals usually with two scale organs, one elongate and located posteriorly on medial side of keel (i.e., to left of keel on right side of tail, right of keel on left side of tail), another rounded located terminally, but not atop keel; ventrals lacking scale organs; generation glands present.

Snout same color as dorsal head scales. In juveniles, light vertebral and paravertebral stripes absent; dark dorsolateral field absent; dorsolateral light stripe present only on head and disappearing on neck; dark lateral field solid not well defined or absent (lateral field of some specimens broken into irregularly or badly defined blotches; in others, distinct and consisting of large black blotches on sides of neck, scapular region and anterior flanks); upper and lower lateral light stripes absent; thigh with numerous light spots. Adult males lacking light spots or ocelli on flanks; turquoise ventrolateral spots absent; venter with large melanic areas or blotches; juvenile dorsal color pattern present in adult males with moderate modification [= juveniles with better defined dorsal banding, greenish (*Salvator rufescens*) to bright green (*S. merianae*) head and anterior dorsum (condition of juvenile *S. duseni* unknown)].

Hemipenis (based on *Salvator merianae*) bilobed, lacking apical awns, papillae, and basin; single enlarged apical lobe on either side of asulcate expansion pleat; lips of sulcus spermaticus flaring outward as prominent triangular sulcal flaps; 7–8 short grooves roughly perpendicular to apex of each sulcal flap, separated from one another by space roughly equal to width of two laminae; lateral and medial expansion pleats absent; asulcate expansion pleat interrupting 56–71 distal laminae; 33–40 laminae proximal to expansion pleat; discontinuous laminae and basal papillae absent.

Etymology.—Salvator is a masculine Latin noun in the nominative singular. In a somewhat florid footnote to their new name, Duméril and Bibron (1839) explain that "Salvator" was at the time a name frequently used for Jesus Christ in hymns of the Christian Church. The name was no doubt inspired by the common name "Sauvegardes," meaning protector or savior in French and used by Cuvier and his contemporaries, especially in popular literature.

Distribution.—Eastern Andean foothills and lowlands south of the Amazon River in Argentina, Bolivia, Brazil, Paraguay, and Uruguay.

Remarks.—Duméril and Bibron (1839) erected the new genus *Salvator* to accommodate New World species then commonly referred to as *Monitor* Fitzinger or *Tupinambis* Daudin. As they explain on p. 83, they considered this action necessary, because species of *Varanus* were commonly considered congeneric with the New World lizards. La Cepède's (1788) illustration of *Lacerta tupinambis* included *Varanus niloticus*, *V. salvator,* and *Tupinambis*. Duméril and Bibron (1839) recognized two species *S. merianae* and *S. nigropunctatus*. Although "Nobis" appears after each of these names, *Salvator Merianae* was originally proposed as an apparent emendation of *Monitor Meriani* Blainville, and *S. nigropunctatus* was a new generic assignment of *Tupinambis nigropunctatus* Spix (= *Tupinambis teguixin*). Both older names appear in the respective synonymies provided by Duméril and Bibron (1839). Nonetheless, as pointed out by Avila-Pires (1995), Blainville's name is a nomen nudum, so that Duméril and Bibron become the authors of *S. merianae*.

***Tupinambis* Daudin**

Figure 78

Tupinambis Daudin 1802: 20. Type species *Tupinambis monitor* Daudin (=*Tupinambis teguixin*) by subsequent designation (Burt & Burt 1933).
Tutor Goldfuss 1820: 168. Type species *Monitor americanus* Goldfuss.
Custa Fleming 1822: 274. Type species *Lacerta teguixin* Linnaeus by subsequent designation (Peters & Donoso-Barros 1970).
Exypnestes Kaup 1826: 88. Type species *Tupinambis monitor* Daudin.
Ctenodus Wagler 1828: 860. Type species *Tupinambis nigropunctatus* Spix.
Podinema Wagler 1830: 153. Type species *Lacerta teguixin* Linnaeus.
Ctenodon Wagler 1830: 153. Type species *Tupinambis nigropunctatus* Spix.
Teguixin Gray 1831: 29. Type species *Lacerta teguixin* Linnaeus.
Gymnogomphius Wagler 1833: 892. Type species *Lacerta teguixin* Linnaeus.

Diagnosis.—*Tupinambis* can be distinguished from all other teiids by the combination of smooth dorsals, one loreal, a gap of granular scales separating femoral from abdominal pores, and a cylindrical tail with complete annuli alternating with annuli divided on the dorsal and lateral sides of the tail.

Content.—Tupinambis longilineus Avila-Pires, *Tupinambis palustris* Manzani and Abe, *Tupinambis quadrilineatus* Manzani and Abe, and *Tupinambis teguixin* (Linnaeus).

Definition.—Large lizards reaching 400 mm SVL (*Tupinambis teguixin*); tail 1.7–2.1X as long as body; posterior maxillary and dentary teeth longitudinally compressed, tricuspid in juveniles, becoming molariform in adults; pupil reniform.

Prefrontal separated from nasal, contacting first supraciliary; frontal entire, lacking longitudinal ridge; posterior suture of frontal contacting second supraocular; scales of frontoparietal region smooth, outwardly convex to flat; key-hole shaped depression absent; frontoparietals paired; parietals consisting of three regular scales; interparietal entire, variable in size; medial pair of enlarged occipitals absent; occipitals 7–14, larger than or subequal to scales in first row of dorsals; supratemporals forming distinctive row of large, angulate scales behind supraciliaries (*Tupinambis longilineus* and *T. teguixin*) or only moderately enlarged (*T. quadrilineatus* and *T. palustris*); supratemporals separated from parietals by one or more scales (in contact with parietals in holotype of *T. longilineus*).

Rostral groove absent; nostril subcircular to subtriangular, usually positioned somewhat posterior to nasal suture; loreal single; supraoculars eight; first supraocular entire, smaller than or subequal to fourth supraocular, in contact with second supraocular; circumorbital semicircles consisting of 0–2 scales, restricted to posterior border of fourth supraocular when present; supraciliaries subequal, 16–20, in contact with supraoculars (i.e., lateral supraocular granules absent); angulate keel extending from first subocular to suboculars below eye; suboculars 5–7; suboculars below eye contacting supralabials; first subocular contacting first supraciliary and supralabials; scales in front of auditory meatus slightly (*Tupinambis longilineus*, *T. quadrilineatus*, *T. teguixin*) to distinctly (*T. palustris*) enlarged; auricular flap and preauricular fold absent.

Supralabials 13–16; first supralabial usually subequal to second, its ventral margin straight; infralabials 13–16; first pair of chinshields usually in contact with infralabials; first pair of chinshields in medial contact; interangular sulcus absent; anterior gulars 15–24; gular patch absent; posterior gulars 9–12; intertympanic sulcus filled with small granular scales, complete medially; larger anterior gulars undergoing transition to smaller posterior gulars at intertympanic sulcus; mesoptychials not to slightly enlarged, not forming differentiated transverse row or serrated edge of gular fold.

FIGURE 78. *Tupinambis longilineus* from Juruti, Pará, Brazil (A, B, photo by F. E. Pimenta, courtesy of A. Lima), *T. quadrilineatus* from Mato Grosso, Brazil (C, photo by P. Bernardo), *T.* cf. *teguixin* from Tocatins, Brazil (D, photo by P. Bernardo), *T. teguixin* from Hato El Cedral, Apure and Puerto Cocha, Zulia, Venezuela (E and F respectively, photos by C. L. Barrio-Amorós).

Dorsals round and flat, smooth; scales on flank subequal to middorsals, not supported by small apical granules; scales on rump slightly smaller than proximal subcaudals; scales of chest large and flat; pectoral sulcus absent; ventrals smooth, in 31–36 transverse and 20–28 longitudinal rows; subrectangular scales lateral to ventrals gradually decreasing in size on flanks, bordering transverse folds of skin; preanals 5–8; preanal plate present (*Tupinambis longilineus* and *T. teguixin*) or absent (*T. palustris* and *T. quadrilineatus*); preanal spurs and postanal plates absent; postcloacal buttons present in males; scales on dorsolateral edge of tail like those on top and sides, denticulate edge and dorsolateral crests absent; complete caudal annuli alternating with annuli complete ventrally but divided on sides and dorsum of tail; proximal subcaudals smooth.

Preaxial, dorsal, and postaxial sides of brachium and antebrachium covered in scales longer than wide; scales on proximal, ventral surface of antebrachium slightly enlarged (scales largest on preaxial and dorsal brachium and antebrachium, grading to granular scales postaxially); subdigital lamellae of hand homogeneous in size, mostly divided, 10–18 under fourth finger.

Prefemorals 18; femoral and abdominal pores 16–33; each compound pore-bearing scale consisting of partially fused prefemoral or abdominal scale and 2 or more granular scales (some pores opening within single scales in

Tupinambis palustris); 2–4 scales separating abdominal pore series medially; distal-most femoral pores usually not separated from others; gap of 3–5 granular scales separating femoral from abdominal pores; scales at heel relatively small and numerous; tibiotarsal spurs and shields absent; lamellae under fourth toe 28–38; distal lamellae of fourth toe smooth; continuous rows of small granular scales separating digital lamellae along postaxial edge of each toe; noticeably enlarged postaxial scales between fourth and fifth toe absent; fifth toe well-developed, base of its claw extending beyond level of skin between third and fourth toes when adpressed, but not surpassing proximal free phalangeal articulation of fourth toe.

β-keratin containing layers of dorsals lacking macrohoneycomb, instead uniformly covered in simple lamellae; long aligned macroridges covering supracaudal scales of hatchlings (at least in *T. teguixin*), lost during ontogeny; large middorsal trunk scales usually with three lenticular scale organs, one on either side of each scale at its posterior one-fourth, one centered at its posterior edge; scales on flanks usually with one lenticular organ positioned near posterior, medial edge; caudals usually with two scale organs, one elongate located posteriorly on medial side of keel (i.e., to left of keel on right side of tail, right of keel on left side of tail), another rounded and located terminally, but not atop keel; ventrals lacking scale organs; generation glands apparently absent.

Snout same color as dorsal head scales. In juveniles, light vertebral stripe absent; light paravertebral stripes absent (most species) or present but conspicuously broken into longitudinal row of spots (*Tupinambis quadrilineatus*); dark dorsolateral field absent; dorsolateral light stripe broken into longitudinal row of spots but extending to tail (*T. longilineus*, *T. quadrilineatus*) or not well defined to absent (*T. palustris*, *T. teguixin*); dark lateral field solid (*T. longilineus*) or not well defined to absent (most species. The dorsolateral and lateral fields of some specimens of *T. teguixin* seem to be broken into irregularly or badly defined blotches, most distinct towards the scapular region); upper and lower lateral light stripes absent; thigh lacking light spots. Adult males lacking spots or ocelli on flanks; turquoise ventrolateral spots absent; venter with large melanic areas or blotches (*T. palustris*, *T. teguixin*) or mostly immaculate (*T. longilineus*, *T. quadrilineatus*); juvenile dorsal color pattern present in adult males without or only slight modification.

Morphology of hemipenis unknown (see Remarks).

Etymology.—The generic name *Tupinambis* is a masculine Latin noun in the nominative singular apparently referring to the Tupinambá indigenous tribe, one of several Tupi ethnic groups that inhabited Brazil at the time of the conquest.

Distribution.—*Tupinambis* extends from the Chocó of Colombia eastward to northern Venezuela, Trinidad, Tobago, and the humid lowlands of Amazonia and the Guianas. Additional species occur south of Amazonia in the Cerrados of Bolivia and southern Brazil. Although *T. teguixin* was recently reported from Playas del Tirano, Isla de Margarita, Venezuela (Rivas *et al.* 2005), its presence on that island is doubtful (Ugueto & Rivas 2010).

Remarks.—Dowling and Duellman (1978, their figure 83.2) published an illustration of the sulcate side of the hemipenis of "*Tupinambis nigropunctatus*." These authors did not provide a museum number and the drawing could be based either on *Tupinambis* or *Salvator*. This small figure does not show most characters of importance. The sulcus flares out into large triangular catchment folds as in *Salvator*. Laminae are visible but cannot be counted. Apical features are not evident in the drawing.

Key to Genera and Species Groups of Extant Teiidae

Based on characters described in this study, we present the following key to teiid genera and species groups. Wherever possible, we relied on highly conservative characters, although a few characters in the key show low levels of polymorphism. Nonetheless, each couplet contains several characters, so that users of the key will not be led astray by specimens having rare character states, missing body parts, or aberrations.

1 Femoral and abdominal pores absent; loreals three or more; 2–3 complete rows of lorilabials separating suboculars from supralabials; prefrontals heavily fractured; vertical fold of skin in front of auditory meatus (Callopistinae) . . . . *Callopistes*

\- Femoral and abdominal pores present; loreals 1–2; one or more suboculars contacting supralabials; prefrontals usually entire; skin in front of auditory meatus without vertical fold. 2

2 Complete caudal annuli alternating with annuli divided dorsally; gap of granular scales separating femoral from abdominal pores; circumorbital scales absent or reduced to 1–3/1–3 circumorbitals at posterior border of fourth supraocular (Tupinambinae) 3

\- Caudal annuli complete; femoral and abdominal pores continuous; circumorbital scales present (Teiinae) 6

3 Pupil round; loreals two; large scale inserted between first subocular, supralabials and posterior loreal; complete row of lateral supraocular granules; supraciliaries 23–28 (count combined from both sides); chinshields usually separated from infralabials by row of granular sublabials; intertympanic sulcus incomplete medially or absent; longitudinal rows of ventrals 30–39; proximal subcaudals keeled 4

- Pupil reniform; loreal single; first subocular contacting supralabials or rarely separated from them by anterior expansion of second subocular; lateral supraocular granules absent; supraciliaries 14–19 (count combined from both sides); chinshields usually in contact with infralabials; intertympanic sulcus complete medially; longitudinal rows of ventral 20–28; proximal subcaudals smooth. 5

4 Ventrals keeled and with subterminal lenticular scale organs positioned atop keel; interangular sulcus complete, containing small granular scales; tail laterally compressed with large scales on dorsolateral edge forming prominent crests; dorsals heterogeneous, consisting of large keeled scales surrounded by smaller scales . . . . *Dracaena*

- Ventrals smooth, lacking lenticular scale organs; interangular sulcus absent; tail cylindrical without dorsolateral crests; dorsals flat and mostly smooth (may be keeled on neck and posterior body), separated by small granular scales . . . . *Salvator*

5 Fifth toe elongate, extending beyond free proximal phalangeal articulation of Toe IV; tail laterally compressed; eight rows of enlarged, keeled scales forming accessory crests at base of tail in addition to pair of dorsolateral crests extending length of tail . . . . *Crocodilurus*

- Fifth toe moderate, not extending beyond free proximal phalangeal articulation of Toe IV; tail cylindrical; accessory and dorsolateral crests absent from tail . . . . *Tupinambis*

6 Posterior maxillary and mandibular teeth oriented transversely and bicuspid 7

- Posterior maxillary and mandibular teeth oriented longitudinally and tricuspid 8

7 Frontoparietals fused; fifth toe reduced but with three free phalanges; distal digital lamellae under fourth toe sharply keeled; hemipenis lacking apical basin . . . . *Dicrodon*

- Frontoparietals paired; fifth toe vestigial, reduced to small nub; distal digital lamellae under fourth toe weakly keeled or smooth; hemipenis with apical basin . . . . *Teius*

8 Suboculars not keeled or with short keel restricted to first and second subocular; dorsals apparently lacking subterminal lenticular scale organs; ventrals keeled; antebrachials small and keeled; scales separating digital lamellae continuing as row of enlarged scales between fourth and fifth toe; hemipenis with relatively long papillae between lobes; apical hemipenial awns absent (*Kentropyx*). 9

- Prominent subocular keel extending to elongate subocular below eye; dorsals with single subterminal lenticular scale organs; ventrals smooth; at least some antebrachials enlarged and plate-like; when present, scales separating digital lamellae not continuing as row between fourth and fifth toes; apex of hemipenis with smooth awns or awns ornamented with short papillae 11

9 At midbody, scales on flanks small, strongly differentiated from enlarged dorsal scales. . . . . *Kentropyx striata* Group

- At midbody scales on flanks gradually increasing in size to middorsal line; no sharp demarcation between scales on flanks and middorsals 10

10 Scales on rump much smaller than proximal caudals; prefemorals 13–19; femoral and abdominal pores (both sides combined) 27–43; subarticular lamellae of hands usually entire; scales between pedal lamellae large and denticulate; lower lateral stripe broken or absent . . . . *Kentropyx calcarata* Group

- Scales on rump slightly smaller than proximal caudals; prefemorals 10–13; femoral and abdominal pores 28 or fewer; subarticular lamellae of hands usually divided; scales between pedal lamellae moderate and serrate; lower lateral stripe solid to groin . . . . *Kentropyx paulensis* Group

11 Subtriangular auricular flap partially covering external auditory meatus; suboculars 2–3; second pair of chinshields in medial contact; preanal plate single, subtriangular, larger than scale in front of it; single row of 3–4 poorly developed tibiotarsal spurs consisting of large triangular scales with raised and pointed distal ends . . . . *Aurivela*

- External auditory meatus not partially covered by auricular flap; suboculars 4 or more; second pair of chinshields separated medially; preanals usually paired or in transverse row; if present, tibiotarsal spurs well-developed and in two rows 12

12 Dorsolateral row of scales at base of tail serrate; subarticular lamellae of hand noticeably enlarged; distal subdigital lamellae of fourth toe sharply keeled; postanal plates usually present in males 13

- Dorsolateral scales at base of tail like adjacent scales, not serrated; subdigital lamellae of hand homogeneous or with divided subarticular lamellae (basal subarticular lamellae enlarged in some *Aspidoscelis*); distal subdigital lamellae of fourth toe smooth or weakly keeled; postanal plates absent except in *Aspidoscelis* 15

13 Cephalic roofing scales fractured and heavily keeled; key-hole shaped depression in frontoparietal region; longitudinal ventral rows 6; scale surfaces covered in short aligned microridges . . . . *Holcosus septemlineatus* Group

- Cephalic roofing scales smooth, mostly entire; scales in frontoparietal region flat or outwardly convex (i.e., key-hole shaped depression absent); longitudinal ventral rows 8; scale surfaces covered in macrohoneycomb 14

14. Frontal replaced by irregular, keeled scales, three subequal shields at heel . . . . *Holcosus orcesi* Group

- Frontal entire, one very wide ventral and one wide postaxial shield at heel. . . . . *Holcosus undulatus* Group

15 First supralabial subequal or longer than second; single pair of preanal spurs in males; continuous row of large keeled scales separating digital lamellae on Toes 2–5; subarticular lamellae of hand divided (*Cnemidophorus*) 16

- First supralabial subequal or smaller than second; preanal spurs absent, except for *Medopheos* with 5–6 pairs; digital lamellae of toes in contact between some phalangeal articulations, separated by continuous row of scales in some *Ameiva*; subarticular lamellae of hand entire 19

16 Interparietal usually partially or completely divided longitudinally; first subocular usually separated from supralabials by anterior expansion of second subocular; ventrals in 10–12 longitudinal rows; postaxial brachials barely enlarged, restricted to

patch near elbow; enlarged antebrachials separated from brachials by large gap of distinctly smaller scales 17

\- Interparietal usually entire; first subocular usually contacting supralabials; ventrals in 8 longitudinal rows; postaxial brachials enlarged, extending beyond center of arm; enlarged antebrachials in contact or only narrowly separated from brachials 18

17 Lateral supraocular granules in 2.5-3 rows; proximal subcaudals smooth; preaxial brachials barely enlarged, restricted to patch near elbow; femoral pores 57–86; flank spots in adult males large . . . . *Cnemidophorus murinus* Group

\- Lateral supraocular granules in single row; proximal subcaudals keeled; preaxial brachials moderately enlarged and extending beyond center of arm; femoral pores 49–58; flank spots in adult males small. . . . . *Cnemidophorus vanzoi* Group

18 Proximal subcaudals keeled; scales on dorsal surface of brachium subtriangular; dorsal stripes of juveniles complete or broken in few places; ventral surfaces of adult males pale, never black. . . . . *Cnemidophorus lemniscatus* Group

\- Proximal subcaudals smooth; scales on dorsal surface of brachium granular; dorsal stripes of juveniles broken into spots; ventral surfaces of adult males black . . . . *Cnemidophorus nigricolor* Group

19 First supraciliary as long or longer than second (except in *Ameivula abaetensis, A. littoralis,* and *A. venetacauda* where first supraciliary is divided); nasal usually in contact with prefrontal; postanal plates absent; small teiids less than 75 mm SVL from south and east of Amazonia 20

\- First supraciliary shorter than second; third, fourth, or second and third supraciliaries enlarged; nasal usually separated from prefrontal in South American species (usually in contact in North American species); postanal plates present in males or absent; small to very large teiids from North America, the Caribbean, and South America 21

20 Tail usually relatively short (1.5–2.1 times as long as SVL); parietals usually three; first supralabial usually subequal to second, its ventral margin straight to curved; three scales at heel; when adpressed, claw of Toe V passing skin between Toes III and IV . . . . *Contomastix*

\- Tail long (2.1–2.3 times as long as SVL); parietals usually five; first supralabial shorter than second, its ventral margin “toothy;” scales at heel small and numerous; Toe V reduced . . . . *Ameivula*

21 Nasal usually in contact with prefrontal; parietals usually three; postanal plates present in males . . . . *Aspidoscelis*

\- Nasal usually separate from prefrontal; parietals usually five; postanal plates absent 22

22 Ventrals in 8 longitudinal rows at midbody; 5–6 pairs of preanal spurs in males; three relatively large, subequal scales at heel; western Ecuador and Peru . . . . *Medopheos*

\- Ventrals in 10–20 longitudinal rows at midbody (8 in few Caribbean species); preanal spurs absent; scales at heel relatively small and numerous; Neotropical but absent from western Ecuador and Peru (*Ameiva*) 23

23 Frontal transversely divided; nasal suture in front of nostril; frontal ridge well developed . . . . *Ameiva bifrontata* Group

\- Frontal usually entire; nostril in front of nasal suture or suture passing through nostril; frontal ridge absent or poorly developed 24

24 Nasal suture passing through nostril; ventral margin of first supralabial curved; fifth toe reduced (=when adpressed, not surpassing skin between Toes 3 and 4); pedal lamellae separated by continuous row of granular scales along postaxial edge of digits; black edged ocelli on flanks . . . . *Ameiva ameiva* Group

\- Nostril in front of nasal suture (except in *A. wetmorei*); ventral margin of first supralabial toothy (except in *A. lineolata* series); fifth toe long (except in some specimens of *A. griswoldi*); pedal lamellae in contact at least distally (except in *A. fuscata* and some *A. chrysolaema*); black edged ocelli absent (except in *A. fuscata*) 25

25 Interparietal usually entire; parietals long; pectoral sulcus absent; enlarged brachials usually narrowly separated from antebrachials (except in *A. dorsalis*); femoral and anal pores 20–48 . . . . *Ameiva dorsalis* Group

\- Interparietal frequently divided longitudinally; parietals short and square; pectoral sulcus present; enlarged brachials separated from antebrachials by four or more rows of small scales; femoral and anal pores 39–78 . . . . . . *Ameiva erythrocephala* Group

Conclusion and Some Directions for Future Research

In recent years, herpetologists have discovered numerous new species of South American Teiidae, and we are aware of many others awaiting description. We consider the synopsis of morphological characters to be the most important contribution of our study, because it defines a large suite of characters that will help resolve persistent problems in teiid systematics. We urge future authors to report each of these characters in descriptions of new species. Character suites such as folding of the β-keratin containing layers, distribution of scale organs, presence and type of generation glands, and teiid hemipenial morphology may not be familiar to most readers. Nonetheless, their study is relatively simple, they provide valuable diagnostic information, and they should not be omitted from future systematic publications. When preserving specimens, field biologists should evert and tie-off hemipenes of teiid lizards so that characters of importance can be easily viewed. We strongly urge field biologists to preserve some specimens with their mouths partly open so that tongue morphology can be studied. As we point out, this suite of characters has been a source of confusion in the past, and its study has been hampered by the prevailing practice of preserving teiids with their mouths tightly closed.

At least since 2002, herpetologists realized that *Ameiva* and *Cnemidophorus* were polyphyletic, however characters that might be used to define natural groups were limited at best. In this study, we provide detailed definitions of monophyletic groups of teiids. The various phylogenetic analyses published to date often disagree regarding relationships among these groups. However, this disagreement should come as no surprise. We are reminded of research cycles involving pitviper systematics (reviewed by Gutberlet & Harvey 2004; see also Fenwick *et al*. 2009). As in viperids, many monophyletic groups were identified long before our understanding of intergeneric relationships stabilized. We provide a relatively long list of morphological characters, however we have yet to even consider most types of internal anatomy such as osteology and musculature. Moreover, we point to several interesting character suites requiring further study such as tongue morphology, hand-waving and other types of antipredator behavior, and apparent breeding coloration exhibited by certain groups of *Ameiva* and *Cnemidophorus*. These and other under-studied sources of phylogenetic data will add to our database in future research cycles involving teiids.

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Appendix

Specimens Examined

Ameiva ameiva: **BOLIVIA**: **Santa Cruz**: Finca Dos Milanos (UTA R-34735–39), El Refugio (UTA R-38077–79). **PERU: Loreto:** Yarinacocha, Río Ucayali (FMNH 56026, 56030–34). **VENEZUELA: Amazonas:** Tamatama, Rio Orinoco (NMNH 80653–56); Boca Mavaca, 84 km SSE of La Esmeralda (NMNH 162756–59). **Anzoátegui:** Corrientoso, near Carapa (NMNH 80615–16); Soledad (NMNH 80621-24). **Bolivar:** Ciudad Bolivar (NMNH 80602–04); Santa Maria de Erebato (NMNH 561200–06).

Ameiva atrigularis: **VENEZUELA: Distrito Capital:** El Valle (USNM 128914). **Guarico:** Parque Nacional Guatopo, 15 Km NW of Altagracia de Orituco (USNM 217032). **Miranda:** Quebrada Siquire, 11 Km ENE of Santa Lucia (USNM 121197); 1 Km S of Rio Chico (USNM 216981); Curupao, 5 Km NNW of Guarenas (USNM 217033–34); Hacienda Bejuquero, 1 Km S of Rio Chico (USNM 217060–62); Santa Lucia, 11 km ENE on Quebrada Siquire (CM S 7445–48). **Nueva Esparta:** Isla de Margarita, 3 Km NNE of La Asuncion (USNM

217051); Isla de Margarita, near Salamanca, 2 Km N and 1 Km E of La Asuncion (USNM 217052). **Sucre:** Manacal, 26 Km ESE of Carupano (USNM 217053); Cumanacoa (MCZ 9993, holotype of *A. a. melanocephala*). **Vargas:** La Guaira (USNM 22526). **TRINIDAD: Unspecified locality**: MCZ 186018–19 (syntypes of *A. atrigularis*). **Tunapuna/Piarco:** St. George, Mount Saint Benedict (CM S 4845, 4947–53, 6498–501, 6503, 6505–509).

Ameiva auberi: **BAHAMAS**: **Bimini**: North Bimini, Paradise Point (UF 16593, 16596**);** North Bimini, Alice Town (UF 16598–99)**;** Gun Cay (UF 17934). **Andros Island:** Lighthouse along road from Smith's place (USNM 28007), Gibson Cay (USNM 159602, 159604). **New Providence Island:** no other data (USNM 55352). **No other data:** no other data (USNM 14575). **CUBA: Pinar del Rio**: Mariel(USNM 27669). **La Habana:** Marianao (USNM 28007). **Santa Clara**: Cienfuegos (USNM 136096). **Oriente:** Guantanamo Bay US Naval Base (USNM 524103). **Guantánamo:** 8.9 km SW of Hatibonico (USNM 306540).

Ameiva bifrontata: **VENEZUELA: Bolívar:** Caicara (AMNH 38371). **Falcón:** Paraguana Peninsula (FMNH 242238–42). **Nueva Esparta:** Isla Cubagua (SDMNH 34906, 34941–46); Isla de Margarita, Los Robles (USNM 79217–21). **Sucre:** Carupano (UMMZ 107086). **Trujillo:** Sabana Mendoza (UMMZ 57436–42). **Yaracuy:** San Felipe (UMMZ 55532). **COLOMBIA: Cesar:** Valle Dupar, Santa Marta Mountains (UMMZ 55024–30).

Ameiva chrysolaema: **DOMINICAN REPUBLIC: Independencia:** 22 km SE Duverge (KU 232034, 232026, 232024); 4 km SE Duverge (KU 232040, 232039); 2.2 mi W Duverge (KU 232016, 232020); 22 km SE Duverge (KU 232025, 232035, 232029).

Ameiva concolor: **PERU: Cajamarca:** 3500 ft, Paipoy on Rio Crisnejas, 15 mi from Rio Marañon (UMMZ 59193–94); junction between Crisnejas River and Marañon River opposite Tingo de Pauca (UMMZ 59195).

Ameiva corvina: **BRITISH WEST INDES: Sombrero:** Sombrero Island, no other data (UF 19417–21).

Ameiva dorsalis: **JAMAICA: Saint Andrew:** Long Mt. Kingston (UF 18424–25, 18524); Kingston, Sandy Gully (UF 18571–72).

Ameiva erythrocephala: **LESSER ANTILLES**: **St. Kitts:** Basseterre (UF 11387), Golden Rock Airport, 1.5 mi N. Basseterre (UF 11388–89).

Ameiva fuscata: **DOMINICA: St. Patrick:** Pointe Mulatre Estate (UF 15855–56).

Ameiva griswoldi: **LESSER ANTILLES: Antigua:** St. John, St. Johns (UF 11361); St. Paul, English Harbour, Nelson's Dockyard (UF 11362). **Barbuda:** Codrington (UF 11374–75, 14942).

Ameiva lineolata: **HAITI: Artibonite:** 5.0 km NW Desalines (UF 45743).

Ameiva pantherina: **VENEZUELA: Monagas:** Hato Mata de Bejuco, 54 Km SSE of Maturin (USNM 216982, 217048–50); Hato Mata de Bejuco, 55 Km SSE of Maturin (USNM 217047); 42 Km SE of Maturin, LACM (31414–21); 60 Km SE of Maturin, (LACM 31422–41).

Ameiva pluvianotata: **LESSER ANTILLES: Montserrat:** Plymouth (UF 11364–65).

Ameiva praesignis: **VENEZUELA: Apure:** Hato Cariben, Rio Cinaruco, 60 Km NW of Puerto Paez (USNM 162760). **Aragua:** Pie del Cerro La Victoria (USNM 121195–96); El Limon (NMHN 142391–93). **Carabobo:** Sabana Aguirre, 5.5 Km SE of Montalban (USNM 217028–29). **Cojedes:** Finca La Coromoto, Camoruco, Municipio Cojedes (FMNH 127284, FMNH 155874). **Guarico:** San Juan de Los Morros (USNM 72752); Palenque (USNM 128915); Estacion Biologica de los Llanos, 9 Km SE of Calabozo (USNM 217035–45); Calabozo Airport, Distrito Miranda (LACM 130661). **Mérida:** Coromoto, 4 km S and 6.5 Km E of Tabay (USNM 162761–62). **Portuguesa:** San Jorge, Municipio Piritu (FMNH 127284–89). **Trujillo:** El Dividive, 28 Km NW of Valera (USNM 162764); El Dividive, 30 Km NW of Valera (USNM 162790); Valle Verde near Santa Apolonia, 52 Km WNW of Valera (USNM 162791–94). **Vargas:** El Limon (USNM 121194, 162763). **Zulia:** Caño Azul, El Rosario, 65 Km WNW of Encontrados (USNM 217054); Hacienda Platanal, near Cerro Azul, 33 Km NW of La Paz (USNM 217055–56); near Cerro Azul, 39 Km NW of La Paz (USNM 217057). **COLOMBIA: Cesar:** Valle Dupar, Santa Marta Mountains (UMMZ 54915–16); Vallencia, Santa Marta Mountains (UMMZ 54917–21). **PANAMA: Canal Zone:** El Vigia (UMMZ 76012); Gatuncillo (UMMZ 76013); Alhajuela (UMMZ 76014 four specimens); Madden Dam (UMMZ 76015 two specimens).

Ameiva plei analifera (10).—**LESSER ANTILLES**: ST MARTIN: 2.5 mi W, 0.25 mi N Philipsburg (UF 11403, 11404 four specimens: 3, 5, 6, 8); Philipsburg (UF 11405 four specimens: 1, 2, 3, 4); Great Bay, E side (UF 15785).

Ameiva plei plei: **LESSER ANTILLES**: **Anguilla:** 1.0 mi E., 0.5 mi N. Road Bay (UF 11399–400).

Ameivula ocellifera: **BRAZIL: Bahia:** Bahia (AMNH R-36373, 36375). **Ceará:** Fortaleza (FMNH

64387–64390). **Mato Grosso:** confluence of Rio Araguaia and Tapirapé, Tapirapé village (AMNH R-87903). Santa Rosa, west of Descalvados (FMNH 9119–9125); Urucum (FMNH 9199). **Paraiba:** Independencia (FMNH 64384-64385). **Pernambuco:** Olinda (FMNH 42088); Recife (FMNH 64383). **Rio Grande do Norte** Baixa Verde (FMNH 64371–64375), Ceara Mirim (FMNH 64368–64370), Natal (FMNH 64376–64382). **BOLIVIA: Santa Cruz:** La Brecha, ca 104–120 km NE Charagua, Izozog Region (AMNH R-141485, 141497). **PARAGUAY: Central:** Asunción (FMNH 13155–56). **Unknown:** Fotrín Guachala, Río Pilcomayo (FMNH 44149, 44152–44153, 44156).

Aspidoscelis angusticeps: **MEXICO: Yucatan:** Cholul (UTA 29397).

Aspidoscelis burti: **USA: ARIZONA: Santa Cruz:** Santa Rita Mountains, Gardner Canyon (UTA 28876–78). **Pima:** Santa Catalina Mountains (UTA 32038–39).

Aspidoscelis deppi: **GUATEMALA: Huehuetenango:** along road to Chacaj, 4.7 mi W by road jct Nentón-Gracias a Dios road (UTA 52187–98).

Aspidoscelis exsanguis: **MEXICO: Chihuahua:** Sierra San Luis, Cañon del Oso (UTA 17568–69). **USA: TEXAS: Brewster:** Chisos Mountains (UTA 29), 8.0 km N Alpine (UTA 92, 93, 95), Hess Ranch (UTA 44529–31).

Aspidoscelis gularis: **USA: TEXAS: Parker:** Mineral Wells, Lake Mineral Wells State Park (UTA 32588).

Aspidoscelis guttatus: **MEXICO: Oaxaca:** : vicinity of Mixtequilla (UTA 52686, 52689, 52696), Area Santo Domingo Tehuantepec-Albaro Obregon (UTA 52691).

Aspidoscelis inornatus: **USA: TEXAS: Brewster:** Black Gap Wildlife Management Area (UTA 44255–56), S side Dove Mountain road, ca 200 m E jct US 385 (UTA 17675–77), 8.0 km N Alpine (UTA 94, 97–99).

Aspidoscelis laredoensis: **USA: TEXAS: Starr:** SE of Falcon Dam (UTA 14931–32), Rancho Falcon, near Falcon Dam (UTA 33690).

Aspidoscelis marmorata: **USA: NEW MEXICO: Dona Ana:** Madamna High School (UTA 44102); 3.2 km W 'A' Mtn (UTA 44103); Picacho Peak, N side at base (UTA 44105). **TEXAS: Brewster:** Black Gap WMA (UTA 44087); Black Gap WMA, 6.4 km E Maravillas Creek on R¡o Grande River (UTA 44089).

Aspidoscelis mexicanus: **MEXICO: Oaxaca:** 5.8 mi S Sola de Vega (UTA 3465), El Tejocote (UTA 4231), 3–5 mi E Mitla (UTA 51915, 51917).

Aspidoscelis montaguae: **GUATEMALA: Baja Verapaz:** Salamá (UTA 42055–56), Rabinal (UTA 42058–60).

Aspidoscelis neomexicanus: **USA: TEXAS: El Paso:** jct St Hwy 20 and I-10 (UTA 28880). **NEW MEXICO: Bernalillo:** Bernalillo (UTA 30527–28).

Aspidoscelis parvisocius: **MEXICO: Puebla:** Zapotitlan (UTA 52732–33), 3.5 mi SSW of Zapotitlan on MX 125 (UTA 8805, 8776), 5.1 km SSW Zapotitlan Salinas (UTA 11947).

Aspidoscelis sexlineata: **USA: TEXAS: Anderson:** Engling Wildlife Management Area (UTA 17918, 17920–21). **Brewster:** Rt 33 near McDade 30.25903 N; 97.22383 W (UTA 58737). **Parker:** Brazos River at Interstate Hwy 20, Littlefield Bend (UTA 16999); 3.5 km NW jct I-20 and Brazos River, eastern Gilbert Valley (UTA 17124). *Aspidoscelis tigris*: **USA: NEVADA: Clark:** Virgin Mts., near Whitney Pockets (UTA 51038); Newberry Mts., in wash between Secondary State Route 76 and power line road (UTA 51037). **Lincoln:** White River Narrows (UTA 51042). **Nye:** Bullfrog Hills, Beatty (UTA 45110); foothills between High Peak and Stewart Valley outside of Pahrump (UTA 51043).

Aurivela longicauda: **ARGENTINA: Buenos Aires:** Bahia Blanca (AMNH 17020).

Aurivela tergolaevigata: **ARGENTINA: Catamarca:** arid section (FMNH 10836–40). **La Rioja:** Famatina, 9.9 km W Atinaco (AMNH 144524–25).

Callopistes flavipunctatus: **PERU: Piura:** Verdun Alto (FMNH 41584), Talara (FMNH 41586), Lobito (FMNH 41588). **Unspecified:** Parinas Valley, ca 6 m N Talara, near Negritos (FMNH 8382); plains back of Talara (FMNH 37369).

Callopistes maculatus: **CHILE: Atacama:** no other data (FMNH 9921). **Santiago:** San Jose de Maipo (FMNH 5877); no other data (FMNH 9934). **UNSPECIFIED:** no other data (FMNH 223689–90).

Cnemidophorus arenivagus: **VENEZUELA: Falcón:** Paraguaná Peninsula, 6 km S Adicora on Coastal Rd. (AMNH 142582); ca. 4 km N Moruy (AMNH 142585); Capatarida (USNM 217099). **COLOMBIA: La Guajira:** Merochon, 5 km SE Uribia (AMNH 109992–94).

Cnemidophorus arubensis: **DUTCH ANTILLES: Aruba:** near Oranjestad (UMMZ 57225–26, 57232); Seroe Caneshito (UMMZ 57227–28); Rooi Lamoenchi (UMMZ 57229–31); near Boedoei (UMMZ 57233–34), 57241–42, 57244); "Aromd Campo West Punt" (UMMZ 57235–42).

Cnemidophorus cf. *nigricolor:* **VENEZUELA: Dependencias Federales:** Islas Las Aves (LACM 114859, CM S8132); Aves de Sotavento (LACM 108876, 109458).

Cnemidophorus lemniscatus espeuti: **COLOMBIA: Isla de San Andrés:** "San Andres Island near Big Pond" (UMMZ 127880).

Cnemidophorus lemniscatus gaigei: **COLOMBIA: Cesar:** Badillo, Santa Marta Mountains (UMMZ 54890–91); Valle Dupar, Santa Marta Mountains (UMMZ 54892–99). **La Guajira:** Merochon, 5 km SE Uribia (AMNH 106218).

Cnemidophorus flavissimus: **VENEZUELA: Dependencias Federales:** Archipielago Los Frailes (MBUCV 980, 983–88, 3422; MCZ 50206).

Cnemidophorus gramivagus: **COLOMBIA: Arauca:** Cravo Norte (AMNH 97411, 97416–19, 97423). **VENEZUELA: Apure:** 6.0 km W San Fernando de Apure (TCWC 46125–26, 46145, 46155–56, 46159, 46161, 46166–67, 46130).

Cnemidophorus lemniscatus lemniscatus: **VENEZUELA: Anzoátegui:** Puerto La Cruz (FMNH S7268–72). **Aragua:** Pie del Cerro La Victoria (USNM 121187, CM 7401, 7406, 7409, 7419, 7423). **Distrito Federal:** Puerto La Cruz (CM 7269–71, 7299–300, 7343). **Miranda:** Quebrada Siquire, 11 km ENE of Santa Lucia (USNM 121188); Petare (CM 7429). **Sucre:** Cumanacoa (FMNH S7907–14, CM 7898, 7907–13, 7932); Ensenada Cauranta, 9 km NE of Guiria (USNM 217102). **Vargas:** La Guaira (USNM 27809–16); Puerto La Cruz (USNM 121189–91).

Cnemidophorus lemniscatus splendidus: **VENEZUELA: Falcón:** Paraguana Peninsula, 6 km W Pueblo Nuevo, Monte Cano Biological Reserve (FMNH 242236); Paraguana Peninsula, Aguaque, "Casa Colonial," off road to Vinculo (FMNH 252723).

Cnemidophorus leucopsammus: **Venezuela: Dependencias Federales:** Isla La Blanquilla, Playa La Falucha (MCZ 133533); Isla La Blanquilla, no specific locality (LACM 138126, YPM 6742).

Cnemidophorus murinus: **DUTCH ANTILLES: Curaçao**: (FMNH 2649, three of four specimens), Scharloo (UMMZ 57245-53), North side of Ronde Klip (UMMZ 57254); Hills W of Ent to Laguma near Willembrodus [= Sint Willibrodus] (57285–87).

Cnemidophorus nigricolor: **VENEZUELA: Dependencias Federales:** Los Roques Archipelago (AMNH 111057, 111056–57, 111059–60, LACM 109456–57, 109494, 113728, MCZ 38183–84, UCM 59594, USNM 79232); Gran Roque, Los Roques Archipelago (UCM 45296–300, 45302–303, 45308–309, 45311, 45314, 45316–319, 45321, 45329, 45336); Cayo Tortuga, Los Roques Archipelago (LACM 128378); Dos Mosquites, Los Roques Archipelago (LACM 128380).

Cnemidophorus rostralis: **VENEZUELA: Dependencias Federales:** Isla La Tortuga (SDNHM 34885–95).

Cnemidophorus ruthveni: **DUTCH ANTILLES: Bonaire:** no other data (UMMZ 57264–66), Seroe Wassau beyond El Goto (UMMZ 57267–68), Seroe Grandi (UMMZ 57269–74, 57280), Santa Barbara beyond El Hato (UMMZ 57281). **Klein Bonaire:** no other data (UMMZ 57272–79).

Cnemidophorus senectus: **VENEZUELA: Nueva Esparta:** Cubagua (SDNHM 34907–10); Isla de Margarita, El Valle (MCZ 9914–17); Isla de Margarita, Los Robles (USNM 79222–23); Isla de Margarita, Porlamar (MBUCV 327–329, 331–332); Isla de Margarita, Porlamar Airport (USNM 217101); Isla de Margarita, no specific locality (SDNHM 34896–905, 34954; MBUCV 1017-19; 339-40).

Cnemidophorus vanzoi: **LESSER ANTILLES: St. Lucia:** Vieux Fort, Maria Islands (KU 234871–74, 234876).

Contomastix charrua: **ARGENTINA: Rocha:** Cabo Polonia (AMNH R-116321).

Contomastix lacertoides: **ARGENTINA: Cordoba:** Achiras (AMNH 65209–65211). **BRAZIL: Rio Grande do Sul** 10 km SE Osorio (FMNH 80092–80095). **URUGUAY: Maldonado:** Maldonado (FMNH 10110, 10135, 10138, 10191, 10193; AMNH R-115938); 10 km NW Garzón, Arroyo Garzón (FMNH 10292); Sierra de Animas (FMNH 217269). **Tacuarembó:** Pozo Hondo, Tambores (FMNH 216406).

Contomastix leachei: **ARGENTINA: Jujuy:** Estancia Cachupunco, Sierra de Santa Barbara, Departamento Santa Barbara (FML 855-2); Angosto del Río Pescado, Finca Arrazayál, Departamento Orán (FML 907-1); Camino entre Libertador General San Martín y Caimancito, desde Ruta Provincinal 194 hacia Estancia La Realidad

(359 m), Departamento Ledesma, 23° 45’ 46.4” S, 64° 32’ 58.7” W. **Salta:** Sección de Aguas Negras, Parque Nacional Calilegua, Departamento Ledesma (FML 7344).

Contomastix serrana: **ARGENTINA: Catamarca:** Departamento Ambato, El Rodeo (MVZ 12754–57).

Contomastix vittata: **BOLIVIA: Chuquisaca:** Yotala, Oropeza Province, 2600 m, 19° 09'23.61" S, 65° 16'04.08" W (MHNC-R 198). **Cochabamba:** Pacata, Cercdo Province, 2550 m, 17° 21'43.62" S, 66° 7'18.60" W (MHNC-R 199); Caramarca, Quillacollo Province, 2600 m, 17° 27'10.42" S, 66° 17'49.03" W (BMNH 1946.8.31.13, MHNC-R 197, 201, 203,; Parotani, Quillacollo Province, 2475 m, 17° 34'15.12" S, 66° 20'35.98" W (MHNC-R 186, 205); Cerro Cota, 1.5 Km NE Vinto Chico, Quillacollo province, 17.423386º S, 66.307409º W, 2770 m, (UTA 58472–58480); Vinto Chico, 2500 m, 17° 25'57.61" S, 66° 19'6.90" W (MHNC-R 200, 202). **Santa Cruz:** Mataral, “La Laguna,” Florida Province, 1452 m, 18° 6’ 50” S, 64° 12’ 56” W. (MNK 1669); Pampagrande, Florida Province, 1471 m, 18° 5’ 22” S, 64° 6’ 42” W (MNK 1005).

Crocodilurus amazonicus: **BRAZIL: Amazonas:** Nova Olinda, Rio Madeira (USNM 200689). **NO DATA:** no data (USNM 89371; UTA 7233).

Dicrodon guttulatum: **ECUADOR: Manabi:** Manta (FMNH 53835–36, 53849, 53853. **PERU: Lambayeque:** 3 km SE Morrope (MVZ 82415, 82417). **Piura:** Talara (FMNH 53856); 4 km SE Bayovar (MVZ 82419); Parinas, 7 km N and 15 km E Talara (MVZ 82423); 5 km E Las Lomas, 60 km ENE Sullana (MVZ 82425).

Dicrodon heterolepis: **PERU: Ancash:** 5 km SE Casma, Ruinas de Sechin (KU 163770–72); 13 km S Nasca (KU 163776). **La Libertad:** Chan Chan, near Trujillo (FMNH 34244, 34257 two specimens). **Ica:** Hacienda San Jacinto, near Ica (FMNH 39356–57).

Dracaena guianensis: **PERU: Loreto:** 5 km NNE Iquitos (TCWC 42022); Iquitos (TCWC 44554); Moropon (TCWC 38119–21), Centro Union, Rio Aucayo (TCWC 38170).

Holcosus anomalus: **COLOMBIA: Cauca:** Quebrada Guanguí, about 0.5 km above its junction with Río Patia, in upper Río Saija drainage, 100–200 m (AMNH 107908–09, 109685, 109694). **Chocó:** Rio San Juan (AMNH 108993); Pangala, ca 40 km (by river) N of Palestina, lower Rio San Juan (AMNH 111042); Quebrada Taparal, ca 12 km (by river) N of Palestina, lower Rio San Juan (AMNH 111052). **Valle:** Anchicaya (KU 152678–81).

Holcosus bridgesii: **COLOMBIA: Nariño:** Rio Mataje, Pacific coast during archaeological excavation (site CHP-57) (FMNH 165155–57); Tumaco, El Morro, Pacific coast (FMNH 166245); mouth of Rio Curay, 1.5 hours N of Tumaco (FMNH 166246); Tangareal Tumaco (KU 192691). **ECUADOR: Carchi:** Cantón Tulcán, Parroquia Tobar Donoso, 223 m (MECN 6725).

Holcosus festivus: **COLOMBIA: Chocó:** Pizarro (FMNH 43816, 43818, 43821, 43826–27). **GUATEMALA**: **Izabal:** Morales, Sierra de Caral, San Miguelito (UTA 39978, 39979, 37537, 37529, 33265, 37533, 37528); Puerto Barrios, Finca El Jabalí (UTA 39975); Livingston, Sierra de Santa Cruz, Cerro 1019 (lado este) (UTA 39981); Montañas del Mico, Las Escobas, 5.1 road km WSW Puerto Santo Tomás (UTA 29347); Los Amates, Sierra del Espíritu Santo, Aldea San Antonio (UTA 29342, 37530–31, 37535, 29344).

Holcosus leptophrys: **PANAMA: Darién:** SG VIII site (FMNH 170100); Rio Lara site (FMNH 170101); Santa Fe camp (FMNH 170102); Yavitza (MVZ 83218, 83221–22, 83224–25, 83227–28, 83230–32).

Holcosus niceforoi: **COLOMBIA: Tolima:** Honda (AMNH 35300); Salado (KU 210030, 210028).

Holcosus orcesi: **ECUADOR: Azuay:** 1.4 km NE Abdon Calderon, 1420 m (KU 152686).

Holcosus quadrilineatus: **COSTA RICA: Limon:** beach between mouth of Rio Tortuguero and town of Tortuguero, E side of River (MVZ 149853). **Puntarenas:** Rincon (MVZ 82976, 82980, 82990, 82995–99). **Unspecified:** Rio Puerto Nuevo, 13.7 mi NE Palmar del Norte (UTA 338).

Holcosus septemlineatus: **ECUADOR: Esmeraldas:** San Mateo, 100 m (FMNH 27667–68; 27678–80); Santo Domingo de los Colorados, 30 km (airline) NNW of, Hacienda Equinox (USNM 152408); 1 30 52 S, 80 32 13 W (USNM 193242). **Los Rios:** Vinces (USNM 222796); Quevedo (USNM 193264); ca. 1 km E of Jauneche (USNM 285778). **Manabí:** Parque Nacional Machalilla (MECN 5959–60); 22 km S of Jipijapa, near Jipijapa-Nobol Highway (USNM 193242). **Pinchincha:** km 124 on Quito-SantoDomingo de Los Colorados road (USNM 152424).

Holcosus undulatus: **GUATEMALA: Alta Verapaz:** Finca Rubelpec (UTA 46890, 46733); Finca San Juan (UTA 46734, 46733, 52199)

Kentropyx altamazonica: **BOLIVIA: Santa Cruz:** El Refugio, Velasco Province (UTA 59487–88). **PERU: Loreto:** Belen, on Rio Itaya (TCWC 38122); Iquitos (TCWC 38124, 40401, 42833–34); Central Union (TCWC 42767); Central Union, Rio Aucayo (TCWC 39033); Moropon (TCWC 40402, 42768,); Indiana (TCWC 40403–04);

Kentropyx borckiana: **GUAYANA: Demarara:** Georgetown (TCWC 58530, 58532–34, 58536–39, 58603, 58611).

Kentropyx calcarata: **VENEZUELA: Bolivar:** 120 km S El Dorado, near Salto del Danto (TCWC 60142–43).

Kentropyx lagartija: **ARGENTINA: Tucumán:** Rio Sali, San Miguel de Tucumán (MVZ 127395, 127397, 127399–406).

Kentropyx pelviceps: **PERU: Loreto:** Moropon (TCWC 38130); Mishana, on Rio Nanay (TCWC 39041–42, 39045–46, 39050, 39052, 39055, 42025–26).

Kentropyx striata: **FRENCH GUIANA: Cayenne:** 1.6 km W, 1.8 km S Iracoubo (TCWC 65653; 65656–57). **VENEZUELA: Apure:** Rio Cinaruco, Laguna Larga (TCWC 83029–30); 6 km W San Fernando de Apure (TCWC 46236); Hato la Guanota, 4 km W San Fernando de Apure (TCWC 44880). **Bolivar:** 16 km N El Manteco (TCWC 59191).

Kentropyx viridistriga: **ARGENTINA: Corrientes:** Villa Ilinares (TCWC 70293). **PARAGUAY: Amambay:** Parque Nacional Cerro Cora, ca. 32 km WSW of Pedro Juan Caballero (USNM 341984). **Canindeyu:** Mbaracayu Reserve + or - 22 km E Villa Ygatimi (TCWC 72220).

Kentropyx vanzoi: **BOLIVIA: Santa Cruz:** El Refugio, Velasco Province (UTA 59489–90).

Medopheos edracanthus: **ECUADOR: El Oro:** Machala (FMNH 197961). **Guayas:** 8 km S Guayaquil, Puerto Maritimo (KU 121149); Cerro Santa Ana (KU 121142–44, 121147). **Manabi:** Manta (FMNH 53860); **Manabi:** Parque Nacional Machalilla (MECN 5961–62, 6059). **PERU: Piura:** near Huasimal, on Cascadero Trail, near Ecuador border, Amotape Mts near edge of humid zone (FMNH 9830–32).

Salvator merianae: **BOLIVIA: Santa Cruz:** El Refugio, Velasco Province (UTA 59492). **PARAGUAY: Concepción:** Pozo Barreto, along Rio Aquidaban, W of town (TCWC 90540, 90550–52, 90554-56, 90563).

Salvator rufescens: **ARGENTINA: Córdoba:** Departamento Rio Primero, ca. 10 km N La Puerta (MVZ 128169); Departamento Capital, La Carolina, ca. 2 km SE Villa Warcalde (MVZ 128171).

Teius oculatus: **URUGUAY: Montevideo:** Montevideo (USNM 65575) **Cerro Largo:** no other data (65613–14) **No other data:** no other data (USNM 12320, 73533).

Teius teyou: **BOLIVIA: Santa Cruz:** Chiquitos, Santiago, serranía y cerca (FMNH 195978–79, 195985, 195988, 195991). **BRAZIL: Mato Grosso:** Urucum (FMNH 9199). **PARAGUAY: Chaco:** Fortin Guachalla, Rio Pilcomayo (FMNH 44154–55).

Tupinambis palustris: **BOLIVIA: Santa Cruz:** El Refugio, Velasco Province (UTA 59492).

Tupinambis teguixin: **ECUADOR: Sucumbios:** Santa Cecilia (KU 175382). **GUYANA:** No other data (UF 61477).