SYSTEMATICS OF NORTH AMERICAN COLUBRID SNAKES RELATED TO *TANTILLA PLANICEPS* (BLAINVILLE)

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ABSTRACT

Examination of numerous characters (primarily of head coloration, hemipenes, scutellation, and size and proportions) of more than 750 specimens suggests that *Tantilla planiceps*, as recognized by Tanner (1966), actually represents four distinct species: *Tantilla planiceps* (Blainville, 1835), of southern California and Baja California; *Tantilla yaquia* Smith, 1942, of southeastern Arizona and northwestern Mexico; *Tantilla atriceps* (Günther, 1895), of southern Texas and northeastern Mexico; and *Tantilla hobartsmithi* Taylor, "1936" [1937], which is broadly distributed in the southwestern United States and northern Mexico and usually has been considered synonymous with *T. atriceps*. Synonymies, diagnoses, descriptions, illustrations, range maps, and ecological notes are presented for each of these species.

Tantilla atriceps and *T. hobartsmithi* are sibling species with strikingly different hemipenes. They also are the only species of the complex for which sympatry (in Coahuila) has been documented. Future collecting may well demonstrate sympatry at the periphery of the ranges of *T. planiceps* and *T. hobartsmithi* and of *T. yaquia* and *T. hobartsmithi*.

Analysis of variation indicates that some classical taxonomic characters used previously (e.g., number of ventral scales) are not particularly reliable for distinguishing among species of *Tantilla*. The best specific characters we found are in anatomy of the hemipenes. Variation in hemipenial features usually is correlated with variation in head coloration. Because *T. atriceps* and *T. hobartsmithi* are sibling species, now known to differ consistently only in hemipenial characters, and because they exhibit sympatry at the periphery of their ranges, specific identification of females is a problem that requires additional investigation.

Once it appeared that male copulatory organs would provide important, diagnostic characters for the four species formerly assigned to *T. planiceps*, we examined hemipenes on as many specimens (258) as were reasonably available. These included pertinent type-specimens and outgroup comparisons with *T. gracilis*, *T. nigriceps*, and *T. wilcoxi*; hemipenes of these species are distinctive also, and examples of all are described and illustrated (excepting *T. wilcoxi*). One problem that remains under investigation is the specific relationship between *T. atriceps* and southern populations of *T. nigriceps*. No such problem exists between *T. hobartsmithi* and *T. nigriceps*, however, as they differ rather consistently in hemipenes and head coloration, and they are sympatric in the western part of the range of *T. nigriceps*.

We also examined maxillary bones, sex ratio, and karyotypes (including that of *T. coronata*) in addition to the characters mentioned above. Most of these data are not taxonomically useful, due either to lack of significant variation or lack of comparative data from congeners.

A preferred cladogram of phylogenetic relationships of *T. wilcoxi*, *T. planiceps*, *T. yaquia*, *T. nigriceps*, *T. atriceps*, *T. hobartsmithi*, and *T. gracilis* is presented, as is a key to all species of *Tantilla* known to occur in the western United States and northern Mexico.

The most useful characters for distinguishing species of *Tantilla*, particularly in North America, appear to be in the hemipenes and head coloration. Hereafter, all taxonomic studies within *Tantilla* routinely should include examination of hemipenes of the specimens examined. When possible, males should be selected as type-specimens.

INTRODUCTION

In 1963 we found a young *Tantilla* in riparian habitat in Guadalupe Canyon of the Guadalupe Mountains, Hidalgo County, New Mexico. In the course of identifying that snake, we became impressed by the lack of information concerning the species of *Tantilla* occurring in the southwestern United States and northern Mexico. Although some distribution maps at that time did not indicate its occurrence in the area of Guadalupe Canyon, the traits of head coloration and number of ventral scales indicated that our specimen was *Tantilla atriceps* (Günther, 1895). We were concerned, however, that apparently one of the best indicators that it was not a specimen of the morphologically similar *Tantilla utahensis* Blanchard, 1938 was that we found the snake

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in New Mexico instead of Utah! At that time there had been no analyses of geographic variation in these forms, and thus we initiated this investigation to test the working hypothesis that *T. atriceps* and *T. utahensis* are conspecific.

We began borrowing specimens of *T. atriceps* and *T. utahensis* from various institutions and recording data on external morphology. Our intent was to re-examine their taxonomic status with an understanding of the local and geographic variation in a variety of traits. Several important events led to adjustments in procedures during the course of our work: (1) Tanner (1966) concluded that *T. atriceps, T. utahensis,* and several additional named populations of *Tantilla* in western North America are subspecies of *Tantilla planiceps* (Blainville, 1835). Tanner's study did not include comparisons of local population samples, which we considered necessary for analyzing this difficult problem, and thus we continued our efforts. However, his inclusion of *atriceps* and *utahensis* as subspecies in a complex with several other forms required expanding the scope of our investigation, so we borrowed additional material. (2) McDiarmid (1968), in a detailed study of intraspecific variation, concluded that *Tantilla yaquia* Smith, 1942 was not conspecific with either *T. planiceps* or *T. atriceps,* although Tanner (1966) had included *yaquia* among the subspecies of *T. planiceps.* McDiarmid suggested additional characters to examine and shared our belief that a more thorough understanding of geographical variation was necessary to clarify and stabilize the taxonomy of these snakes. (3) Colleagues (Dr. S. B. McDowell and Dr. C. W. Myers) advised us to examine hemipenes for characters that could be vital to our investigation. Telford (1966) also had considered hemipenes as important for distinguishing some species of *Tantilla* in the southeastern United States.

Thus, the present study is an investigation of geographic variation in several species of *Tantilla,* a taxonomic review of selected forms, and an evaluation of the characters used to recognize them. The taxonomic instability of this group of snakes has resulted

from: extensive geographic variation, perhaps resulting from a highly secretive, fossorial way of life with low vagility; evolution of sibling species (cryptic or symmorphic species; McCafferty and Chandler, 1974); and utilization of unreliable characters in earlier studies.

We hope this revision will result in taxonomic stability for the species considered here and will contribute to an understanding of their evolutionary relationships. Nevertheless, we realize we have not solved all the basic problems pertaining to these species. For example, we recognize many species primarily on the basis of color pattern of the head in combination with morphology of the male copulatory organs. In instances where head coloration alone will not suffice to identify specimens, one must rely on hemipenial traits. In some instances, therefore, it is virtually impossible to identify individual females to species. Nevertheless, as a consequence of having examined variation in numerous characters and more than 750 specimens, we believe that the difficulties in identifying certain females and using hemipenial characters in the key are imposed on us by the biological realities of the material studied. The challenge of discovering reliable characters for identifying problematical specimens of the sibling species remains for future endeavors.

BRIEF TAXONOMIC HISTORY

The genus *Tantilla* Baird and Girard, 1853 may be defined as follows: Size usually small, body slender, head not conspicuously distinct from body; typical colubrid cephalic scutellation with one preocular, one or two postoculars, one (at least partly divided) or two nasals, but loreal lacking on each side; smooth dorsal scales in 15 rows and lacking apical pits; anal plate divided; subcaudals paired; two enlarged, grooved fangs situated posteriorly on the maxilla and separated by a small diastema from the other maxillary teeth; pupil round. Hardy and Cole (1968) discussed variation of these characters in *Tantilla gracilis* Baird and Girard, 1853.

The junior synonym *Homalocranion* Du-

méril, 1853[1] was emended without comment or explanation to *Homalocranium* by Günther (1862).[2] Subsequent authors often have used either *Homalocranium* (e.g., Boulenger, 1896; Mocquard, 1899) or *Tantilla* (e.g., Cope, 1861, "1876" [1875]; Stejneger and Barbour, 1917), without explaining the basis for their decision as to which generic name to employ. However, Brown (1901) specified a preference for *Tantilla* because it was originally described more thoroughly than *Homalocranion*. Assuming it is correct that both *Tantilla* Baird and Girard and *Homalocranion* Duméril were published in 1853 as printed on the publications, *Tantilla* has priority since Baird and Girard's publication is dated "January, 1853," whereas no month is specified for Duméril's publication. This is in accordance with Article 21 (b) of the International Code of Zoological Nomenclature.

The genus *Tantilla,* which includes approximately 50 species recognized today, has an overall geographic range extending from the southern United States through Mexico, Central America, and South America to northern Argentina (Peters and Orejas-Miranda, 1970). The 10 species currently recognized as occurring at least in part in the United States are the following:

Tantilla coronata Baird and Girard, 1853: We do not consider the status of this species in the present paper. It occurs in the southeastern United States and was reviewed recently (Telford, 1966).

Tantilla oolitica Telford, 1966: This species occurs only in southern Florida and is not considered here.

Tantilla relicta Telford, 1966: This species occurs only in peninsular Florida and is not considered here.

Tantilla gracilis Baird and Girard, 1853: The status of this species, which occurs in the midwestern United States and northern Mexico (Savitzky and Collins, 1971) has not

been questioned recently, and we recognize it as a valid species. We describe the hemipenis of *T. gracilis* and aspects of its variation in this paper. We discussed variation in other characters elsewhere, and we do not recognize subspecies (Hardy and Cole, 1968).

Tantilla nigriceps Kennicott, 1860: The status of this species, which occurs in the midwestern and southwestern United States and northern Mexico (Smith, 1942) has not been questioned recently, and we recognize it as a valid species. We describe the hemipenis of *T. nigriceps* and aspects of its variation in this paper. Considering the present knowledge of geographic variation in other species, the subspecies of *T. nigriceps,* recognized primarily on numbers of ventral and subcaudal scales (*T. n. nigriceps* and *T. n. fumiceps*; see Smith, 1942), are not based on a thorough understanding of variation and are not sufficiently distinctive to warrant recognition. We hereby propose treating *Tantilla nigriceps* as a monotypic species hereafter, unless and until future analyses of variation should indicate otherwise.

Tantilla rubra Cope, "1876" [1875]: In the present paper we do not question the status of this Mexican species, which barely reaches the United States in southern Texas. We concur with Smith and Werler (1969) that *Tantilla diabola* Fouquette and Potter, 1961 is best considered a junior synonym of *T. rubra* unless and until more detailed analyses of variation may indicate otherwise. Whether or not *Tantilla cucullata* Minton, 1956 is conspecific with either or both of these forms, as suggested by Degenhardt, Brown, and Easterla (1976), is not entirely clear to us and is beyond the scope of this paper. Examination of hemipenes probably will be instrumental in solving the difficult taxonomic problems involving *rubra, diabola,* and *cucullata.*

Tantilla wilcoxi Stejneger, 1902: The status of this Mexican species, which barely enters the United States in southern Arizona, has not been questioned recently, and we recognize it as a valid species. We describe the hemipenis of *T. wilcoxi* and aspects of its variation in this paper. The subspecies of *T.*

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[1] Peters and Orejas-Miranda (1970) cited the year of publication as 1854, but we were unable to verify that date. The date 1853 is printed on the volume containing this work, and Vanzolini (1977) accepted this date also.

[2] Peters and Orejas-Miranda (1970) cited a subsequent paper for the emendation (Günther, 1863).

TABLE 1
Status of Names of Snakes Formerly and Presently Referred to *Tantilla planiceps*

Original combination	Author, date	Proposed status
planiceps, Coluber	Blainville, 1835	*Tantilla planiceps*
atriceps, Homalocranium	Günther, 1895	*Tantilla atriceps*
eiseni, Tantilla	Stejneger, "1895" [1896]	Synonym of *T. planiceps*
hobartsmithi, Tantilla	Taylor, "1936" [1937]	*Tantilla hobartsmithi*
utahensis, Tantilla	Blanchard, 1938	Synonym of *T. hobartsmithi*
yaquia, Tantilla	Smith, 1942	*Tantilla yaquia*
bogerti, Tantilla	Hartweg, 1944	Synonym of *T. yaquia*
transmontana, Tantilla eiseni	Klauber, 1943	Synonym of *T. planiceps*

wilcoxi, recognized primarily on numbers of ventral and subcaudal scales (*T. w. wilcoxi* and *T. w. rubricata*; see Smith, 1942), are not based on a thorough understanding of variation and are not sufficiently distinctive to warrant recognition. We hereby propose treating *Tantilla wilcoxi* as a monotypic species hereafter, unless and until future analyses of variation should indicate otherwise.

Tantilla yaquia Smith, 1942: This Mexican species barely enters the United States in southern Arizona. It is one of the western forms whose status has vacillated in recent years. Tanner (1966) considered two different populations of *T. yaquia* as subspecies of *Tantilla planiceps.* However, we concur with McDiarmid (1968) and Hardy and McDiarmid (1969), who concluded that *T. yaquia* is specifically distinct from *T. planiceps* and that the clinal variation in *T. yaquia* is not consistent with the recognition of subspecies. We describe the hemipenis of *T. yaquia* and discuss aspects of its variation in this paper.

Tantilla planiceps (Blainville, 1835): The present paper is directed at clarifying the relationships of the snakes presently included in *T. planiceps.* Tanner (1966) visualized *planiceps* as a polytypic species with seven subspecies: *T. p. planiceps, T. p. eiseni, T. p. transmontana, T. p. utahensis, T. p. atriceps, T. p. yaquia,* and *T. p. bogerti.* Another form (*Tantilla hobartsmithi* Taylor, "1936" [1937]) was considered by Tanner as a junior synonym of *T. planiceps atriceps.* Prior to Tanner's review, all of these nominal

forms, excepting *Tantilla eiseni transmontana* Klauber, 1943, had been considered as separate species. Since Tanner's review, McDiarmid (1968) and Hardy and McDiarmid (1969) have elevated *yaquia* to specific status, relegated *bogerti* to the synonymy of *yaquia,* and suggested that probably *planiceps* and *atriceps* are specifically distinct; nevertheless, they refrained from making formal proposals concerning *atriceps,* pending completion of the present study.

We conclude that none of the past taxonomic arrangements proposed for the forms in the *planiceps* complex has reflected their relationships properly at the species level. Our present understanding of these forms is that even after the proper removal of *T. yaquia* (see McDiarmid, 1968), *T. planiceps* as visualized by Tanner (1966) consists of three separate species: *T. planiceps* (including *eiseni* and *transmontana*), which occurs in Baja California and California; *T. atriceps,* which occurs in southern Texas and northeastern Mexico (primarily Coahuila, Nuevo León, and San Luis Potosí); and *T. hobartsmithi* (including *utahensis* and most populations formerly considered as *atriceps*), a sibling species of *T. atriceps* that occurs widely in the southwestern United States and northern Mexico (primarily Coahuila, Chihuahua, and Sonora). We do not recognize subspecies within any of these three species (table 1).

We present our taxonomic conclusions early so we can use the names properly throughout the rest of the paper, where we attempt to justify our conclusions.

ACKNOWLEDGMENTS AND MATERIALS

We have examined more than 730 snakes of the *Tantilla planiceps* complex. These specimens have been accumulating for more than 135 years in 52 herpetological collections. Specimens examined include the holotype of *Coluber planiceps* Blainville, 1835, the syntypes of *Homalocranium atriceps* Günther, 1895, the holotype of *Tantilla eiseni* Stejneger, "1895" [1896], the holotype of *Tantilla hobartsmithi* Taylor, "1936" [1937], the holotype of *Tantilla utahensis* Blanchard, 1938, the holotype of *Tantilla bogerti* Hartweg, 1944, and the holotype of *Homalocranion praeoculum* Bocourt, 1883 (1870–1909).

The abbreviations listed below are used throughout this report in reference to specimens from the respective collections; we are grateful to our colleagues (in parentheses) who facilitated examination of these specimens.

AIM, Texas A and I University, Kingsville (Dr. Allan H. Chaney)

AMNH, American Museum of Natural History, New York

ASDM, Arizona-Sonora Desert Museum, Tucson (Mr. Merritt S. Keasey, III; Mr. William H. Woodin, III)

ASU, Arizona State University, Tempe (Dr. M. J. Fouquette)

BCB, private collection of Dr. Bryce C. Brown, Waco, Texas

BMNH, British Museum (Natural History), London (Dr. Alice G. C. Grandison; Dr. Colin J. McCarthy)

BYU, Brigham Young University, Provo, Utah (Dr. Wilmer W. Tanner)

CA, Chicago Academy of Sciences, Illinois (Dr. W. J. Beecher)

CAS, California Academy of Sciences, San Francisco (Dr. Steven C. Anderson; Dr. Alan E. Leviton)

CCNP, Carlsbad Caverns National Park, Carlsbad, New Mexico (Mr. Philip F. Van Cleave)

CM, Carnegie Museum, Pittsburgh, Pennsylvania (Dr. Clarence J. McCoy)

CU, Cornell University, Ithaca, New York (Dr. James N. Layne)

DEH, private collection of Mr. Donald E. Hahn, Cottonwood, Arizona

DMNH, Dallas Museum of Natural History, Texas (Mr. Wayne Seifert)

EAL, private collection of Mr. Ernest A. Liner, Houma, Louisiana

FMNH, Field Museum of Natural History, Chicago, Illinois (Dr. Robert F. Inger, Mr. Hymen Marx)

FSM, Florida State Museum, University of Florida, Gainesville (Dr. Walter Auffenberg)

FWMSH, Fort Worth Museum of Science and History, Texas (Dr. William J. Voss)

GCNPM, Grand Canyon National Park Museum, Arizona (Dr. Merrill D. Beal)

IPN, Instituto Politechnic Nacional, Mexico City (Mr. Ticul Alvarez)

JFC, private collection of Mr. Joseph F. Copp, La Jolla, California

KU, University of Kansas, Lawrence (Dr. William E. Duellman; Mr. Joseph T. Collins)

LACM, Natural History Museum of Los Angeles County, California (Dr. John W. Wright)

LBSC, Long Beach State University, California (Dr. Richard B. Loomis)

LSU, Louisiana State University, Baton Rouge (Dr. Douglas A. Rossman)

LSUS, Louisiana State University in Shreveport

MALB, Museum of Arid Land Biology, University of Texas at El Paso (Dr. Robert G. Webb)

MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (Dr. Ernest E. Williams)

MNA, Museum of Northern Arizona, Flagstaff (Mr. Steven W. Carothers)

MNHN, Muséum National d'Histoire Naturelle, Paris (Dr. Jean Guibé)

MVZ, Museum of Vertebrate Zoology, University of California, Berkeley (Dr. Robert C. Stebbins; Dr. David B. Wake)

OPCNM, Organ Pipe Cactus National Monument, Arizona (Mr. Larry E. Henderson)

RGW, private collection of Dr. Robert G. Webb, El Paso, Texas

RSF, private collection of Mr. Richard S. Funk, Edwardsville, Illinois

SDSNH, San Diego Society of Natural History, California (Dr. Allan J. Sloan)

SFA, Stephen F. Austin State University, Nacogdoches, Texas (Dr. Fred L. Rainwater)

SM, Strecker Museum, Baylor University, Waco, Texas (Dr. Bryce C. Brown)

SRSU, Sul Ross State University, Alpine, Texas (Dr. James F. Scudday)

TCWC, Texas Cooperative Wildlife Collection, Texas A and M University, College Station (Dr. James R. Dixon)

TNHC, Texas Natural History Collection, University of Texas, Austin (Dr. W. Frank Blair)

TT, Texas Technological College, Lubbock (Dr. John S. Mecham)

UAZ, University of Arizona, Tucson (Dr. Charles H. Lowe; Dr. Michael D. Robinson; Dr. Thomas R. Van Devender)

UCM, University of Colorado Museum, Boulder (Dr. T. Paul Maslin; Dr. Clarence J. McCoy)

UIMNH, University of Illinois Museum of Natural History, Urbana (Dr. Donald F. Hoffmeister)

UMMZ, University of Michigan Museum of Zoology, Ann Arbor (Dr. Charles F. Walker)

UNM, University of New Mexico, Albuquerque (Dr. William G. Degenhardt)

USL, University of Southwestern Louisiana, Lafayette (Dr. William D. Reese)

USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C. (Dr. James A. Peters; Dr. George R. Zug)

UTA, University of Texas at Arlington (Dr. William F. Pyburn; Mr. John L. Darling; Dr. Harry W. Greene)

UU, University of Utah, Salt Lake City (Dr. John M. Legler)

UWZ, University of Wisconsin, Madison (Dr. Richard C. Vogt)

ZMB, Institut für Spezielle Zoologie und Zoologisches Museum der Humboldt-Universität, Berlin (Dr. Günther Peters)

In addition, we are grateful to Mrs. Frances Waite Gibson, who illustrated most of the hemipenes figured herein.

METHODS

We attempted to study all characters under investigation on nearly every specimen examined. Sample sizes vary for different characters, however, because not all have been included since initiation of the work, and damage on some specimens precluded observing all features.

The following data were obtained precisely as in our investigation of variation in *Tantilla gracilis* (see Hardy and Cole, 1968): Total length; tail length; body length; number of supralabials and infralabials; number of preoculars, postoculars, and temporals; condition of the nasal; possible contact between prefrontals and particular supralabials; which supralabials are in contact with the eye; whether the mental is in contact with the anterior pair of genials (chin-shields); number of rows of dorsal scales; number of ventrals and subcaudals; and characters of the maxillary bones. In addition, we recorded the

vertical position of the nostril within the nasal scale (i.e., halfway between the lower edge and the upper edge, two-thirds of the way up, etc.; estimates for the two sides were consistently similar).

Nearly all the species considered here have characteristic patterns of dark (brown or black) and light (white, cream, or gray) colors on the head and neck. Thus we examined several characters of color pattern and recorded data for statistical analysis. The following features were recorded as described by McDiarmid (1968) for *Tantilla yaquia*: Length of dark head cap (number of vertebral scales posterior to posterior end of suture between parietal scales); presence and width of light nuchal collar immediately posterior to dark head cap; presence and number of distinct brown spots posterior to nuchal collar; presence and amount (number of scales) of ventral extension of dark head cap below angle of mouth (average for both sides); and percent (estimated; average for both sides) of light color on the anterior temporal and on the last three supralabials (numbers 5–7), when the normal number of seven was present. In addition, we recorded shape of the posterior edge of the dark head cap according to the generalized forms illustrated in figure 22.

Sex of nearly all specimens was determined by presence of hemipenes (males) or ovaries and oviducts (females). On rare occasions, a specimen was concluded to be female based only on its lacking hemipenes. In some instances, sex of males was verified by examining testes and/or vasa deferentia. No examples of intersexuality were found.

Once we turned to examining hemipenes, we studied them on nearly all males available. Although these organs are small in *Tantilla,* they can be studied in detail with a dissecting microscope, and they are of considerable taxonomic importance. Organs were studied and described in both the everted and retracted conditions, using the methods and terminology of Dowling and Savage (1960) and Myers (1974). Well-everted organs either required no preparation prior to study or were injected with colored liquid latex (Dowling and Savage, 1960). We studied retracted organs *in situ,* using an incision on the midventral line of the tail and the midventral line of the hemipenis (Myers, 1974).

We used Student's t-tests and χ^2 tests for association in contingency tables (Simpson, Roe, and Lewontin, 1960) for comparing certain population samples, rejecting the null hypothesis if $P < 0.05$.

IDENTIFICATION

The following key is for identifying specimens of *Tantilla* from west of the Mississippi River and from the following states and territories that comprise approximately the northern half of Mexico: Baja California del Norte, Baja California del Sur, Chihuahua, Coahuila, Durango, Nayarit, Nuevo León, Sinaloa, Sonora, Tamaulipas, and Zacatecas.

See Telford (1966) for identifying specimens from east of the Mississippi River, although one species that scarcely crosses the Mississippi into southwestern Illinois (*T. gracilis*) was not included in his key. *Tantilla gracilis* is the only species of the genus having populations on both sides of the Mississippi River.

KEY TO THE SPECIES OF *TANTILLA* OCCURRING IN THE WESTERN UNITED STATES AND NORTHERN MEXICO[3]

1. Top of head slightly darker brown than dorsal body (beige to light brown; fig. 1A); supralabials 6-6 2
   Top of head strikingly darker (brown, black) than dorsal body (beige to light brown),

[3] Table 28 also will be useful for identifying members of the *T. planiceps* complex.
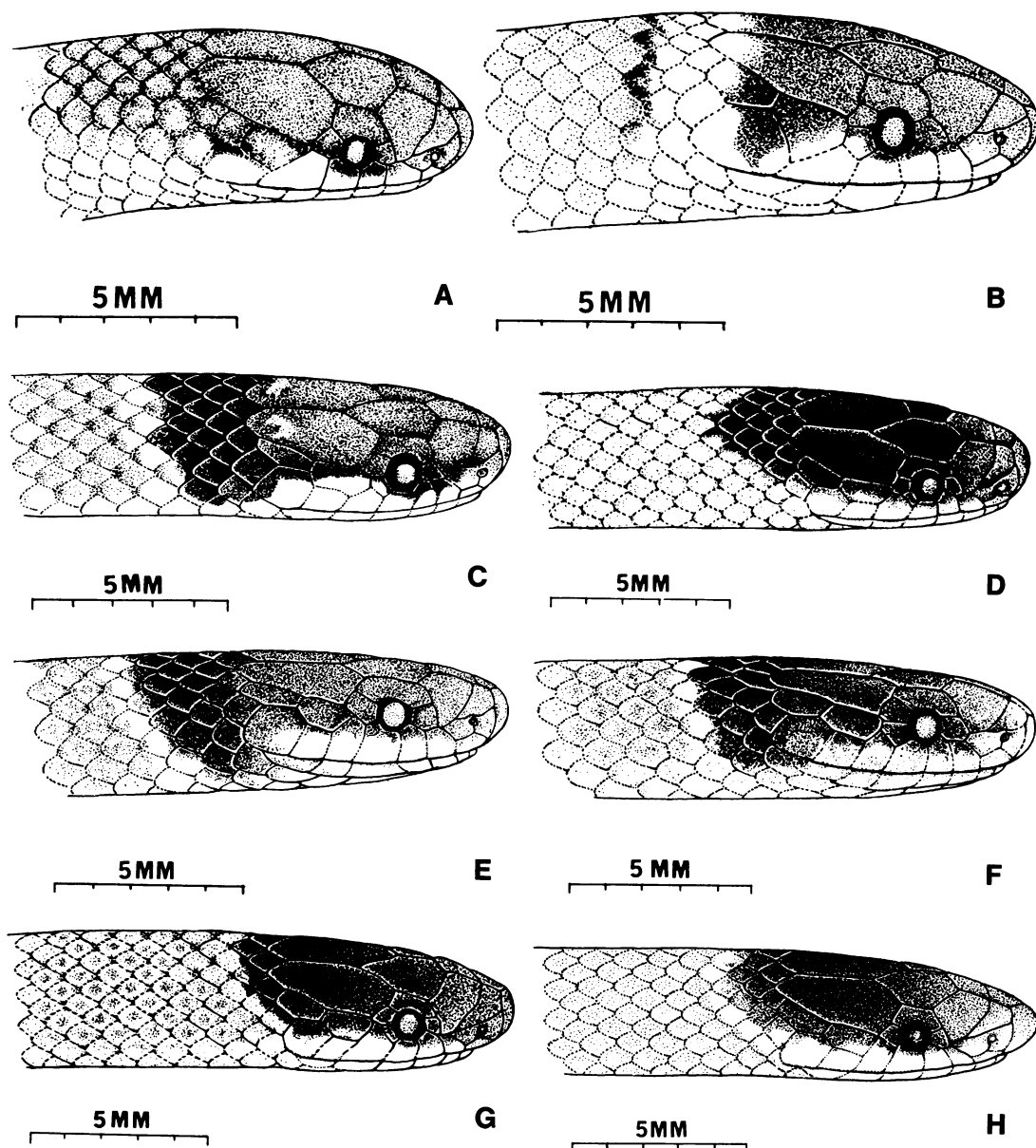
FIG. 1. Color pattern of head and neck of seven species of *Tantilla*. A. *T. gracilis*, AMNH 103805. B. *T. wilcoxi*, AMNH 15066. C. *T. yaquia*, AMNH 109531. D. *T. nigriceps*, AMNH 108917. E. *T. planiceps* (Baja California Sur), AMNH 97174. F. *T. planiceps* (California), AMNH 93381. G. *T. hobartsmithi*, AMNH 107377. H. *T. atriceps*, CM 42823.

their colors meeting abruptly at parietal region of head or on neck, possibly separated by a light (white, gray) collar; supralabials 7-7 3

2(1). Dorsal and lateral body coloring uniform

beige or light brown, without stripes; temporals 1+1 [midwestern United States; northern Mexico] .... *T. gracilis*

Body with three faint but clear dark brown stripes (one vertebral and one lateral on

each side); one temporal [western Mexico]
.... *T. calamarina*

3(1). Dark head coloration stops at or near (within 1 dorsal scale length of) posterior tips of parietals; dark head cap followed immediately by bold, light (cream, white) collar, 1–3 scales wide; light collar followed immediately by dark (brown, black) collar (fig. 1B) 4

Dark head coloration extends uninterruptedly 1–5 scales past end of interparietal suture; dark head cap possibly followed by light (white, gray) collar, ½ to 2 scales wide, which may be subtle; light collar (or dark head cap, if collar absent) followed by dorsal body color (beige to light brown), although some small brown smudges may be present 5

4(3). Dark nape collar (posterior to light collar) very narrow, not exceeding 1 scale width (fig. 1B) .... *T. wilcoxi*

Dark nape collar (posterior to light collar) relatively broad, 2–5 scales wide ....
.... *T. rubra*

5(3). Dark (brown, black) head cap extends ventrad to below angle (corner) of mouth (figs. 1C, E, F) 6

Dark head cap not extending below angle of mouth (figs. 1D, G, H) 8

6(5). Below angle of jaw, dark head cap color sweeps anteriad through gular region, including the infralabial, mental and genial scales .... *T. cucullata*

Dark head cap color stops ½ to 3½ scales below angle of jaw; gular region light (white to beige) excepting some brown smudges on some individuals 7

7(6). 25% or more of anterior temporal light in color (white, cream, gray); supralabials 5 and 6 100% light in color (fig. 1C); mental separated from anterior pair of genials by first pair of infralabials; origin of m. retractor penis magnus at level of subcaudals 20–28; basal hemipenial spines (dis-

tinctly proximal to spinose midsection) very large and two in number (e.g., fig. 6C) .... *T. yaquia*

20% or less of anterior temporal light in color; supralabials 5 and 6 with dark pigment (brown, black) near dorsal edges (usually involving at least 10% to 20% of scale area; figs. 1E, F); mental in contact with anterior pair of genials; origin of m. retractor penis magnus at level of subcaudals 29–39; basal hemipenial spines (distinctly proximal to spinose midsection) very small, if present, varying in number from 0–2 (figs. 6E, F) ..... *T. planiceps*

8(5). Dark head cap extends 3–5 scales past posterior end of interparietal suture (fig. 1D); posterior edge of dark head cap angular in shape (fig. 22); dark head cap not followed by light collar (fig. 1D); origin of m. retractor penis magnus usually between subcaudals 32–39 ... *T. nigriceps*

Dark head cap extends only ½ to 3 scales past end of interparietal suture (figs. 1G, H); posterior edge of dark cap usually convex or straight (fig. 22); dark head cap followed by light (white, gray) collar, ½ to 2 scales wide (possibly faint; figs. 1G, H); origin of m. retractor penis magnus usually between subcaudals 20–32 9

9(8). Hemipenis capitate; usually fewer than 30 spines in spinose midsection of hemipenis; usually 1 (rarely 2) row of spines around hemipenis in spinose midsection (figs. 6H, I); postoculars usually 2; mental usually touching anterior pair of genials
.... *T. hobartsmithi*

Hemipenis not capitate; usually 30–40 spines in spinose midsection of hemipenis; a minimum of 3 (rarely 2) rows of spines around hemipenis in spinose midsection (fig. 6G); postoculars usually 1; mental usually separated from anterior pair of genials by first pair of infralabials .... *T. atriceps*

ACCOUNTS OF THE FOUR SPECIES FORMERLY INCLUDED IN *TANTILLA PLANICEPS*

Tantilla planiceps (Blainville)
Figures 1E, F (head and neck);
2 (range map); 6E, F (hemipenis)

Coluber planiceps Blainville, 1835, pp. 294, 295, pl. 27, figs. 3, 3a, 3b (dorsal, ventral, and lateral views of scutellation of head).

Homalocranion planiceps (Blainville): Duméril, 1853, p. 490. Jan, 1862, p. 51; 1866, pl. 2, fig. 2 (dorsal, ventral, and lateral views of scutellation and color pattern). Bocourt, 1883 (1870–1909), pp. 581, 582, pl. 36, figs. 7–7d (dorsal, ventral, and lateral views of scutellation and color pattern of head and neck).

Tantilla planiceps (Blainville): Cope, 1861, p. 74. Garman, 1884, p. 31. Stejneger and Barbour, 1917, p. 105 (part). Van Denburgh, 1922, pp. 880–882. Blanchard, 1938, p. 371. Smith and Taylor, 1945, p. 141. McDiarmid, 1968, p. 174. Stebbins, 1972, p. 131, pl. 6d (illustrated in color).

Tantilla nigriceps (not of Kennicott): Yarrow, 1882, p. 85 (part). Cope, 1900, pp. 1113, 1114 (part).

Homalocranium planiceps (Blainville): Günther, 1895, pp. 145, 146. Boulenger, 1896, pp. 226, 227 (part).

Tantilla eiseni Stejneger, "1895" [1896], pp. 117, 118 (holotype, USNM 11766, adult female, from Fresno, California; G. Eisen, collector). Van Denburgh, 1922, pp. 876–878, pl. 97 (three photographs of a specimen from "near Campo, San Diego County, California"). Blanchard, 1938, p. 371. Perkins, 1938, p. 47 (photograph); 1949, p. 65 (photograph; same material as in Perkins, 1938). Stebbins, 1954, p. 449, fig. 48 (scutellation and color pattern of head and neck), p. 504, pl. 100 (range map, primarily for U.S.A.); 1966a, p. 35, pl. 3d (head, neck, and anterior part of body illustrated in color). McDiarmid, 1968, p. 174.

Tantilla eiseni eiseni Stejneger: Klauber, 1943, pp. 71–74. Smith and Taylor, 1945, p. 138. Wright and Wright, 1957, p. 736, fig. 215 (seven photographs of material from San Diego, California). Staedeli, 1972, p. 18 (color photograph, dorsolateral view of head and neck).

Tantilla eiseni transmontana Klauber, 1943, pp. 71–74 (holotype, SDSNH 29273, adult male [not seen], from one mile east of Yaqui Well, San Diego County, California; Charles E. Shaw and Cyrus B. Perkins, collectors, June 6, 1938, at 8:10 P.M.). Smith and Taylor, 1945, p. 138.

Tantilla planiceps planiceps (Blainville): Tanner, 1966, pp. 135–149, fig. 1E (dorsolateral view of scutellation and color pattern of head and neck), fig. 2 (range map).

Tantilla planiceps eiseni Stejneger: Tanner, 1966, pp. 135–149, fig. 1F (dorsolateral view of scutellation and color pattern of head and neck), fig. 2 (range map). Stebbins, 1966b, pl. 35 (dorsolateral view of scutellation and color pattern of head and neck), map 173 (range in U.S.A.). Bostic, 1971, p. 259. Shaw and Campbell, 1974, p. 318, pl. 50 (color photograph of head, neck, and anterior part of body).

Tantilla planiceps transmontana Klauber: Tanner, 1966, pp. 135, 137–145, 148–150, fig. 1D (dorsolateral view of scutellation and color pattern of head and neck), fig. 2 (range map).

HOLOTYPE: Blainville specified that he examined only one specimen, an adult male, at the Muséum National d'Histoire Naturelle, Paris, "rapportées de la Californie par M. P. E. Botta" (Blainville, 1835, p. 283). Mme. Rolande Roux-Estève of the Muséum National informed us that the holotype is MNHN 818, for which catalogue data read, "Californie, Botta, type de Blainville." Examination of the specimen confirmed that it is an adult male with 137 ventral scales and 57 subcaudals (tail complete), which are consistent with restriction of the type-locality to southern Baja California Sur (Smith and Taylor, 1950, p. 322; see our table 15, figs. 24–27).

DIAGNOSIS: *Tantilla planiceps* differs from all other species of *Tantilla* in possessing the following combination of characters: Top of head strikingly darker (brown, black) than dorsal body color (beige to light brown); dark head cap extending ventrolaterally 0.5–2 scales below angle (corner) of mouth; supralabial 5 with some dark pigment (usually at least 10% of area); supralabial 6 with dark pigment (usually at least 15% of area); less than 20% (usually 0–10%) area of anterior temporal light in color; dark head cap extending on middorsal line 2–3 scales beyond posterior end of interparietal suture; posterior edge of dark head cap usually convex or straight, followed by light (white, cream) collar 0.5–1 scale wide; often several distinct brown spots along posterior edge of collar; origin of m. retractor penis magnus at subcaudal 30–38; retracted hemipenis extending to subcaudals 9–15; hemipenis subcylindrical to bulbous when everted, not capitate, usually with one basal spine (small to large); no spinules on hemipenis proximal to basal spine; 45–73 spines in 3–5 rows (minimum) approximately encircling spinose midsection of hemipenis, except at sulcus; supralabials 7; infralabials 6; naris usually medial (vertical axis) in nasal; postoculars 2; temporals 1+1; mental usually touching anterior pair of genials. Most similar to *T. yaqui*; differing strikingly in hemipenial characters and lateral head coloration.

DISTRIBUTION: Southern California in the United States, and Baja California, Mexico
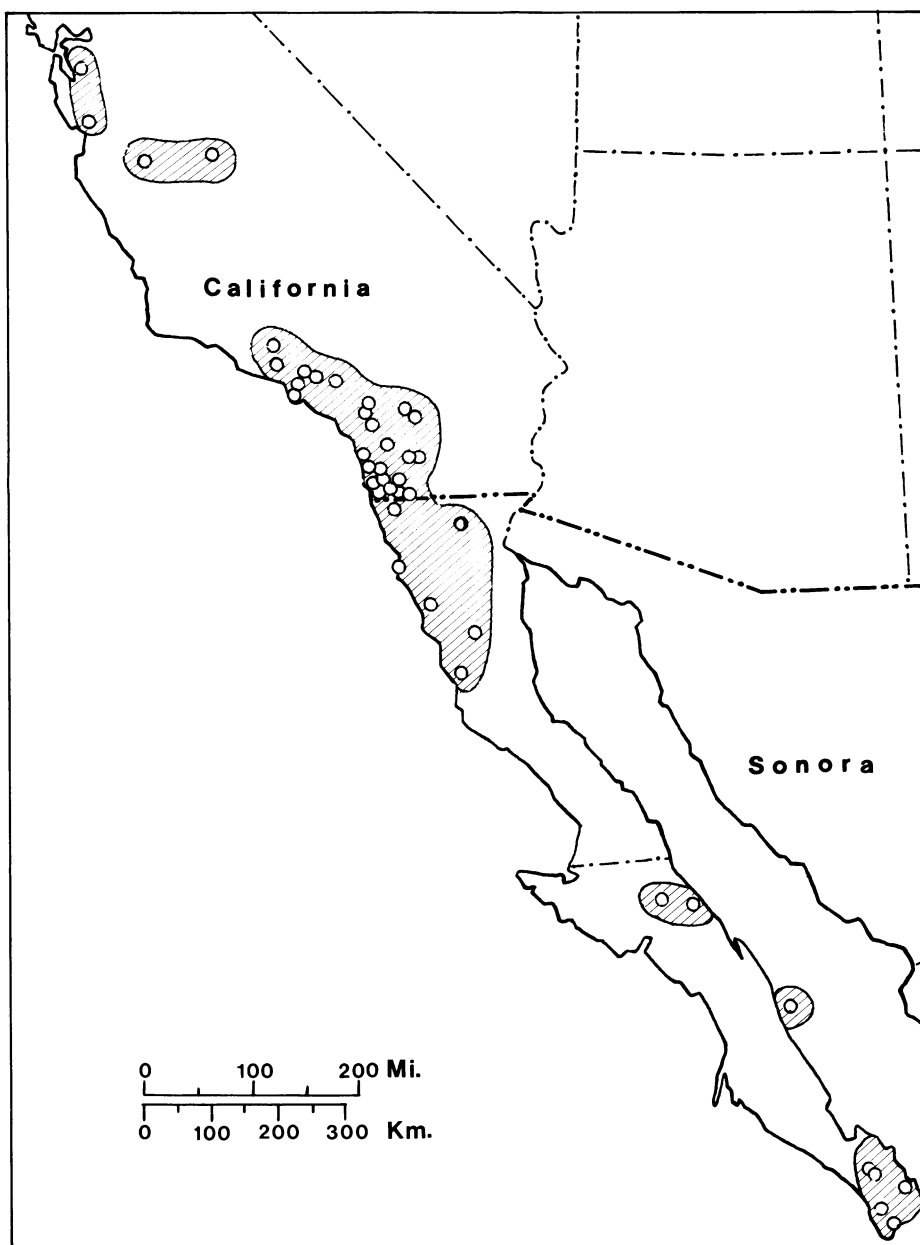
FIG. 2.   Geographic distribution of *Tantilla planiceps*. Hollow circles indicate localities from which we examined specimens.

(fig. 2).   Possibly *T. planiceps* and *T. hobartsmithi* are sympatric in California, although this has not been documented. Additional collections are needed from the southern Sierra Nevada, particularly its western flanks, from the San Joaquin Valley, and from Joshua Tree National Monument (see Remarks in account of *T. hobartsmithi*).

GENERAL DESCRIPTION: Except where specified otherwise, the following descrip-

tion is based on pooled observations from 142 specimens examined from throughout the range; analyses of variation are presented later in this paper. When ranges of data or alternatives are presented, sample size follows (in parentheses).

Maximum total length 386 mm. (N = 109); maximum snout to vent (body) length 301 mm. (N = 140); tail comprising 20.3–26.8% of total length of males (62), 18.1–23.8% of females (43).

Coloration was described by Van Denburgh (1922, p. 877) as follows: "The ground color is pale brownish gray or grayish brown, above, the edges of the scales being lighter. The top and sides of the head and the neck for a distance of about two or three scale-lengths behind the parietal plates is dark grayish or blackish brown. Behind this area a narrow whitish transverse band or collar about one scale wide crosses the nape. This may be bordered behind by a few dark dots. The labials and lower surfaces of the head and neck are grayish white. The rest of the lower surfaces are coral red, fading to grayish white in alcohol." Klauber (1931, 1943) noted that specimens from arid localities generally are lighter than others.

Characteristics of head coloration for the specimens we examined follow: dark head cap extending ventrolaterally 0–3 (140) scales below angle (corner) of mouth; 0–40% (136) anterior temporal light in color; 5–75% (131) seventh supralabial light in color; 16–100% (131) sixth supralabial light in color; 40–100% (131) fifth supralabial light in color; dark head cap extending on middorsal line 2–3.5 (139) scales beyond posterior end of suture between parietals; posterior edge of dark head cap convex (90), straight (46), pointed (3), or concave (1); dark head cap followed by light collar (137 out of 138 specimens) 0–1.5 (137) scales wide; a few dark spots along posterior edge of collar (78 out of 129 specimens).

Hemipenes are described under Variation. Those of the holotype are described below (see Redescription of Holotype).

The following details of scutellation are essentially invariant, unless indicated otherwise: supralabials 7, with 3+4 entering orbit; infralabials 6; preoculars 1; postoculars 2; temporals 1+1; mental touching both anterior genials (109 out of 139 specimens); prefrontals not touching supralabials (107 out of 139 specimens); naris medial (vertical axis) in nasal (109 out of 131 specimens); nasal usually divided only below naris (85 out of 131 specimens), often divided both above and below (33 out of 131 specimens); dorsal scales in 15 rows throughout, except variable (13–18 rows) immediately anterior to anal plate. Ventrals and subcaudals with considerable sexual dimorphism and geographic variation (figs. 24–27): ventrals of males 134–184 (N = 78), females 148–197 (55); subcaudals of males 57–73 (61), females 49–70 (44); ventrals + subcaudals of males 194–257 (61), females 197–260 (41).

Maxillae are described under Variation.

REDESCRIPTION OF HOLOTYPE: Snout-vent length 179 mm.; tail length 59 mm. (tail complete); tail comprising 24.8% total length; dark head cap extending ventrad about ½ scale (unclear) below angle of mouth; essentially unpigmented anterior temporal (unclear); about 55% seventh supralabial light in color; dark head cap extending on middorsal line 3.25 scales beyond posterior end of suture between parietals; posterior edge of dark head cap convex; dark head cap followed by light collar 1 scale wide; coloration otherwise largely faded, specimen gray.

The right hemipenis is retracted, the left one slightly everted. The right organ was dissected, using left subcaudals as reference points, unless specified otherwise: M. retractor penis magnus originating at right subcaudal 38; hemipenis length to suture of subcaudals 13 and 14; organ single; sulcus spermaticus simple, curving abruptly from medial surface at cloaca, to ventral surface, then to lateral surface, continuing to apex; basal region nude, with longitudinal folds; no basal spines; spinulate region at subcaudals 6–9; spinose midsection at 9–11, with 62 medium to large spines densely distributed in 3–6 rows (minimum) approximately encircling organ, except at sulcus; spinules numerous on edges of sulcus in spinose midsection; apical region calyculate; basal

calyces spinulate, distal ones more fleshy (papillate), perhaps with calcified tips; organ not capitate.

Dorsal scales smooth; apical pits lacking; cephalic scutellation essentially normal; supralabials 7, with 3+4 entering orbit; infralabials 6; preoculars 1; postoculars 1; temporals 1+1; mental touching both anterior genials (barely, on left); left prefrontal not touching any supralabials; right prefrontal touching right supralabial 2; naris medial (vertical axis) in nasal; nasal divided only below naris; dorsal scales in 15 rows throughout; anal divided; ventrals 137; subcaudals 57, third and fourth pairs fused across midventral line; ventrals + subcaudals 194.

ECOLOGY: *Tantilla planiceps* occurs "principally in the Lower and Upper Sonoran life-zones in arid and semiarid environments" (Stebbins, 1954, p. 450). Brief habitat notes exist for specimens collected in chaparral (Banta and Morafka, 1968) and desert (Klauber, 1939; Bostic, 1971), but remarkably few specifics have been stated on habitats of this species. Individuals have been found in all months of the year (Klauber, 1939; Leviton and Banta, 1964), and most were found beneath rocks or other objects, or while excavating (Klauber, 1924, 1931; Stebbins, 1954; Leviton and Banta, 1964; Banta and Morafka, 1968). Klauber (1939) reported only one found alive on the road (8:10 P.M., June), in nearly 3000 miles of night driving; perhaps this was the holotype of *T. p. transmontana* Klauber (1943, p. 71). Klauber (1931, p. 72) also found one "crawling about in the open at 1:30 A.M."

There are few reports on other aspects of natural history. Stebbins (1954, p. 451) reported that a specimen measuring 6.5 inches (165 mm.) in total length "contained a centipede 2 inches long." Perkins (1938, p. 47) said it "eats earthworms in captivity."

ETYMOLOGY: Blainville (1835, p. 294) named this species with reference to its flat head.

REMARKS: Justification for our taxonomic treatment of this form among the four species previously included in *T. planiceps* is presented under Taxonomic Judgments.

Although there is local variation and geographic variation in a few characters, we do not recognize subspecies (see Taxonomic Judgments).

The specimens we examined include the holotype of *Tantilla eiseni* Stejneger, "1895" [1896] (USNM 11766) and five of the paratypes (USNM 55387–55391), including a male whose hemipenis we studied. We also examined all six paratypes of *Tantilla eiseni transmontana* Klauber, 1943, including the hemipenes of both males (L. M. Klauber nos. 2633 and 2634 of the SDSNH).

Tantilla yaquia Smith
Figures 1C (head and neck); 3 (range map); 6C, D (hemipenis)

Tantilla yaquia Smith, 1942, p. 41. Smith and Taylor, 1945, p. 142. Fowlie, 1965, p. 117 (photograph; range map for Arizona). McDiarmid, 1968, pp. 159–175, fig. 1 (range map), fig. 3 (dorsolateral view of scutellation and color pattern of head and neck). Hardy and McDiarmid, 1969, p. 203, 238, fig. 84 (range map for Sinaloa). Shaw and Campbell, 1974, p. 319, pl. 51 (color photograph of head, neck, and anterior part of body).

Tantilla bogerti Hartweg, 1944, pp. 1–4 (holotype, AMNH 62259, male, from Acaponeta, Nayarit, Mexico; Charles Bogert, collector, November 18–19, 1939). Smith and Taylor, 1945, p. 137.

Tantilla yaquia yaquia Smith: Zweifel and Norris, 1955, p. 243, fig. 2 (dorsal and lateral views of scutellation and color pattern of head and neck).

Tantilla yaquia bogerti Hartweg: Zweifel and Norris, 1955, p. 243.

Tantilla atriceps (not of Günther): Wright and Wright, 1957, p. 729, fig. 212 (four photographs of a specimen from Bisbee, Arizona; misidentification).

Tantilla planiceps yaquia Smith: Tanner, 1966, pp. 135, 137, 138, 140–143, 145–148, 151, fig. 2 (range map). Stebbins, 1966b, pl. 35 (dorsolateral view of scutellation and color pattern of head and neck), map 173 (range in U.S.A.).

Tantilla planiceps bogerti Hartweg: Tanner, 1966, pp. 135, 138, 140–142, 145, 148, 151, fig. 2 (range map).

HOLOTYPE: "Museum of Comparative Zoology no. 43274, female, collected at Guasaremos, Río Mayo, Chihuahua, by H. S.
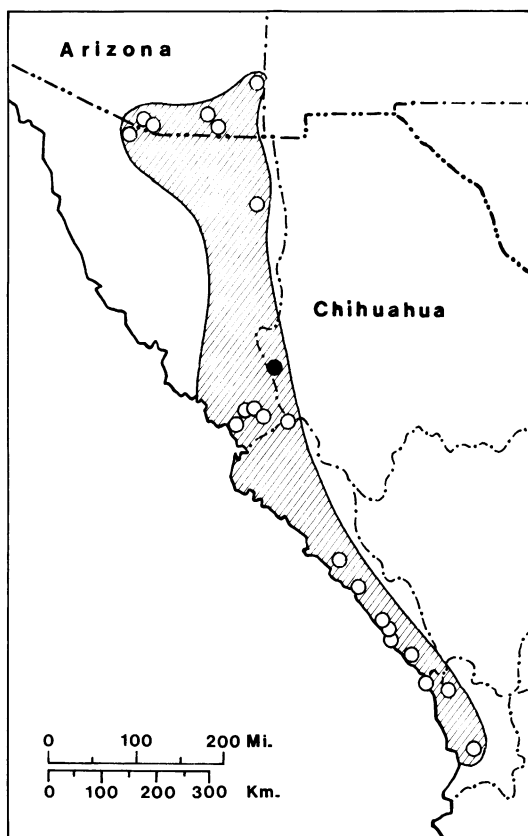
FIG. 3. Geographic distribution of *Tantilla yaquia*, slightly modified from McDiarmid (1977, p. 198.1). Hollow circles indicate localities represented by specimens. Solid circle designates type-locality.

Gentry, in August, 1936" (Smith, 1942, p. 41). We did not examine this specimen, as it was examined by McDiarmid (1968).

DIAGNOSIS: *Tantilla yaquia* differs from all other species of *Tantilla* in possessing the following combination of characters: Top of head strikingly darker (brown, black) than dorsal body color (beige to light brown); dark head cap extending ventrad 0.5–3 scales below angle (corner) of mouth; 100% area of supralabial 5 light (white, gray) in color; 100% supralabial 6 light in color; at least 25% anterior temporal light in color; dark head cap extending on middorsal line 2–4 scales beyond posterior end of suture between parietals; posterior edge of dark head cap usu-

ally straight, followed by light (white, cream) collar 0.5–1.5 scales wide; often several distinct brown spots along posterior edge of collar; origin of m. retractor penis magnus at level of subcaudal 22–24; retracted hemipenis extending to subcaudal 6–9; hemipenis subcylindrical to clavate when everted, semicapitate, with two very large basal spines; no spinules on hemipenis proximal to basal spines; 37–58 spines in 2–4 rows (minimum) approximately encircling spinose midsection of hemipenis, except at sulcus; supralabials 7; infralabials 6; naris usually in upper half of nasal; postoculars 2; temporals 1+1; mental usually separated from anterior pair of genials by midventral contact of anterior pair of infralabials. Most similar to *T. planiceps*; differing strikingly in hemipenis and lateral head coloration.

DISTRIBUTION: Extreme southeastern Arizona in the United States, and the following states, or parts thereof, in Mexico: western Chihuahua; Nayarit; Sinaloa; and Sonora (fig. 3). Probably *T. yaquia* and *T. hobartsmithi* are sympatric in southern Arizona, although this has not been documented (McDiarmid, 1968, pp. 174, 175).

GENERAL DESCRIPTION: We have combined our observations on nine specimens of *T. yaquia* with McDiarmid's (1968) data on 40 specimens from throughout the range.

Maximum total length 325 mm.; tail length comprises 21.2–27.5% of total length of males, 17.2–28.5% of females. The proportionate tail length varies geographically (McDiarmid, 1968, p. 169).

The following description is partly quoted from McDiarmid (1968, p. 162): "In preservative, the dorsal surface of the body is light brown to brownish-tan, fading slightly on the lateral surfaces . . . . The ventral coloration of three live specimens was pinkish-orange," brightest posteriorly, gradually fading anteriorly. "The anterior quarter of the ventral surface, the throat, and the chin are creamy white." Top and sides of head and neck dark brown to black (lighter anteriorly), with strongly contrasting creamy white area on posterior supralabials and primary temporal; light collar, along posterior edge of dark head cap.

Dark head cap extending ventrad 0.5–3 scales below angle of mouth; 14–75% anterior temporal light in color; 25–100% seventh supralabial light in color; usually 100% sixth and fifth supralabials light in color; dark head cap extending on middorsal line 2–4.25 scales beyond posterior end of suture between parietals; posterior edge of dark head cap usually straight; dark head cap followed by light collar 0.5–1.5 scales wide; often a few dark spots along posterior edge of collar, but with geographic variation (McDiarmid, 1968, p. 165).

Hemipenes are described under Variation.

The following details of scutellation are essentially invariant, unless indicated otherwise: supralabials 7, with 3+4 entering orbit; infralabials 6; preoculars 1; postoculars 2; temporals 1+1; mental usually separated from anterior pair of genials by midventral contact of anterior pair of infralabials; prefrontals usually not touching supralabials (four out of six specimens); naris usually in upper half of nasal; nasal often divided both above and below naris (four out of six specimens); dorsal scales in 15 rows throughout. Ventrals and subcaudals with considerable sexual dimorphism and geographic variation (McDiarmid, 1968, pp. 160, 161): ventrals of males 134–157, of females 145–165; subcaudals of males 50–73, of females 46–75.

ECOLOGY: McDiarmid (1968, p. 169) reported that in the north, "*T. yaquia* is characteristically found above 1000 m in evergreen and riparian woodland," and further south is found "at lower elevations" in "deciduous short tree forest," "thorn woodland," and "tropical semiarid and dry forests." McDiarmid (1968, pp. 169, 170) reviewed other ecological notes and concluded that "apparently it is a nocturnal, secretive form, that spends much of its time beneath rocks and in crevices." No specifics on food habits are known, but body size and geographic distribution preclude the possibility that *T. yaquia* normally eats wart hogs.

REMARKS: The color notes presented by Wright and Wright (1957, p. 726) for a specimen of "*T. atriceps*" from Bisbee, Arizona, actually are based on a specimen of *T. yaquia* (see their fig. 212, p. 729).

The specimens we examined include the holotype of *Tantilla bogerti* Hartweg, 1944 (AMNH 62259).

Tantilla atriceps (Günther)
Figures 1H (head and neck); 4 and 38 (range maps); 6G (hemipenis)

Homalocranium atriceps Günther, 1895, pp. 146, 147, pl. 52, fig. B (dorsal, ventral, and lateral views of scutellation and color pattern of head, neck, and anterior part of body).

Tantilla atriceps (Günther): Amaral, "1929" [1930], p. 219. Taylor, "1936" [1937], pp. 339, 340 (part). Smith, 1942, p. 34 (part). Smith and Taylor, 1945, p. 136 (part). McDiarmid, 1968, pp. 159, 160, 171–175 (part; see Remarks).

Tantilla planiceps atriceps (Günther): Tanner, 1966, pp. 135, 146–148, 150 (part; see Remarks).

SYNTYPES: Two BMNH specimens, BMNH 1946.1.8-81 and 1946.1.8-82 (previously 89.7.3.36 and 89.7.3.37, respectively), from "MEXICO, Nuevo Leon" (Günther, 1895, p. 146), obtained from W. Taylor, Esq. Both specimens are males.

DIAGNOSIS: *Tantilla atriceps* differs from all other species of *Tantilla* in possessing the following combination of characters: top of head strikingly darker (brown, black) than dorsal body color (beige to light brown); dark head cap not extending ventrolaterally below angle (corner) of mouth; dark head cap extending on middorsal line 1–2 scales beyond posterior end of suture between parietals; posterior edge of dark head cap usually convex or straight, followed by light (white, cream) collar 1 scale wide; no dark band or dark spots along posterior edge of collar; origin of m. retractor penis magnus at level of subcaudals 25–32; retracted hemipenis extending to subcaudals 9–14; hemipenis subcylindrical when everted, not capitate, with two medium to large basal spines; no spinules on hemipenis proximal to large basal spines; 26–40 spines in 2–3 rows (minimum) approximately encircling spinose midsection of hemipenis, except at sulcus; supralabials 7; infralabials 6; naris in upper half of nasal; postoculars 1 (sometimes 2); temporals 1+1; mental usually separated from anterior pair of genials by midventral contact of anterior
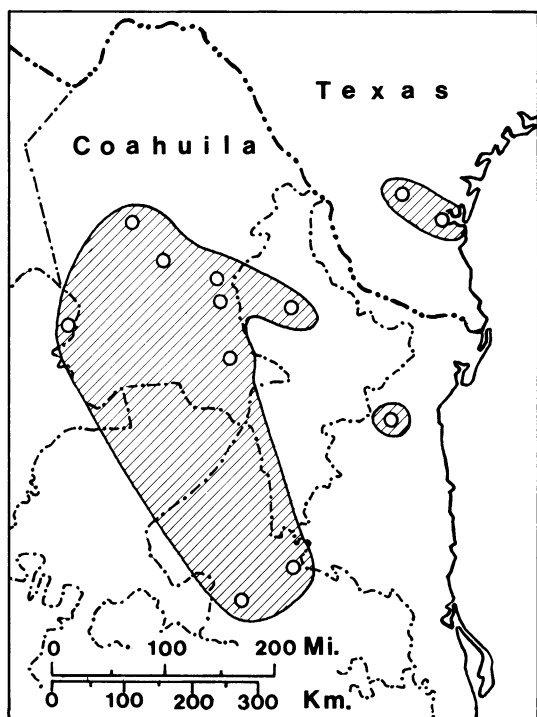
FIG. 4. Geographic distribution of *Tantilla atriceps*; interpretation as in figure 2.

pair of infralabials. Most similar to *T. hobartsmithi*; differing strikingly in hemipenis.

DISTRIBUTION: The few specimens from the United States are from southern Texas; all others are from the following states in Mexico: Coahuila; Durango; Nuevo León; San Luis Potosí; Tamaulipas; and Zacatecas (tables 29, 30; figs. 4, 38). *Tantilla atriceps* and *T. hobartsmithi* are sympatric in Coahuila.

In the course of this work, we borrowed six specimens of *Tantilla* from the British Museum (Natural History), all of which were collected by W. Taylor prior to 1900 and either presented to or, depending on the specimen, purchased by the Museum; W. Taylor corresponded from San Diego, Texas (C. J. McCarthy, *in litt.*), which is in Duval County. In addition to the two syntypes of *T. atriceps* from "Nuevo Leon," these specimens included three male *T. atriceps* and a female *T. nigriceps* (BMNH 87.1.4.25) from

"Duval County, Texas." Initially, we were reluctant to accept these data as representative of where the specimens were collected for three reasons: (1) the holotype of a lizard, *Lysoptychus lateralis* Cope, 1888, said to be from San Diego, Texas, was provided by William Taylor (Cope, 1888); *L. lateralis* is a synonym of *Sceloporus couchii* Baird (see Smith, 1939, pp. 240–242), which is known from northern Mexico, including Nuevo León, but for which no additional specimens have been reported from the United States. (2) We had seen no other specimens of *T. atriceps* (as we understand it and diagnose it here) from the United States. And (3) we had seen no other specimens of *T. atriceps* from Nuevo León. More recently, however, we have examined males of *T. atriceps* from southern Texas (AIM 931) and from Nuevo León (FSM 39626), so we have confirmed the occurrence of *T. atriceps* in those areas. Nevertheless, confirmation that *T. atriceps* and *T. nigriceps* are specifically distinct and literally sympatric in Duval County, Texas, awaits further study (see Additional Problems).

GENERAL DESCRIPTION: Except where specified otherwise, the following description is based on pooled data from the 14 males comprising population sample A (table 5; Specimens Examined) from throughout the range, including the syntypes. The difficulty of identifying females is discussed later (see Additional Problems). Two additional males (TCWC 48207; FSM 39626) that we examined subsequent to the data reductions are similar. Since many of these characters show geographic variation in other species of *Tantilla,* one must allow for the likelihood of such variation in *T. atriceps* also. When ranges of data or alternatives are presented, sample size follows (in parentheses).

Maximum total length 230 mm.; maximum body length 183 mm.; tail length comprising 20.4–30.6% of total length (9 males).

We are not aware of any color notes that were definitely taken from a living *T. atriceps,* but examination of preserved specimens suggests that coloration is similar to or indistinguishable from that of *T. hobartsmithi* (see following account). Taylor

("1936" [1937], p. 339) described a specimen he collected (no. 4555; now FMNH 105319 [Hymen Marx, *in litt.*]), as follows: "Slightly brownish gray, somewhat pinkish white below; head slate-black, somewhat lighter anteriorly, the dark color involving posteriorly one row of scales behind the parietals, this bordered by a narrow, dim yellowish line apparently not reaching down on sides of neck to ventrals."

Characteristics of head coloration for the specimens we examined follow: dark head cap not extending ventrad below angle of mouth; 0–50% (10) anterior temporal light in color; 33–100% (11) seventh supralabial light in color; 70–100% (11) sixth supralabial light in color; 57–100% (11) fifth supralabial light in color; dark head cap extending on middorsal line 1–2 (14) scales beyond posterior end of suture between parietals; posterior edge of dark head cap convex (12) or straight (2), followed by light collar (10 out of 14 specimens) 0–1.5 (11) scales wide; no dark band or dark spots along posterior edge of collar (10 out of 11 specimens).

Hemipenes are described under Variation, but those of the syntypes are described below (see Redescription of Syntypes).

The following details of scutellation are essentially invariant, unless indicated otherwise: supralabials 7, with 3+4 entering orbit; infralabials 6; preoculars 1; postoculars 1–2; temporals 1+1; mental separated from anterior pair of genials by midventral contact of anterior pair of infralabials (10 out of 14 specimens); prefrontals touching (5) one or more supralabials or not (8); naris in upper half of (8) or medial (3) (vertical axis) in nasal; nasal usually divided only below naris; dorsal scales in 15 rows throughout; ventrals 123–140 (13 males); subcaudals 45–66 (9 males); ventrals + subcaudals 179–194 (8 males).

Maxillae are described under Variation.

REDESCRIPTION OF SYNTYPES: The two syntypes are identical in the following features for which only one character state is mentioned. If two traits are given, the first is for BMNH 1946.1.8-81 and the second (in parentheses) is for BMNH 1946.1.8-82.

Snout-vent length 126 mm. (123 mm.); tail length 47 mm. (45 mm.); tail complete; tail length comprising 27.2% (26.8%) of total length; dark head cap not extending ventrad below angle of mouth; 0% (8%) anterior temporal light in color; 45% (73%) seventh supralabial light in color; 70% (98%) sixth supralabial light in color; 60% (90%) fifth supralabial light in color; dark head cap extending on middorsal line 1 scale beyond posterior end of suture between parietals; posterior edge of dark head cap straight (convex); dark cap not clearly (clearly) followed by light collar (1 scale wide); no dark band or dark spots along posterior edge of dark cap or light collar.

Neither hemipenis is everted. The right organ was dissected, using left subcaudals as reference points, unless specified otherwise: M. retractor penis magnus originating at right subcaudal 29 (25); hemipenis length 10; organ single; sulcus spermaticus simple, continuous to apex, on ventrolateral surface (similar on second specimen after curving from ventral surface proximal to basal spine); basal spine medium to large (large) at level of subcaudal 4 (suture of 4+5); second basal spine at 5 on opposite side, somewhat smaller; spinose midsection at subcaudals 6+7, with 35 (26) medium to large (mostly) spines densely distributed in 3 (2) rows (minimum) approximately encircling organ except at sulcus; spinules scattered between spines and on edges of sulcus, extending toward base to level of second basal spine (base of spinose midsection, with one spinule at level of basal spines); apical region calyculate, neither abruptly nor clearly differentiated from spinose midsection; basal calyces spinulate, with large spinules; distal calyces papillate; organ not capitate.

Cephalic scutellation essentially normal; supralabials 7, with 3+4 entering orbit; infralabials 6; preoculars 1; postoculars 2; temporals 1+1; mental separated from anterior pair of genials by midventral contact of anterior pair of infralabials; prefrontals not touching any supralabials (prefrontal touching supralabial 2, each side); naris high in nasal; nasal divided only below naris (on second specimen, left nasal also grooved above naris); dorsal scales in 15 rows throughout;

ventrals 123 (128); subcaudals 56 (58); ventrals + subcaudals 179 (186).

REMARKS: Justification for specific recognition of this form among the four species previously included in *T. planiceps* is presented under Taxonomic Judgments. The relationship of *T. atriceps* and *T. nigriceps* is discussed in Additional Problems. We do not consider it advantageous to designate a lectotype for *T. atriceps* until its specific distinctness from *T. nigriceps* is better resolved. Nevertheless, it may prove helpful to note that of the syntypes, BMNH 1946.1.8-81 best matches the illustrations presented by Günther (1895, pl. 52, fig. B) and is in better condition than the other syntype.

We include the references to Tanner (1966) and McDiarmid (1968) in the synonymy because they involve changes in name combinations, even though all the specimens those authors referred to as *T. planiceps atriceps* or *T. atriceps* actually are *T. hobartsmithi*, which Tanner (1966, p. 147) considered a synonym of *T. atriceps* (see below). Also, instances where specimens of *T. hobartsmithi* have been illustrated and identified as *T. atriceps* (or other species) are cited in the following synonymy.

Tantilla hobartsmithi Taylor
Figures 1G (head and neck); 5 (range map);
6H, I (hemipenes)

Tantilla nigriceps (not of Kennicott): Van Denburgh and Slevin, 1913, pp. 423, 424. Van Denburgh, 1922, p. 880. Tanner, 1927, p. 57.
Tantilla planiceps (not of Blainville): Stejneger and Barbour, 1917, p. 105 (part).
Tantilla nigriceps eiseni (not of Stejneger): Woodbury, 1931, pp. 107, 108, fig. 49 (dorsal view of scutellation and color pattern of head and neck).
Tantilla atriceps (not of Günther): Taylor, "1936" [1937], pp. 339, 340 (part). Blanchard, 1938, p. 372. Smith, 1942, p. 34 (part). Smith and Taylor, 1945, p. 136 (part). Stebbins, 1954, pp. 449–452, fig. 48 (scutellation and color pattern of head and neck), p. 504, pl. 100 (range maps) (part). Wright and Wright, 1957, pp. 725–728 (part). Fowlie, 1965, pp. 109, 110 (photograph of specimen from near Tucson, Pima County, Arizona, and range map for Arizona). Raun and

Gehlbach, 1972, p. 981. Conant, 1975, pp. 222, 223, pl. 33 (photograph, probably of *T. hobartsmithi*), map 168 (part).
Tantilla hobartsmithi Taylor, "1936" [1937], pp. 340–342, fig. 2 (dorsal, ventral, and lateral views of scutellation of head and neck). Smith, 1942, p. 36. Smith and Taylor, 1945, p. 138.
Tantilla utahensis Blanchard, 1938, pp. 372, 373 (holotype, CAS 55214, adult female, from St. George, Washington County, Utah; V. M. Tanner, collector). Stebbins, 1954, pp. 449, 451, 452, fig. 48 (scutellation and color pattern of head and neck), p. 504, pl. 100 (range map). Wright and Wright, 1957, pp. 750–752. Fowlie, 1965, p. 113 (photograph of specimen from St. George, Washington County, Utah, and range map for Arizona).
Tantilla nigriceps nigriceps (not of Kennicott): Smith, 1956, p. 269, fig. 204 (photograph of specimen from Congress Junction, Arizona; misidentification). Fowlie, 1965, p. 111 (photograph of specimen from Mesa, Maricopa County, Arizona; misidentification).
Tantilla eiseni (not of Stejneger): Miller and Stebbins, 1964, pp. 424, 425. Baker and Bradley, 1966, p. 308.
Tantilla planiceps atriceps (not of Günther): Tanner, 1966, pp. 135–143, 145–148, 150, 151, fig. 1A (dorsolateral view of scutellation and color pattern of head and neck), fig. 2 (range map). Stebbins, 1966b, p. 181, pl. 35 (dorsolateral view of scutellation and color pattern of head and neck), map 173 (range in U.S.A.).
Tantilla planiceps utahensis Blanchard: Tanner, 1966, pp. 135–146, 150, fig. 1B (dorsolateral view of scutellation and color pattern of head and neck), fig. 2 (range map). Stebbins, 1966b, pp. 180, 181, pl. 35 (dorsolateral view of scutellation and color pattern of head and neck), map 173 (range).

HOLOTYPE: UIMNH 25066, a male, "collected near La Posa, 10 mi. northwest of Guaymas the night of July 3, 1934. E. H. Taylor, collector" (Taylor, "1936" [1937], p. 340). The locality is in the state of Sonora, Mexico (Taylor, *op. cit.*, p. 341). Taylor ("1936" [1938], p. 497) later reported that the holotype "was taken at a point about two miles north of La Posa, back of the first low range on the bank of a dry stream bed at night."

DIAGNOSIS: *Tantilla hobartsmithi* differs from all other species of *Tantilla* in possessing the following combination of characters:
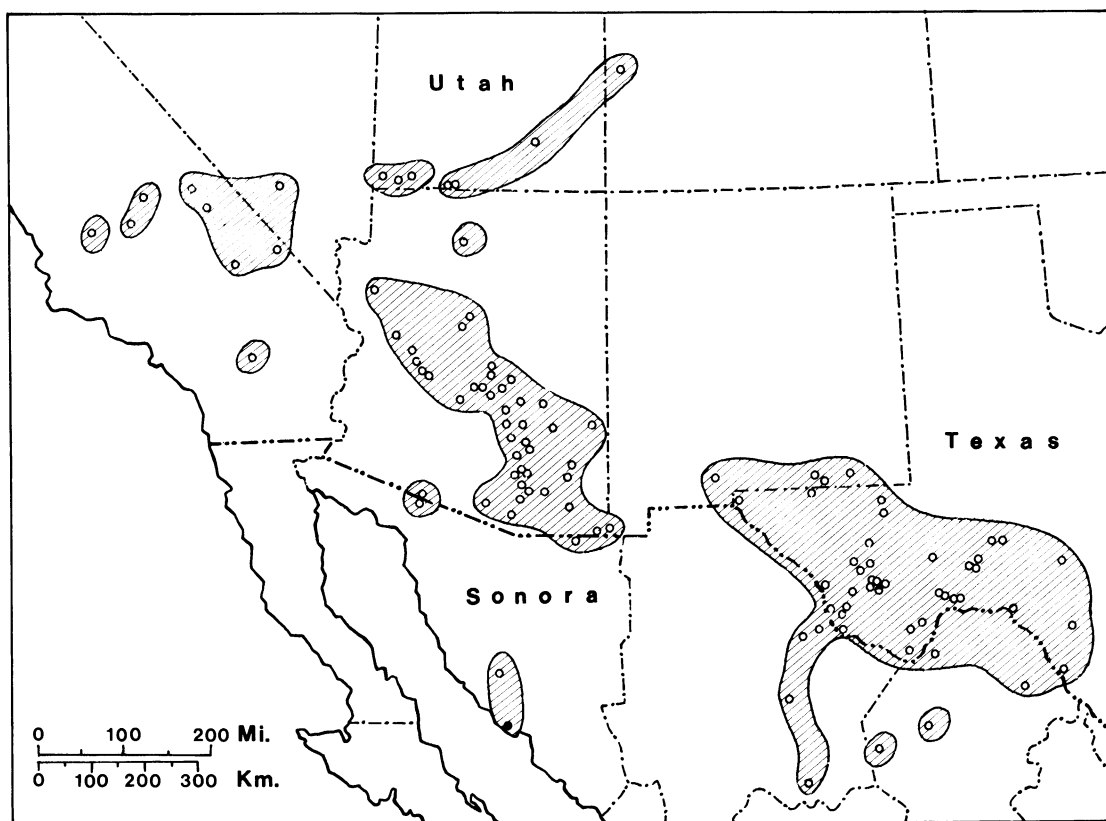
FIG. 5. Geographic distribution of *Tantilla hobartsmithi*. Hollow circles indicate localities from which we examined specimens. Solid circle designates type-locality.

Top of head strikingly darker (brown, black) than dorsal body color (beige to light brown); dark head cap not extending ventrolaterally below angle (corner) of mouth; dark head cap extending on middorsal line 0.5–3 scales beyond posterior end of suture between parietals; posterior edge of dark head cap usually convex or straight, followed by light (white, cream) collar 0.5–2 scales wide; no dark band or dark spots along posterior edge of collar; origin of m. retractor penis magnus at level of subcaudals 20–34; retracted hemipenis extending to subcaudals 7–14; hemipenis subcylindrical to clavate when everted, capitate, with two medium to large basal spines; no spinules on hemipenis proximal to basal spine; 16–37 spines in 1–3 rows (minimum) approximately encircling spinose midsection of hemipenis; supralabials 7; infra-labials 6; naris in upper half of nasal; postoculars usually 2; temporals 1+1; mental usually touching anterior pair of genials. Most similar to *T. atriceps*; differing strikingly in hemipenis.

DISTRIBUTION: Specimens are from the following states, or parts thereof, in the United States: Arizona; southern California; western Colorado; southern Nevada; southern New Mexico; southern Texas; and southern Utah. Specimens are from the following states in Mexico, also: Chihuahua; Coahuila; and Sonora (fig. 5). Although there are no certain records, *T. hobartsmithi* also may occur in one or more of the following Mexican states: Durango; Nuevo León; San Luis Potosí; and Zacatecas (table 29; fig. 38). *Tantilla hobartsmithi* and *T. atriceps* are sympatric in Coahuila; *T. hobartsmithi*

might also be sympatric with *T. planiceps* in California and with *T. yaquia* in southern Arizona (see Remarks, below).

GENERAL DESCRIPTION: Except where specified otherwise, the following description is based on pooled data from 577 specimens examined from throughout the range; variation is discussed later in this paper. When ranges of data or alternatives are presented, sample size follows (in parentheses).

Maximum total length 313 mm.; maximum body length 238 mm.; tail length comprising 19.4–31.3% (216) of total length of males, 18.3–27.4% (164) of females.

Taylor ("1936" [1937], p. 341) described color of the holotype as follows: "Head brown, a light tan or yellow-tan on the snout, becoming black-brown or an indefinite brown on back part of head. White nuchal spots or collar; body anteriorly tan, becoming more faun posteriorly, each scale with some small brownish flecks forming indefinite lines on all save outer scale row . . . . Whitish on the underside of head and anterior part of body; cream to cream yellow posteriorly." In life, the majority of the ventral surface is bright coral-red, orange-red, or pink (fading to grayish white in preservative), as seen on individuals from Arizona, Colorado, New Mexico, Texas, and Utah (Van Denburgh and Slevin, 1913, p. 424; Woodbury, 1931, p. 108; McCoy, Knopf, and Walker, 1964, p. 136; Conant, 1975, p. 223; and personal observ.).

We recorded the following notes from four living specimens from Val Verde County, Texas, contributed by Dr. Robert Wayne Van Devender. "Dorsal Body: One specimen is grayish-tan; another is orangish-tan; the other two snakes are different shades in between. Dorsal Head: Very dark brown on all specimens, gradually becoming lighter anteriorly; collar is simply a lighter tan than the body. Ventral Surfaces: Chin and throat (through first few ventrals) light gray; rest of venter, to tip of tail, reddish-orange. The bright ventral color begins gradually anteriorly, first as a midventral streak, soon broadens and covers all the ventral surface." Unusual specimens rarely are found with dark pigmentation on the infralabials and

chin (e.g., CM 40416 from Cochise Co., Arizona).

Characteristics of head coloration for the specimens we examined follow: dark head cap not extending ventrad below angle of mouth; 0–45% (316) anterior temporal light in color; 5–97% (328) seventh supralabial light in color; 0–100% (326) sixth supralabial light in color; 37–100% (328) fifth supralabial light in color; dark head cap extending on middorsal line 0–3 (576) scales beyond posterior end of suture between parietals; posterior edge of dark head cap usually convex (280 out of 577 specimens), straight (120 out of 577 specimens), pointed (94 out of 577 specimens), or angular (69 out of 577 specimens); dark head cap followed by light collar (502 out of 572 specimens) 0–2 (561) scales wide; no dark band or dark spots along posterior edge of collar (304 out of 331 specimens).

Hemipenes are described under Variation, but those of the holotype are described below (see Redescription of Holotype).

The following details of scutellation are essentially invariant, unless indicated otherwise: supralabials 7, with 3+4 entering orbit; infralabials 6; preoculars 1; postoculars 1–2, usually 2; temporals 1+1; mental touching both anterior genials (449 of 574 specimens); prefrontals usually not touching any supralabials (327 of 566 specimens), but often touching one or more supralabials on each side (167 of 566 specimens); naris in upper half of (272 of 328 specimens) or medial in (56 of 328 specimens) nasal; nasal usually divided only below naris on both sides (253 of 318 specimens), sometimes divided below and grooved above naris on both sides (25 out of 318 specimens), sometimes divided both below and above naris on both sides (20 out of 318 specimens); dorsal scales in 15 rows throughout. Ventrals and subcaudals with considerable sexual dimorphism and geographic variation (figs. 24–27): ventrals of males 124–166 (N = 305), of females 130–169 (246); subcaudals of males 48–74 (220), of females 47–67 (164); ventrals + subcaudals of males 180–239 (216), of females 186–231 (162).

Maxillae are described under Variation.

REDESCRIPTION OF HOLOTYPE: The specimen is highly desiccated, brittle, and discolored, apparently having dried out in the past. Thus, many features are obscure and indeterminate, especially if one is not to risk tearing or breaking the specimen.

Snout-vent length 146 mm.; dark head cap extending on middorsal line 1 scale beyond posterior end of suture between parietals; posterior edge of dark head cap convex.

Neither hemipenis is everted. Because the specimen is so brittle, the right hemipenis was examined *in situ* only sufficiently to check critical characters: Organ single; spinose midsection with few spines, being relatively small (relative to *T. atriceps*); only one row (minimum) of spines approximately encircling organ except at sulcus spermaticus; apical region calyculate, abruptly and clearly differentiated from spinose midsection; basal calyces with very small spinules; organ capitate.

Cephalic scutellation essentially normal; supralabials 6–7, with 3+4 entering orbit; infralabials 6; preoculars 1; postoculars 1–2, lower right one being tiny; temporals 1+1; mental touching both anterior genials; prefrontals not touching any supralabials; naris high in nasal; nasal divided both above and below naris; dorsal scales in 15 rows throughout; number of ventrals uncertain, probably 131, definitely not more than 133; subcaudals 36+; ventrals + subcaudals approximately 167.

ECOLOGY: For Arizona, *T. hobartsmithi* has been reported to occur "in pinon-juniper habitat" (Hulse, 1973, p. 281), "in the chaparral-woodland zone" near Roosevelt Dam (Little, 1940, p. 264), and, "around Tucson, . . . it is frequently encountered under loose boards, logs or pieces of wood amongst mesquite thickets or sycamore stands, usually within a few hundred feet of the river bed" (Fowlie, 1965, p. 110); we have collected it in mesquite-*Yucca* grassland also. In California the species has been found in the piñon belt, with some trees higher than 20 feet, with "clumps of bunch grass and numerous large boulders scattered about" (Miller and Stebbins, 1964, p. 424); also in the "sage-greasewood complex. Dominant plant species

included *Artemisia tridentata, Salvia carnosa* [=*Salvia dorrii*], *Vitis girdiana, Sarcobatus vermiculatus, Eriogonum inflatum*" (Banta, 1962, p. 188). In Colorado, *T. hobartsmithi* has been found where "the vegetation on the sandy, rock-laden soils . . . consists of an assemblage of xerophytic shrubs, especially *Sarcobatus vermiculatus, Artemisia tridentata,* and *Atriplex canescens,* and various species of grasses and forbs" (McCoy, Knopf, and Walker, 1964, p. 135). For Texas, individuals have been reported from "the Piñon-Juniper-Oak association," where it "is extremely rocky with steeply sloping sides" (Degenhardt and Milstead, 1959, p. 159; also see Minton, "1958" [1959]) and in the following associations: cedar-ocotillo; persimmon-shinoak; mesquite-creosote; and cedar-savannah (Milstead, Mecham, and McClintock, 1950). Specimens from Utah have been reported from "the juniper-pinyon pine community" (Tanner, 1954, p. 92). Most individuals are found beneath objects such as rocks, logs, boards, and fallen *Yucca, Agave,* and sotol (Woodbury, 1931; Schmidt and Smith, 1944; Milstead, Mecham, and McClintock, 1950; Woodin, 1953; Tanner, 1954; Minton, "1958" [1959]; Axtell, 1959; Lindner, "1962" [1963]; Miller and Stebbins, 1964; and Fowlie, 1965), but "one was found swimming in the water of a small stream" (Murray, 1939, p. 12). Collecting dates involving all 12 months of the year are included among the specimens we examined. Taylor ("1936" [1937], p. 341) described finding the holotype at night as follows: "The specimen was observed running with most surprising rapidity over rough, gravelly terrain, under low shrubs. I succeeded in capturing it only with the greatest difficulty."

Few specifics have been published regarding food and feeding of *T. hobartsmithi*. Minton ("1958" [1959], p. 50) mentioned that the stomach of one specimen contained a "beetle larva, another contained a centipede," and that both prey items were relatively "quite large." Our observation of a beetle larva in the stomach of FMNH 75850 may well be of the same one. Tanner (1954, p. 92) stated: "A recently ingested centipede

(*Scolopendra polymorpha* Wood), measuring 44 mm., was regurgitated soon after one of the larger specimens (BYU 11279) was collected.'' We determined the snout-vent length of BYU 11279 as 198 mm., so the food item in this case was 22.2% of its body length. Milstead, Mecham, and McClintock (1950, p. 556) reported: ''the remains of a half grown millipede were in the stomach of one individual.'' Lindner (''1962'' [1963], p. 32) examined digestive tracts of 37 individuals from one locality and concluded: ''Apparently, only lepidopterous and coleopterous larvae were eaten by these specimens . . . in spite of the fact that many other suitable food items were available in the snakes' environment. This indicates that *atriceps* is a selective feeder and does not eat anything that moves and is of the 'right' size and shape for ingestion by a small, extremely slender snake.'' Stebbins (1954, p. 452) reported that *T. hobartsmithi* has eaten ''mealworms'' in captivity.

Conversely, Vitt and Hulse (1973) reported that *Micruroides euryxanthus* will eat ''*T. planiceps*'' (probably actually *T. hobartsmithi*) in captivity. We found no record of predation on this species in nature.

Tantilla hobartsmithi is oviparous. Stebbins (1954, p. 452) noted that two collected in California on June 3 ''each contained a single large egg. These eggs measured approximately 4 by 17 mm.'' Similarly, Minton (''1958'' [1959], p. 50) noted that ''a female collected [in Texas] June 1 contained one large egg nearly ready for deposition.'' Easterla (1975) presented the following information on oviposition by three females from Texas: (1) one egg (28 × 7 mm.) laid 28 July 1973 (♀ caught 23 July 1973); (2) one egg (27 × 7 mm.) laid 4 August 1973 (♀ caught 29 July 1973); and (3) one egg (23 × 6 mm.) laid 23 June 1974 (♀ caught 20 June 1974).

REMARKS: Justification for specific recognition of this form among the four species previously included in *T. planiceps* is presented under Taxonomic Judgments; also see Additional Problems. Although there is local variation and geographic variation in a few characters, we do not recognize subspecies (see Taxonomic Judgments).

It is possible that *T. hobartsmithi* and *T. planiceps* are sympatric in California. The only two specimens of *Tantilla* we have seen from Joshua Tree National Monument (both LBSC specimens; different localities) are intriguing. One, bearing apparently a field catalogue number HSL (H. S. Logsdon; although collected by E. L. Sleeper) 630525-4 may actually be LBSC 1070, which Loomis and Stephens (1967) reported as a ''*Tantilla eiseni transmontana*'' with 188 ventrals and 67 subcaudals. The snake, however, which died in a can trap, is in poor condition, and we were unable to make reliable ventral and subcaudal counts on it; nor could we discern other important characters, so we identified this specimen as either *T. hobartsmithi* or *T. planiceps*. The other specimen also bears apparently a field catalogue number—WCW (W. C. Welbourn) 690717-1. It is a male with 166 ventrals, 73 subcaudals, and aspects of head coloration that characterize *T. hobartsmithi*. Another interesting specimen from California is MVZ 83454, a *T. hobartsmithi* from the San Joaquin Valley (Kings Co.); in view of the records for *T. planiceps* in Fresno County, it seems likely that these species are sympatric in that valley. Additional specimens from Joshua Tree National Monument and the San Joaquin Valley are needed.

Probably *T. hobartsmithi* and *T. yaquia* are sympatric in southern Arizona, although this has not been documented (McDiarmid, 1968, pp. 174, 175). The detailed color notes of a specimen of ''*Tantilla atriceps*'' from Arizona (which would be *T. hobartsmithi*) presented by Wright and Wright (1957, p. 726), actually are based on a specimen of *Tantilla yaquia*.

There is no certain fossil record of *T. hobartsmithi*. However, Gehlbach and Holman (1974, p. 194) reported 6 precaudal vertebrae of ''*Tantilla* sp.'' from western Texas and commented that ''*T. atriceps* [= *T. hobartsmithi*] is abundant around Pratt Cave today, while *T. nigriceps* is apparently scarce in the Guadalupe Mountains region.'' Also, Van Devender and Worthington (1977, p. 94) reported 8 vertebrae of ''*Tantilla* sp.'' from southwestern New Mexico and stated that ''the smaller vertebrae may be of sub-

adult *T. nigriceps,* or of the smaller-sized species, *T. planiceps*" [=*T. hobartsmithi*].

The specimens we examined include the holotype of *Tantilla utahensis* Blanchard, 1938 (CAS 55214).

VARIATION

Rather than discuss intraspecific variation in detail separately in each of the foregoing species accounts, we discuss variation within and among species in a comparative fashion here, in order to demonstrate similarities and differences most clearly. Primarily we compare *T. planiceps, T. atriceps,* and *T. hobartsmithi,* but we also include other North American species, particularly *T. yaquia,* as these four species recently were considered conspecific (Tanner, 1966).

Significance and taxonomic utility of the characters examined varies. Some traits are virtually identical in all the species compared and therefore are nondiagnostic. Other characters are so variable that they also are not particularly useful for distinguishing species. Some character states are highly species-specific, but there is no single character whose variation is such that its state is unique in each species. Nevertheless, there are two suites of characters whose variations are correlated so as to be reasonably useful for recognizing taxa at the species level. These are patterns of head coloration, which have been used heavily by previous workers, and structures of hemipenes, which we describe in detail for the first time. Because we find them to be of considerable taxonomic importance in *Tantilla,* we consider anatomy of hemipenes and variation in cephalic coloration first; later we consider variation in scutellation, size and proportions, maxillae, and sex ratios.

HEMIPENES

Shortly after we began examining hemipenes, it was evident that they were potentially important for distinguishing species of *Tantilla.* Therefore, we examined hemipenes of as many specimens in the *planiceps* com-

plex as reasonably possible and of other species of *Tantilla* from western North America for outgroup comparisons. Consequently, we present descriptions of the hemipenes of seven North American species of *Tantilla,* based on examination of these organs on 258 specimens, as follows: *T. gracilis* (N = 8); *T. nigriceps* (N = 16); *T. wilcoxi* (N = 2); *T. yaquia* (N = 5); *T. planiceps* (N = 70); *T. atriceps* (N = 14); and *T. hobartsmithi* (*N* = 143).

GENERAL DESCRIPTION

Features described here characterize all the species examined. The hemipenis is single with a simple sulcus spermaticus that is continuous to the apex. On everted organs, which are symmetrical (mirror images), the sulcus spermaticus emerges from the cloaca on the medial aspect and usually abruptly turns posteriad to the lateral or posterior surface, which is the sulcate side. In retracted organs, the sulcus is on the medial aspect at the cloaca and abruptly turns ventrad to the lateral surface, gradually sloping dorsad as it continues toward the apex.

The hemipenis consists of three general regions: basal section, midsection, and head or apex. The basal section, which bears fine folds or grooves (inconspicuous or absent on fully everted organs), usually is only moderately ornamented. The midsection bears numerous conspicuous spines, which tend to be distributed in one or more rows approximately encircling the organ, except at the sulcus. In counting the number of spines, we disregarded the spinules that may occur in the midsection. The apical region is calyculate, and, depending on the species, the calyces may be spinulate, papillate, or of both
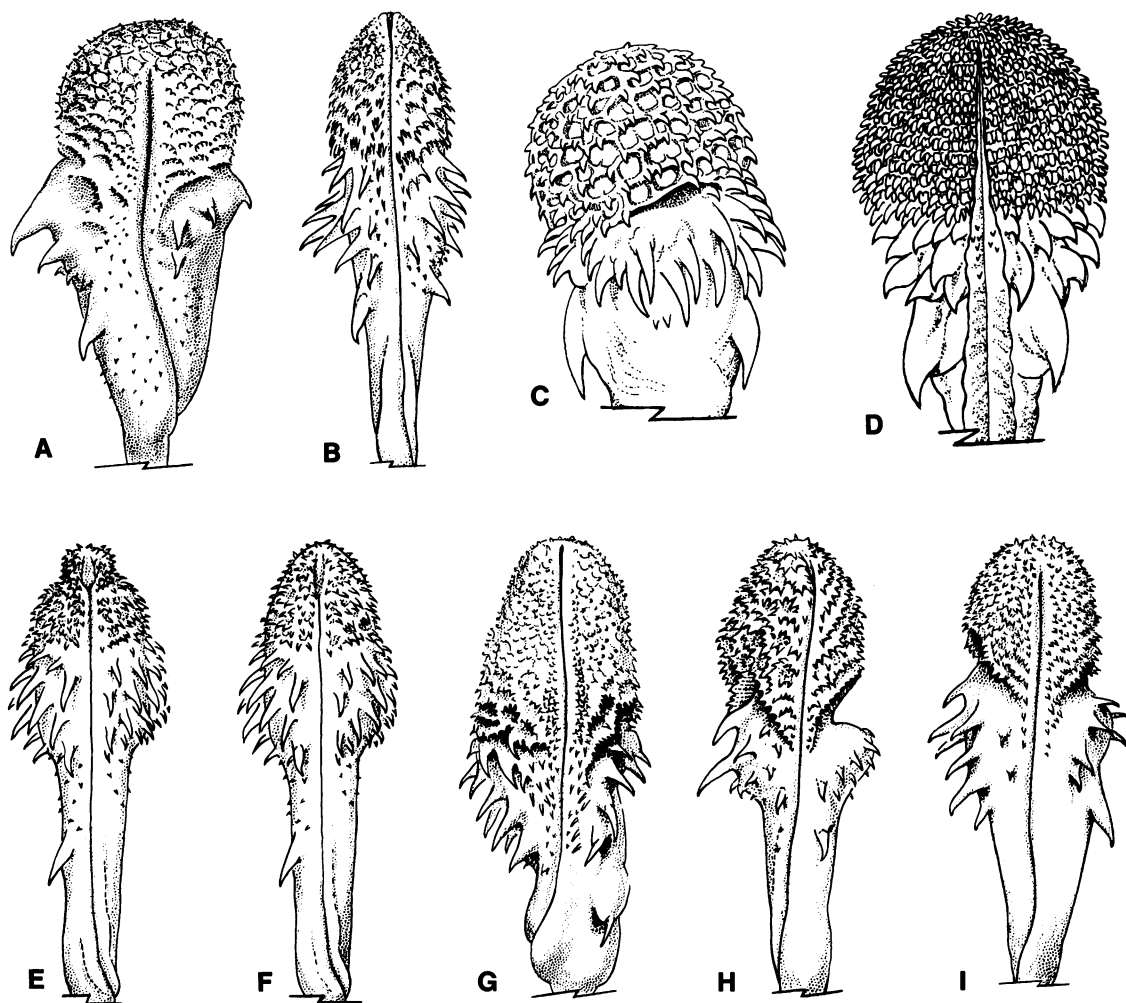
FIG. 6. Hemipenes of six species of *Tantilla*. A. *T. gracilis*, sulcate view, right organ, AMNH 103801. B. *T. nigriceps*, sulcate view, right organ, TCWC 27473. C. *T. yaquia*, asulcate view, left organ, UAZ 40060. D. *T. yaquia*, sulcate view, left organ, UAZ 40060. E. *T. planiceps*, sulcate view, right organ as observed with tip incompletely everted, LBSC 1111. F. *T. planiceps*, same as E, but drawn as if fully everted. G. *T. atriceps*, sulcate view, left organ, UAZ 23763. H. *T. hobartsmithi* (Texas), sulcate view, left organ, TCWC 25904. I. *T. hobartsmithi* (Arizona), sulcate view, left organ, AMNH 108915.

types. Also depending on the species, the hemipenis may be capitate, semicapitate, or noncapitate.

Tantilla gracilis
Figure 6A

The m. retractor penis magnus (major retractor muscle) originates at the level of sub-

caudals 20–23 ($\bar{x}$ = 21.5, N = 6). The everted hemipenis is clavate and extends the length of 5–8 subcaudals ($\bar{x}$ = 7.0, N = 5); the two retracted ones examined extend the length of 7 or 8.

The basal section bears numerous scattered spinules; one conspicuous, moderate-sized, curved spine near the sulcus spermaticus; and another conspicuous, moderate-sized,

curved spine on the opposite side of the organ. The two basal spines are at the level of subcaudals 2–4 ($\bar{x}$ = 3.2, N = 5) on fully everted organs, and at subcaudal 4 (N = 2) in retracted organs. The spinules are widely scattered, occurring in the area between the spines and also proximal and distal to them.

The midsection bears 14–20 ($\bar{x}$ = 16.6, N = 7) small to large, curved spines, most of which are moderate in size. The spines are rather evenly, and not densely, distributed, tending to form one rather neat row (minimum) of spines encircling the organ (viewed on the asulcate side). Some spinules occur among the spines and along the edges of the sulcus. On two retracted organs, the spinose midsection is at the level of subcaudal 5.

The apical region is sharply distinguished from the spinose midsection. In six specimens from Louisiana, all calyces are spinulate; in one from Kansas, the proximal calyces are similarly spinulate but the distal ones are papillate. The proximal and distal calyces are considerably broader than those in between. Indeed, some of the proximal calyces are so broad as to allow the everted organ to flex somewhat and give it a semicapitate appearance, although the organ definitely is not to be regarded as truly capitate.

Tantilla nigriceps
Figure 6B

The major retractor muscle originates at the level of subcaudals 31–38 ($\bar{x}$ = 35.1 ± 0.642, N = 14). The everted hemipenis is subcylindrical and extends the length of 9–13 subcaudals ($\bar{x}$ = 11.0, N = 5); retracted ones extend the length of 8–13 ($\bar{x}$ = 11.2, N = 5).

The basal section bears only a large, conspicuous, curved spine near the sulcus spermaticus and a moderate-sized spine on the opposite side of the organ. The two basal spines are at the level of subcaudals 4–6 ($\bar{x}$ = 4.6, N = 5) on fully everted organs, and also at subcaudals 4–6 (N = 3) in retracted organs. There are no spinules in the basal region.

The midsection is moderately spinose, bearing 31–39 ($\bar{x}$ = 34.4, N = 5) small to

large curved spines. The spines are rather evenly and densely distributed, tending to form at least three (N = 8) rows (minimum) approximately encircling the organ (viewed on the asulcate side). Spinules occur among the spines and along the edges of the sulcus. The total number of spines is difficult to determine on some specimens because of the numerous spinules (not counted) that had to be distinguished from small spines (counted) and because this midsection gradually merges with the following apical region without a sharp area of demarcation. On three retracted organs, the proximal edge of this region is at the level of subcaudals 6–7; the distal edge is at subcaudals 8–10.

The proximal calyces of the apical section are spinulate but the spinules are so large and curved that on some specimens it is difficult to distinguish between the larger spinules on the proximal calyces and some of the adjacent spines of the spinose midsection. The distal calyces are papillate. There is a gradual transition from the large proximal spinules to the small distal papillae on the calyculate apex. The organ is not capitate.

Tantilla wilcoxi

The major retractor muscle originates at the level of subcaudals 26–28 ($\bar{x}$ = 27.0, N = 2). We cannot describe the general shape because we have not seen a fully everted organ. One retracted organ extended the length of 10 subcaudals.

The basal section bears numerous scattered spinules; a conspicuous, very large, thick, curved spine near the sulcus spermaticus; and another conspicuous but somewhat smaller spine on the opposite side of the organ. The basal spines are at the levels of subcaudals 4 and 5, respectively, in one retracted organ. Spinules are numerous on the fleshy base of the largest basal spine and scattered among the two spines and above and below them.

The midsection is very spinose, with curved spines that range from small to very large in size. The smaller spines mostly comprise the proximal part of this section. Most of the spines are rather large, and there are

more than 70 of these on the one organ examined for this character. The spines are very densely distributed, tending to form at least five rows (minimum) approximately encircling the organ (viewed on the asulcate side). The total number of spines is very difficult to count because of their high number, extremely dense distribution, and various sizes, and because this midsection gradually merges with the apical region without a sharp area of demarcation. The edges of the sulcus bear spinules. On one retracted organ, the spinose midsection occurs at the level of subcaudals 6 and 7.

The proximal calyces of the apical region are spinulate but the spinules are so large and curved it is difficult to distinguish them from some of the distal spines in the adjacent spinose midsection. The distal calyces are papillate. The organ is not capitate.

Tantilla yaquia
Figures 6C, D

The major retractor muscle originates at the level of subcaudals 22–24 ($\bar{x}$ = 23.4, N = 5). The one everted hemipenis examined is subcylindrical to clavate and extends the length of 7 subcaudals; inverted ones extend the length of 6–9 ($\bar{x}$ = 7.4, N = 5).

The basal section bears a very large, conspicuous, curved spine near the sulcus spermaticus, and one (also very large) spine on the opposite side of the organ. The two basal spines are at the level of subcaudals 1–2 on one fully everted organ, and subcaudals 3–4 on three retracted organs. Some specimens have a few spinules on the asulcate side between the basal spines.

The midsection is moderately spinose, bearing 37–58 ($\bar{x}$ = 46.3, N = 3) small to large curved spines, most of which are large. The spines are densely distributed, tending to form at least 2–4 ($\bar{x}$ = 2.8, N = 4) rows (minimum) approximately encircling the organ (viewed on the asulcate side). The total number of spines is difficult to count on some specimens because in places this midsection merges with the apical region without a sharp area of demarcation. A few spinules are on the edges of the sulcus, distally. On the one

everted organ examined for this character, the midsection occupies the levels of subcaudals 3 and 4. On four retracted organs, the proximal edge is at the level of subcaudals 3–5 and the distal edge at subcaudals 5–6.

The proximal calyces of the apical region are spinulate but the spinules on some specimens are so large and curved it is difficult in places to distinguish them from some of the distal spines of the spinose midsection. The distal calyces are papillate. There is a gradual transition from the large proximal spinules to the small distal papillae on the calyculate apex. The organ is not capitate, but has one very broad basal calyx on the asulcate side at the base of the apical region (fig. 6C); this allows the everted organ to flex somewhat toward the sulcate side. On retracted organs this appears as an inconspicuous naked pocket at the base of the apical region. Thus, we consider the organ as semicapitate.

Tantilla planiceps
Figures 6E, F

The major retractor muscle originates at the level of subcaudals 30–38 ($\bar{x}$ = 33.7 ± 0.261, N = 62). The everted hemipenis is subcylindrical to somewhat bulbous and the one examined for this character extends the length of 12 subcaudals; retracted ones extend the length of 9–15 ($\bar{x}$ = 12.1 ± 0.156, N = 47).

The proximal half or more of the basal section is essentially naked. The distal part of the basal section, comprising approximately the length of two subcaudals, bears numerous spinules. Usually there is a single, curved, small to large spine near the sulcus at approximately the level of the proximal spinules, but the spine is absent in 12 (23.1%) of 52 specimens. When present on everted organs, the basal spine is at the level of subcaudals 3–4 ($\bar{x}$ = 3.2, N = 5); retracted organs have the spine at the level of 4–6 ($\bar{x}$ = 5.0 ± 0.140, N = 29). In retracted organs the basal spine and numerous spinules usually are concealed within a deep, longitudinal groove adjacent and parallel to the sulcus

spermaticus. On 10 out of 48 specimens (20.8%), there is also a single, curved, smaller spine on the asulcate side of the organ somewhat more distally; this spine is at the level of subcaudals 6–7 ($\bar{x}$ = 6.3, N = 6) on retracted organs. On two specimens there are two such spines close together, one immediately following the other.

The midsection is very spinose, bearing 45–73 ($\bar{x}$ = 57.6 ± 1.484, N = 30) small to very large curved spines. The spines are densely distributed, tending to form 3–5 ($\bar{x}$ = 4.1 ± 0.086, N = 34) rows (minimum) approximately encircling the organ (viewed on the asulcate side). The proximal and distal rows are comprised primarily of the smallest spines. In this section, the lips of the sulcus may be naked, papillate, or spinulate. On retracted organs, the proximal edge of this region is at the level of subcaudals 5–11 ($\bar{x}$ = 7.9 ± 0.168, N = 38), and the distal edge at the level of 8–12 ($\bar{x}$ = 9.6 ± 0.157, N = 38).

The apical region is calyculate and rather sharply demarcated from the spinose midsection. On many specimens all calyces are papillate, but some have the proximal calyces (or some of them) clearly spinulate. Some specimens have basal calyces bearing fleshy papillae on which the tips are pointed and shiny in reflected light, indicating limited calcification. The organ is not capitate.

Anatomy of the hemipenis is basically the same on all specimens of *T. planiceps*, whether they come from the northern part of the range in California (formerly called "*T. eiseni*"), from the Cape region of Baja California Sur, or from any of various localities in between. If any consistent differences characterize the southernmost populations, of which the available sample is small, they appear to be in two relatively unimportant features: (1) five specimens from Baja California Sur have the major retractor muscle originating at the level of subcaudals 36–38 ($\bar{x}$ = 37.0); these are high counts but within the range of the remaining *T. planiceps*, indicating less geographic variation than occurs in *T. hobartsmithi* (fig. 7). (2) Both basal spines are absent on all four specimens from Baja California Sur examined for this char-

acter; however, these spines are also absent on some specimens from elsewhere in the range (e.g., SDSNH [L. M. Klauber specimen] 2634 from San Diego County, California).

We did not notice any obvious differences between left and right organs while examining hemipenes, and on each specimen we dissected (all species) the m. retractor penis magnus of each side originated on the same caudal vertebra. Nevertheless, in the event that we could test for differences on opposite sides, we recorded which organ was examined on each specimen. *Tantilla planiceps* is the only species for which our samples of data obtained from opposite sides of the body are sufficiently large (N = 10 or more) to be analyzed statistically (*t*-tests). There are no significant differences ($P > 0.05$) between right and left hemipenes in all characters tested (length of retracted organ; level of basal spine; and level of proximal and distal ends of spinose midsection). We conclude, therefore, that hemipenial data derived from organs on each side of the body can be used reliably for these snakes.

Tantilla atriceps
Figure 6G

The major retractor muscle originates at subcaudals 25–32 ($\bar{x}$ = 27.6 ± 0.626, N = 14). The everted hemipenis is subcylindrical and extends the length of 9–10 subcaudals ($\bar{x}$ = 9.5, N = 2); retracted ones extend 9–14 ($\bar{x}$ = 10.6 ± 0.452, N = 10).

The basal section bears only a medium to large, conspicuous, curved spine near the sulcus spermaticus and another similar but often somewhat smaller spine on the opposite side of the organ and usually a bit more distal in location. Usually there are some spinules distal to and/or between the two basal spines. The proximal spine is at the level of subcaudal 4 (N = 2) on everted organs, and at subcaudals 3–6 ($\bar{x}$ = 4.3 ± 0.289, N = 9) in retracted organs. The second basal spine, on the opposite side, is at the level of subcaudals 4–5 ($\bar{x}$ = 4.5, N = 2) on everted organs, and at subcaudals 4–7 ($\bar{x}$ = 5.1 ± 0.309, N = 9) in retracted organs.

The midsection is moderately spinose, bearing 26–40 ($\bar{x}$ = 32.4 ± 1.083, N = 14) small to large curved spines. The spines are densely distributed, tending to form 2–3 ($\bar{x}$ = 2.6 ± 0.137, N = 14) rows (minimum) approximately encircling the organ (viewed on the asulcate side). Spinules occur among the spines and conspicuously along the edges of the sulcus. The total number of spines usually is difficult to determine because of the numerous spinules (not counted) to be distinguished from small spines (counted) and because the midsection merges with the apical region without a sharp area of demarcation. In retracted organs the proximal edge of this region is at the level of subcaudals 5–9 ($\bar{x}$ = 6.2 ± 0.401, N = 9) and the distal edge at the level of 6–11 ($\bar{x}$ = 7.7 ± 0.500, N = 9).

The proximal calyces of the apical section are spinulate but the spinules are so large and curved that usually it is difficult to distinguish them from some of the distal spines of the spinose midsection. The distal calyces are papillate. There is a gradual transition from the larger proximal spinules to the small distal papillae on the calyculate apex. The organ is not capitate.

Tantilla hobartsmithi
Figures 6H, I

The major retractor muscle originates at subcaudals 20–34 ($\bar{x}$ = 26.2 ± 0.280, N = 128). The everted hemipenis is subcylindrical to clavate. Retracted organs extend the length of 7–14 subcaudals ($\bar{x}$ = 10.8 ± 0.182, N = 90).

The basal section bears a medium to large, conspicuous, curved spine near the sulcus spermaticus and often another spine (usually smaller) on the opposite side of the organ, usually more distal. A few spinules may occur between the basal spines, but usually such spinules are lacking. In retracted organs, the proximal spine is at the level of subcaudals 2–7 ($\bar{x}$ = 5.1 ± 0.188, N = 48); the second next basal spine, on the opposite side, is at the level of 3–7 ($\bar{x}$ = 5.7 ± 0.239, N = 27).

The midsection is spinose, bearing 16–37

($\bar{x}$ = 23.8 ± 0.576, N = 52) small to large curved spines, most of which are medium to large. The spines, which are not densely distributed, tend to form 1–3 ($\bar{x}$ = 1.2 ± 0.056, N = 66) rows (minimum) approximately encircling the organ (viewed on the asulcate side). Spinules occur among the spines and sparsely along the edges of the sulcus, sometimes limited to the distal portion of the sulcus. In retracted organs the proximal edge of this region is at the level of subcaudals 4–9 ($\bar{x}$ = 6.5 ± 0.193, N = 51) and the distal edge at the level of 5–11 ($\bar{x}$ = 7.8 ± 0.205, N = 51).

The organ is capitate, the apical region being sharply demarcated from the spinose midsection by a naked groove that encircles the organ except at the sulcus spermaticus. Most or all the calyces are papillate. Frequently, however, the proximal calyces bear spinules or fleshy papillae having calcified tips.

A striking feature of the hemipenis of T. hobartsmithi is that it is distinctly capitate, and without exception this is consistent in all specimens examined from diverse localities within its range (Arizona, California, Colorado, Texas, Nevada, New Mexico, Utah, Chihuahua, Coahuila, and Sonora), including the holotype. Nevertheless, our large sample reveals significant geographic variation in some features, such as the number of spines and length of the organ, and positions of certain structures. This is discussed under Comparisons. Note that specimens from the eastern part of the range (Coahuila and Texas) are similar to each other and there is a clinal increase in the various characters from the eastern to the western part of the range; also, specimens from the western part of the range (Arizona and Utah) generally are more similar to each other than to specimens from the eastern part of the range.

COMPARISONS

Of the hemipenes we described above for seven species, the capitate organ of T. hobartsmithi is quite distinctive (table 2). The most similar organs are in T. atriceps and T. nigriceps, which usually are separable on the

TABLE 2

Variation in Occurrence of Basal Spinules and Capitation of Hemipenes of Seven Species of *Tantilla*

Species	Spinules proximal to basal spine?	Capitate?
T. gracilis	Yes	Semi
T. nigriceps	No	No
T. wilcoxi	Yes	No
T. yaquia	No	Semi
T. planiceps	No	No
T. atriceps	No	No
T. hobartsmithi	No	Yes

basis of origin of the retractor muscle; similarities between these two species are discussed later (see Additional Problems). Other than the similarity just mentioned, each species has a species-specific combination of traits that characterize its hemipenis; these characters are included in the diagnoses presented earlier. Comparisons of selected variable characters are presented in tables 3–4 and figures 7–14, and the variation is discussed below.

ORIGIN OF RETRACTOR MUSCLE (table 3; figs. 7, 11): Origin of the m. retractor penis magnus differs among species and varies intraspecifically within *T. hobartsmithi*. Note that the *T. hobartsmithi* from Arizona are not significantly different from the *T. hobartsmithi* that formerly were called "*T. utahensis*," which is consistent with considering these populations as conspecific (fig. 7). Note, however, that *T. atriceps* differs from the geographically nearby populations of *T. hobartsmithi* from Coahuila and Texas, whereas it is similar to *T. hobartsmithi* from Arizona (fig. 7). Also, *Tantilla planiceps* is significantly different from *T. atriceps* and from all three large samples of *T. hobartsmithi* (table 3; fig. 7). *Tantilla yaquia* differs strongly from *T. planiceps* and *T. atriceps*, and is most similar to *T. hobartsmithi* from Coahuila and Texas (table 3; fig. 7). Origin of the m. retractor penis magnus used to-

gether with number of spines in the spinose midsection separates all specimens of *T. atriceps* from all those of *T. planiceps* and *T. yaquia* and from most specimens of *T. hobartsmithi* (fig. 11). Using the same combination of characters, *T. gracilis*, *T. nigriceps*, and *T. wilcoxi* are distinctly different from each other (fig. 11); and *T. nigriceps* and *T. wilcoxi* also differ from *T. atriceps*, *T. planiceps*, *T. hobartsmithi*, and *T. yaquia*. Most of the *T. hobartsmithi* are separable from the *T. gracilis*, although some specimens are similar (fig. 11).

LENGTH OF RETRACTED HEMIPENIS (table 3; fig. 8): There are significant differences between species and between certain populations of *T. hobartsmithi*, but different populations of *T. planiceps* (comparing specimens formerly called "*T. eiseni*" with those from Baja California Sur) are very similar (table 3; fig. 8). Also, the *T. hobartsmithi* from Arizona do not differ from those that
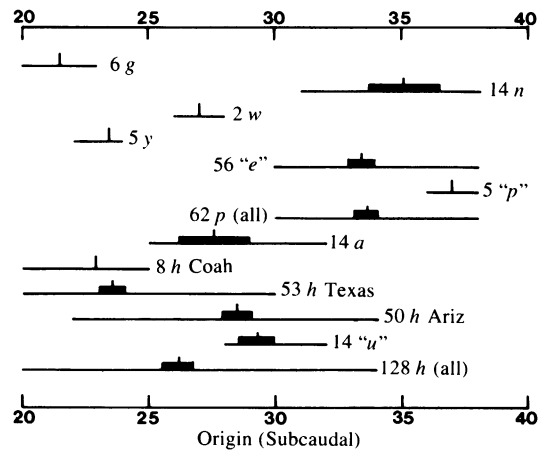
FIG. 7. Origin (subcaudal number) of m. retractor penis magnus in seven species of *Tantilla*: *T. gracilis* (*g*); *T. nigriceps* (*n*); *T. wilcoxi* (*w*); *T. yaquia* (*y*); *T. planiceps* (*p*; "*e*" = specimens previously called *eiseni*; "*p*" = specimens from Baja California Sur); *T. atriceps* (*a*); *T. hobartsmithi* (*h*; "*u*" = specimens previously called *utahensis*). Coah = Coahuila, Mexico; Ariz = Arizona. Horizontal line indicates range, vertical line indicates mean, rectangle indicates 95% confidence interval. Number beside range is sample size.
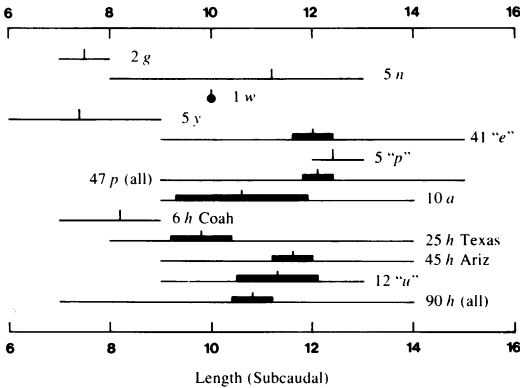
FIG. 8. Length (to subcaudal number) of retracted hemipenis in seven species of *Tantilla*; interpretation as in figure 7.

formerly were called "*T. utahensis.*" *Tantilla yaquia* differs strongly from *T. planiceps* and *T. atriceps,* and is most similar to *T. hobartsmithi* from Coahuila and *T. gracilis* (table 3; fig. 8).

NUMBER OF SPINES IN SPINOSE MIDSECTION (table 4; figs. 9–11): *Tantilla planiceps*

differs strikingly from *T. atriceps* and *T. hobartsmithi.* However, populations of *T. hobartsmithi* are similar to each other, as are different populations of *T. planiceps* (fig. 9). *Tantilla yaquia* differs strongly from *T. hobartsmithi,* perhaps less strongly from *T. atriceps,* and it is most similar to *T. planiceps.* Number of spines in the spinose midsection used together with number of subcaudals (fig. 10), origin of the major retractor muscle (fig. 11), and minimum number of rows of spines in the spinose midsection (fig. 13) separates all specimens of *T. atriceps* from all those of *T. planiceps* and from most specimens of *T. hobartsmithi.* Considering number of spines in the spinose midsection together with number of subcaudals (fig. 10), *T. gracilis* seems to differ from *T. nigriceps,* *T. wilcoxi,* *T. atriceps,* *T. planiceps,* and *T. hobartsmithi*; *T. nigriceps* differs from *T. planiceps* and *T. hobartsmithi*; and *T. atriceps* and *T. hobartsmithi* differ from *T. planiceps* and *T. wilcoxi.* Considering number of spines in the spinose midsection together with origin of the retractor muscle (fig. 11),

TABLE 3

Variation in Origin[a] of Hemipenial Retractor Muscle[b] and in Length of Retracted Hemipenis[a] in Seven Species of *Tantilla*

Sample	Retractor origin			Hemipenis length		
	Mean ± std. error	(Range)	N	Mean ± std. error	(Range)	N
T. gracilis	21.5	(20–23)	6	7.5	(7–8)	2
T. nigriceps	35.1 ± 0.642	(31–38)	14	11.2	(8–13)	5
T. wilcoxi	27.0	(26–28)	2	10.0	(10)	1
T. yaquia	23.4	(22–24)	5	7.4	(6–9)	5
T. planiceps (specimens formerly called "*T. eiseni*")	33.4 ± 0.240	(30–38)	56	12.0 ± 0.175	(9–15)	41
T. planiceps (specimens from Cape area, Baja California Sur)	37.0	(36–38)	5	12.4	(12–13)	5
T. planiceps (all samples combined)	33.7 ± 0.261	(30–38)	62	12.1 ± 0.156	(9–15)	47
T. atriceps	27.6 ± 0.626	(25–32)	14	10.6 ± 0.452	(9–14)	10
T. hobartsmithi (Coahuila)	22.9	(20–25)	8	8.2	(7–9)	6
T. hobartsmithi (Texas)	23.6 ± 0.238	(20–30)	53	9.8 ± 0.307	(8–14)	25
T. hobartsmithi (Arizona)	28.5 ± 0.313	(22–34)	50	11.6 ± 0.210	(9–14)	45
T. hobartsmithi (specimens formerly called "*T. utahensis*")	29.3 ± 0.322	(28–32)	14	11.3 ± 0.376	(9–13)	12
T. hobartsmithi (all samples combined)	26.2 ± 0.280	(20–34)	128	10.8 ± 0.182	(7–14)	90

[a] Number of subcaudals posterior to vent; [b] m. retractor penis magnus.

T. *nigriceps* appears to be distinctive, *T. planiceps* differs from *T. atriceps* and *T. hobartsmithi*, and there is considerable overlap between *T. gracilis* and *T. hobartsmithi*. Considering number of spines in the spinose midsection together with minimum number of rows of spines in the midsection (fig. 13), *T. nigriceps* distinctly differs from *T. planiceps*, *T. wilcoxi*, and *T. gracilis*; *T. gracilis* appears distinctive among all the species except *T. hobartsmithi*; and *T. wilcoxi* appears distinctive among all the species except *T. planiceps*.

MINIMUM NUMBER OF ROWS OF SPINES APPROXIMATELY ENCIRCLING THE SPINOSE MIDSECTION (table 4; figs. 12, 13): *Tantilla planiceps* differs strikingly from *T. atriceps* and *T. hobartsmithi*. However, populations of *T. hobartsmithi* are similar to each other, as are different samples of *T. planiceps* (fig. 12). *Tantilla atriceps* appears to be rather different from most other samples, excepting *T. yaquia* (fig. 12).

POSITION OF DISTAL END OF SPINOSE
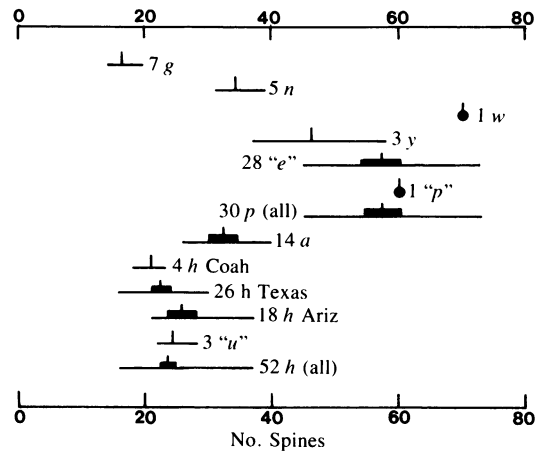
FIG. 9. Number of spines in the spinose midsection of hemipenes of seven species of *Tantilla*; interpretation as in figure 7.

MIDSECTION (table 4; fig. 14): This character (determined by counting number of subcaudals posterior to the vent for retracted organs only) shows a pattern of variation similar to

TABLE 4

Variation in Number of Hemipenial Spines,[a] in Minimum Number of Rows of Hemipenial Spines,[a] and in Position[b] of Distal End of Spinose Midsection of Hemipenis in Seven Species of *Tantilla*

Sample	No. spines			No. rows of spines			End of spinose midsection		
	Mean ± std. error	(Range)	N	Mean ± std. error	(Range)	N	Mean ± std. error	(Range)	N
T. *gracilis*	16.6	(14–20)	7	1.0	(1)	7	5.0	(5)	2
T. *nigriceps*	34.4	(31–39)	5	3.0	(3)	8	8.7	(8–10)	3
T. *wilcoxi*	70+	(70+)	1	5.0	(5)	1	7.0	(7)	1
T. *yaquia*	46.3	(37–58)	3	2.8	(2–4)	4	5.2	(5–6)	4
T. *planiceps* (specimens formerly called "*T. eiseni*")	57.3 ± 1.581	(45–73)	28	4.2 ± 0.083	(3–5)	32	9.6 ± 0.174	(8–12)	33
T. *planiceps* (specimens from Cape area, Baja California Sur)	60.0	(60)	1	4.0	(4)	1	9.8	(9–10)	4
T. *planiceps* (all samples combined)	57.6 ± 1.484	(45–73)	30	4.1 ± 0.086	(3–5)	34	9.6 ± 0.157	(8–12)	38
T. *atriceps*	32.4 ± 1.083	(26–40)	14	2.6 ± 0.137	(2–3)	14	7.7 ± 0.500	(6–11)	9
T. *hobartsmithi* (Coahuila)	21.0	(18–23)	4	1.0	(1)	8	6.0	(5–7)	4
T. *hobartsmithi* (Texas)	22.6 ± 0.736	(16–30)	26	1.1 ± 0.043	(1–2)	32	6.8 ± 0.190	(6–8)	18
T. *hobartsmithi* (Arizona)	25.9 ± 1.056	(21–37)	18	1.5 ± 0.131	(1–3)	21	8.8 ± 0.327	(7–11)	17
T. *hobartsmithi* (specimens formerly called "*T. utahensis*")	24.3	(22–28)	3	2.0	(2)	3	8.7 ± 0.273	(7–10)	11
T. *hobartsmithi* (all samples combined)	23.8 ± 0.576	(16–37)	52	1.2 ± 0.056	(1–3)	66	7.8 ± 0.205	(5–11)	51

[a] In spinose midsection, excluding spinules; [b] number of subcaudals posterior to vent.
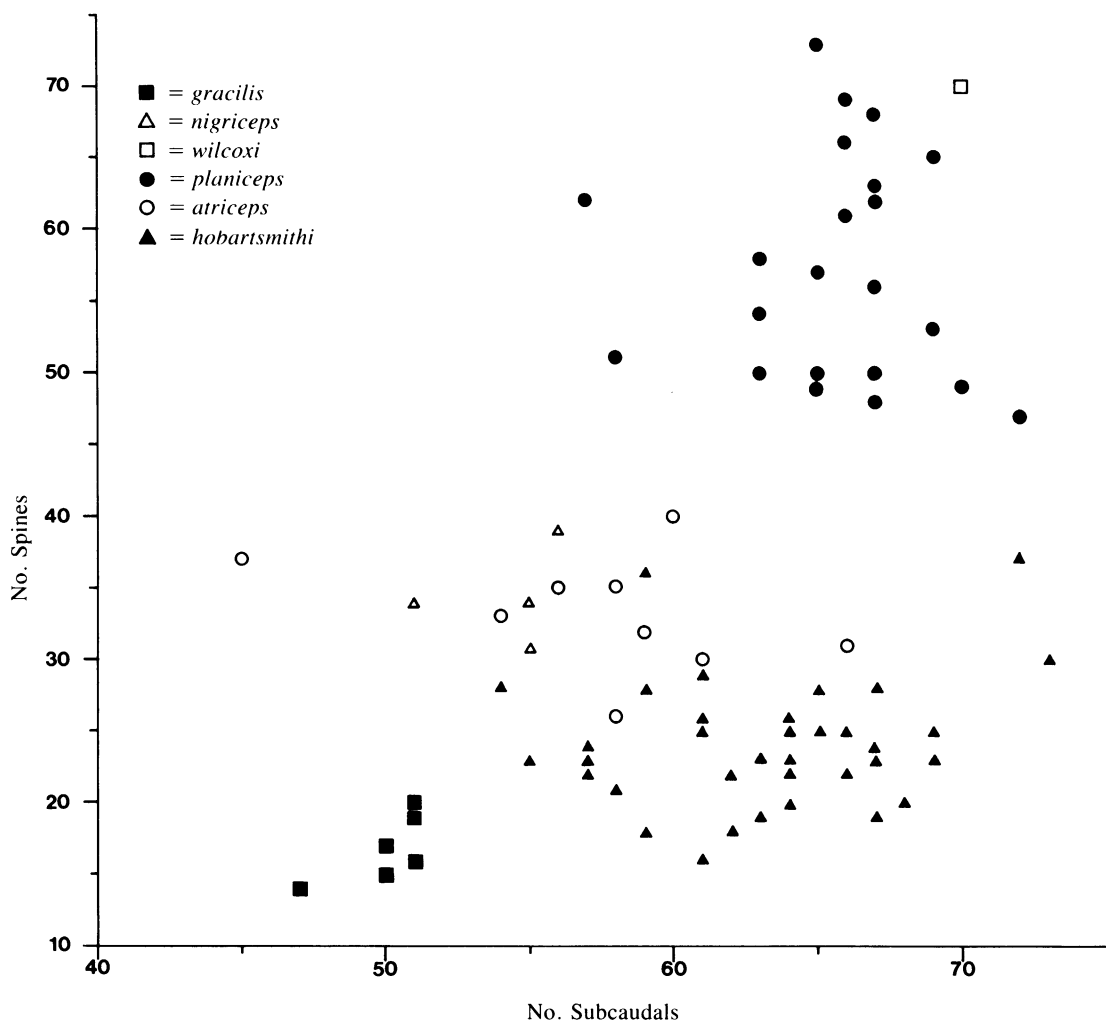
FIG. 10.   Relationship between number of subcaudals and number of spines in the spinose midsection of hemipenes of six species of *Tantilla*. Crowding of symbols in places precluded plotting each individual, but known extremes for all species are shown.

that of length of hemipenis (fig. 8), which may reflect that these, and possibly other topographic features, are not independent and thus should not be treated as such.

In the following sections, comparing characters other than those of hemipenes, we consider head coloration first, as we have found that a combination of hemipenial features and head coloration provides the most reliable way to distinguish between the species considered in this paper. In a later

section, we shall demonstrate that characteristics of scutellation, including numbers of ventrals and subcaudals, are far less reliable for these species.

OTHER CHARACTERS

THE POPULATION SAMPLES

Some characters vary from population to population intraspecifically to such an extent
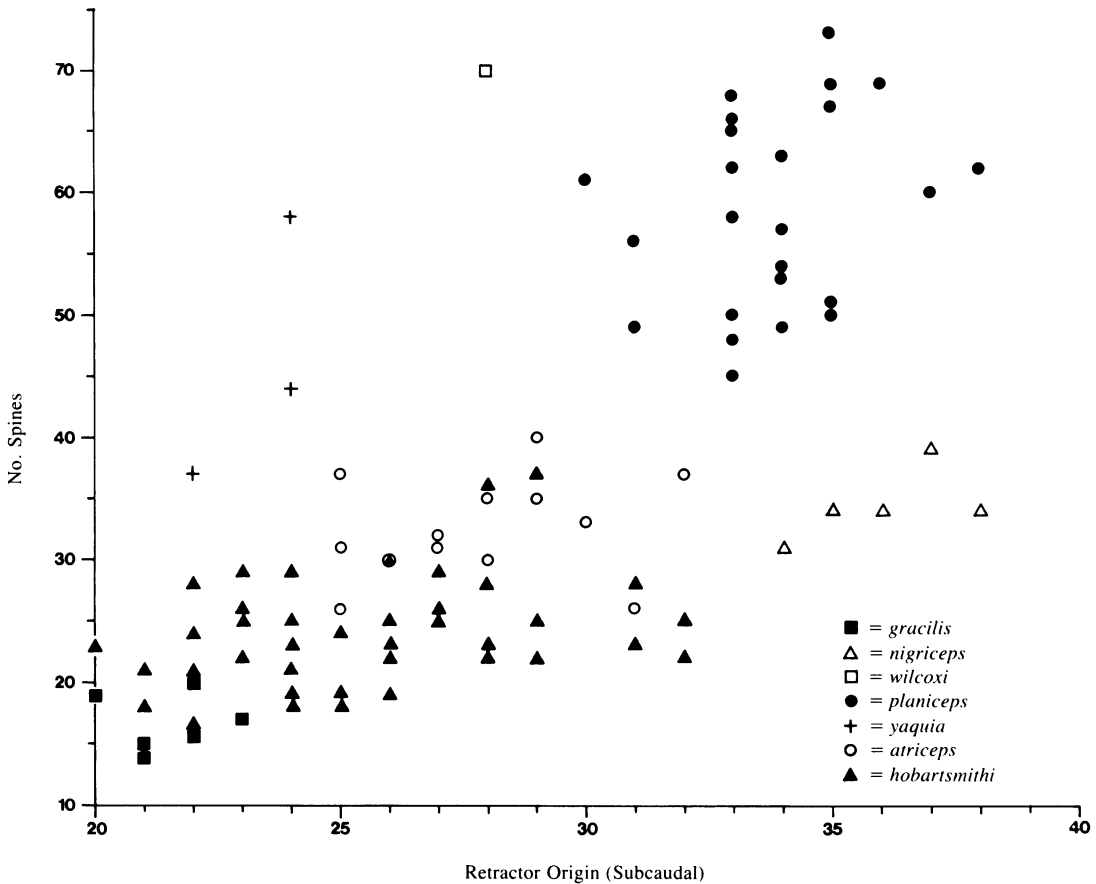
FIG. 11.   Relationship between origin (subcaudal number) of m. retractor penis magnus and number of spines in the spinose midsection of hemipenes of seven species of *Tantilla*. Crowding of symbols in places precluded plotting each individual, but known extremes for all species are shown.

that it would not be reasonable to pool all the data pertaining to each species and compare the pooled samples. Besides, our aim was to develop some understanding of intraspecific variation while determining interspecific differences. Therefore, we scanned the locality data for all specimens of *T. atriceps, T. hobartsmithi,* and *T. planiceps* looking for geographically limited samples that may be regarded as local population samples (table 5; C–Y). Individuals included within a sample are likely to represent a local gene pool. Most of these local population samples (N = 5–70) represent *T. hobartsmithi,* which clearly is the most widespread and most abundant species in the complex, but several

represent *T. planiceps. Tantilla atriceps* is so rare, however, that no local sample was large enough to allow comparison in this fashion; the same problem existed for specimens of *T. hobartsmithi* from northern Mexico, which are important for comparison with *T. atriceps.* Therefore, we pooled the males of *T. atriceps* (sample A) and many Mexican males of *T. hobartsmithi* (from Coahuila; sample B) in an inconsistently broad fashion so they would not be excluded altogether from our comparisons. The 25 samples compared are designated in table 5 and outlined on the map in figure 15. Which individuals were assigned to each sample is noted in Specimens Examined.
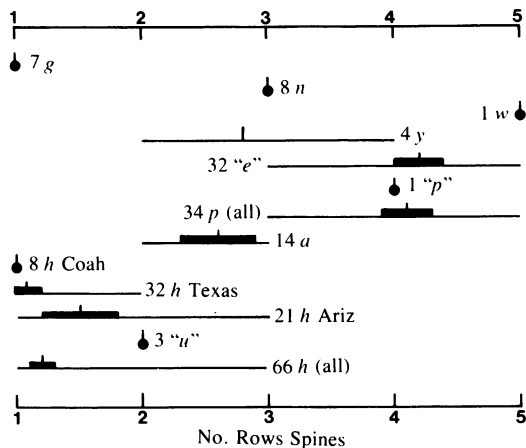
FIG. 12. Minimum number of rows of spines approximately encircling the spinose midsection of hemipenes of seven species of *Tantilla*; interpretation as in figure 7.

Since our emphasis was to recognize and compare local population samples, many of the specimens examined were not utilized in these particular comparisons. However, the data for all specimens were utilized in the species accounts.

HEAD COLORATION

VENTROLATERAL EXTENSION OF HEAD CAP: The dark, dorsal head color does not extend ventrad below the angle of the mouth in either *T. atriceps* or *T. hobartsmithi*, except very rarely (figs. 1H, G, respectively). In nearly all specimens of *T. planiceps*, however, the dark, dorsal head cap extends from one-half to three scales below the angle of the mouth (figs. 1E, F). This is a useful feature for recognizing some species because its variation is well correlated with variation in important hemipenial characters and there is reasonable geographic continuity to this variation (table 6; fig. 16). Comparisons (*t*-tests) of the largest samples (10 or more of each sex compared; samples D, F, N, V, X) failed to indicate sexual dimorphism in any population except sample X, the only sample of *T. planiceps* included ($t = 2.417$; N = 45; $P < 0.05$). Therefore, we pooled the data for both sexes for most comparisons (table 6;

fig. 16). We conclude that there are no significant differences between the samples of *T. hobartsmithi*; the various samples of *T. planiceps* are also similar to each other; but each sample of *T. hobartsmithi* differs from each sample of *T. planiceps*. *Tantilla atriceps* is identical to *T. hobartsmithi* in this feature (figs. 1G, H; table 6; fig. 16), and *T. planiceps* is similar to *T. yaquia* (cf. McDiarmid, 1968, p. 166, and our figs. 1C, E, F).

PERCENTAGE OF ANTERIOR TEMPORAL THAT IS LIGHT IN COLOR: We recorded this only when the normal condition of 1+1 temporals was present on each side. The lateral extent of the dark head cap in the temporal region generally is correlated positively with the ventrolateral extension of the dark head cap. Thus, in *T. planiceps* (figs. 1E, F) usually there is more dark pigment on the anterior temporal than in *T. atriceps* (fig. 1H) and *T. hobartsmithi* (fig. 1G). For consistency, we followed McDiarmid (1968) in expressing this trait as an approximation of the percentage of the anterior temporal that is light (rather than dark) because in comparisons involving *T. yaquia* usually the emphasis is on describing the conspicuous white patch on its posterior supralabials and anterior temporal. Comparisons (*t*-tests) of the largest samples (more than 10 of each sex; samples D, F, N, X) failed to indicate sexual dimorphism in any population of *T. hobartsmithi* or *T. planiceps*. Therefore, we pooled the data for both sexes (table 6; fig. 17). We conclude that there is geographic variation in this character; most samples of *T. hobartsmithi* differ from those of *T. planiceps*; *T. atriceps* is similar to *T. hobartsmithi* in this feature; but *T. yaquia* usually has significantly more of the anterior temporal light than *T. atriceps*, *T. hobartsmithi*, or *T. planiceps* (cf. McDiarmid, 1968, p. 166, and our figs. 1C, E–H).

PERCENTAGE OF SEVENTH SUPRALABIAL THAT IS LIGHT IN COLOR: We recorded this only when the normal number of seven supralabials was present on each side. The lateral extent of the dark head cap in the region of the seventh supralabial generally is correlated positively with the ventrolateral ex-
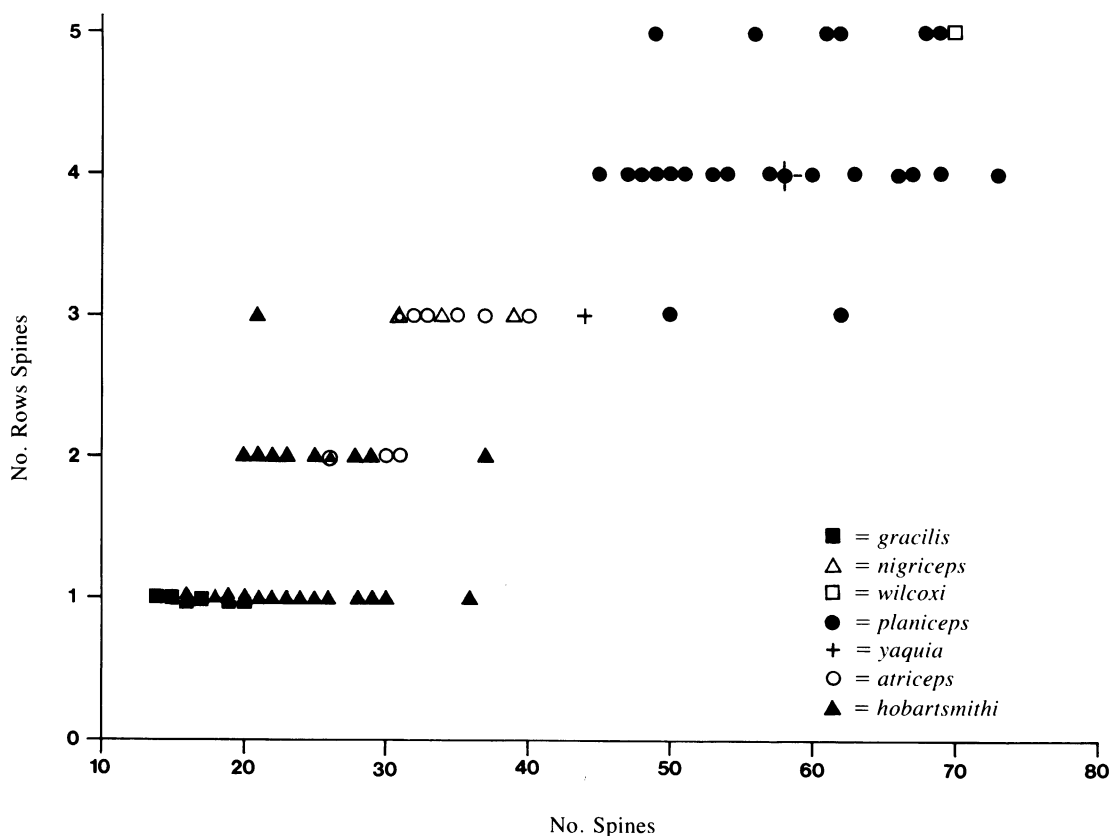
FIG. 13.   Relationship between number of spines in the spinose midsection and minimum number of rows of spines on hemipenes of seven species of *Tantilla*. Crowding of symbols in places precluded plotting each individual, but known extremes for all species are shown.

tension of the dark head cap. Thus, in *T. planiceps* (figs. 1E, F) usually there is more dark pigment on the seventh supralabial than in *T. atriceps* (fig. 1H) and *T. hobartsmithi* (fig. 1G). We followed McDiarmid (1968) in expressing this as an approximation of the percentage of the seventh supralabial that is light in color. Comparisons (*t*-tests) of the largest samples (more than 10 of each sex; samples F, N, X) failed to indicate sexual dimorphism in *T. hobartsmithi* or *T. planiceps*. Therefore, we pooled the data for both sexes (table 7; fig. 18). We conclude that there is geographic variation in this character; the westernmost samples of *T. hobartsmithi* are more similar to other samples of the same species than they are to northern
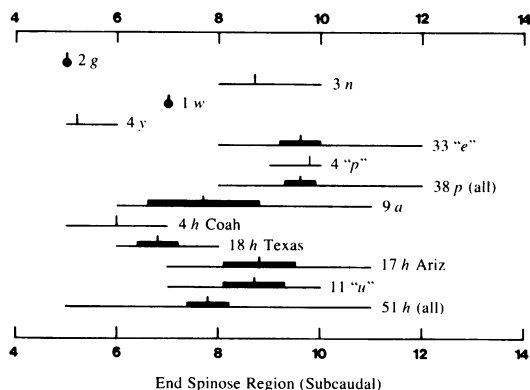
FIG. 14.   Position (subcaudal number) of distal end of the spinose midsection on hemipenes of seven species of *Tantilla*; interpretation as in figure 7.

TABLE 5
Population Samples of *Tantilla* Used for Most Comparisons

Sample	Species	N[a]	♂♂	♀♀	Locality (fig. 15)
A	T. atriceps	14	14	0	Southern Texas, northern Mexico
B	T. hobartsmithi	8	8	0	Coahuila, Mexico
C	T. hobartsmithi	7	3	4	Vicinity of Comstock, Val Verde Co., Texas
D	T. hobartsmithi	27	14	13	Vicinity of Sheffield, Pecos Co., Texas[b]
E	T. hobartsmithi	12	8	4	Vicinity of Sanderson and Dryden, Terrell Co., Texas
F	T. hobartsmithi	70	36	31	Big Bend National Park, Brewster Co., Texas
G	T. hobartsmithi	12	8	3	Davis Mts., Jeff Davis Co., Texas
H	T. hobartsmithi	32	12	20	Guadalupe Mts., W Texas and SE New Mexico
I	T. hobartsmithi	11	5	4	W Texas, S New Mexico
J	T. hobartsmithi	16	9	7	SW New Mexico, SE Arizona
K	T. hobartsmithi	7	5	2	Baboquivari (=Quinlan) Mts., Pima Co., Arizona
L	T. hobartsmithi	53	24	28	Vicinity of Tucson, Pima Co., Arizona
M	T. hobartsmithi	22	16	6	Vicinity of Mammoth and Oracle, Pinal Co., Arizona
N	T. hobartsmithi	60	32	26	Vicinity of Ft. McDowell, Maricopa Co., Arizona
O	T. hobartsmithi	17	8	9	Vicinity of Wickenburg, Maricopa Co., Arizona
P	T. hobartsmithi	7	5	2	Vicinity of Sedona, Coconino Co., Arizona[c]
Q	T. hobartsmithi	20	8	12	Vicinity of Kanab, Kane Co., Utah
R	T. hobartsmithi	14	8	6	Vicinity of St. George, Washington Co., Utah
S	T. hobartsmithi	5	2	1	Tulare Co., California
T	T. planiceps	6	1	5	Vicinity of Fresno, Fresno Co., California
U	T. planiceps	6	2	4	Los Angeles Co., California
V	T. planiceps	13	11	2	Vicinity of Banning and Palm Springs, Riverside Co., California
W	T. planiceps	5	4	1	Anza-Borrego Desert, San Diego Co., California
X	T. planiceps	47	23	23	Vicinity of San Diego, San Diego Co., California
Y	T. planiceps	5	4	1	Southern Baja California del Sur
Total		494	268	214	

[a] Sample sizes for all characters are not the same within each sample because not all traits were ascertainable on all specimens. In instances where N is greater than the sum of the males and females, the difference is the number of specimens for which sex was not determined with certainty; [b] the specimens are from Terrell County; [c] some of the specimens are from Yavapai County.

samples of *T. planiceps*; the southernmost population of *T. planiceps* may be more similar to some samples of *T. hobartsmithi* than to northern populations of *T. planiceps*; and *T. atriceps* is similar to *T. hobartsmithi* in this feature, as is *T. yaquia* (cf. McDiarmid, 1968, p. 167), although the pattern of dark pigment on this supralabial is different in *T. yaquia* (figs. 1C, G, H).

PERCENTAGE OF SIXTH SUPRALABIAL THAT IS LIGHT IN COLOR: We recorded this only when the normal number of seven supralabials was present on each side. Variation in this character is rather similar to that

in color of the seventh supralabial (see above). Comparisons (*t*-tests) of the largest samples (more than 10 of each sex; samples F, N, X) failed to indicate sexual dimorphism in *T. hobartsmithi* or *T. planiceps*. Therefore, we pooled the data for both sexes (table 7; fig. 19). We conclude that there is geographic variation in this character; most samples of *T. hobartsmithi* differ from those of *T. planiceps*; the westernmost samples of *T. hobartsmithi* are more similar to other samples of the same species than they are to northern samples of *T. planiceps*; the southernmost population of *T. planiceps* may be
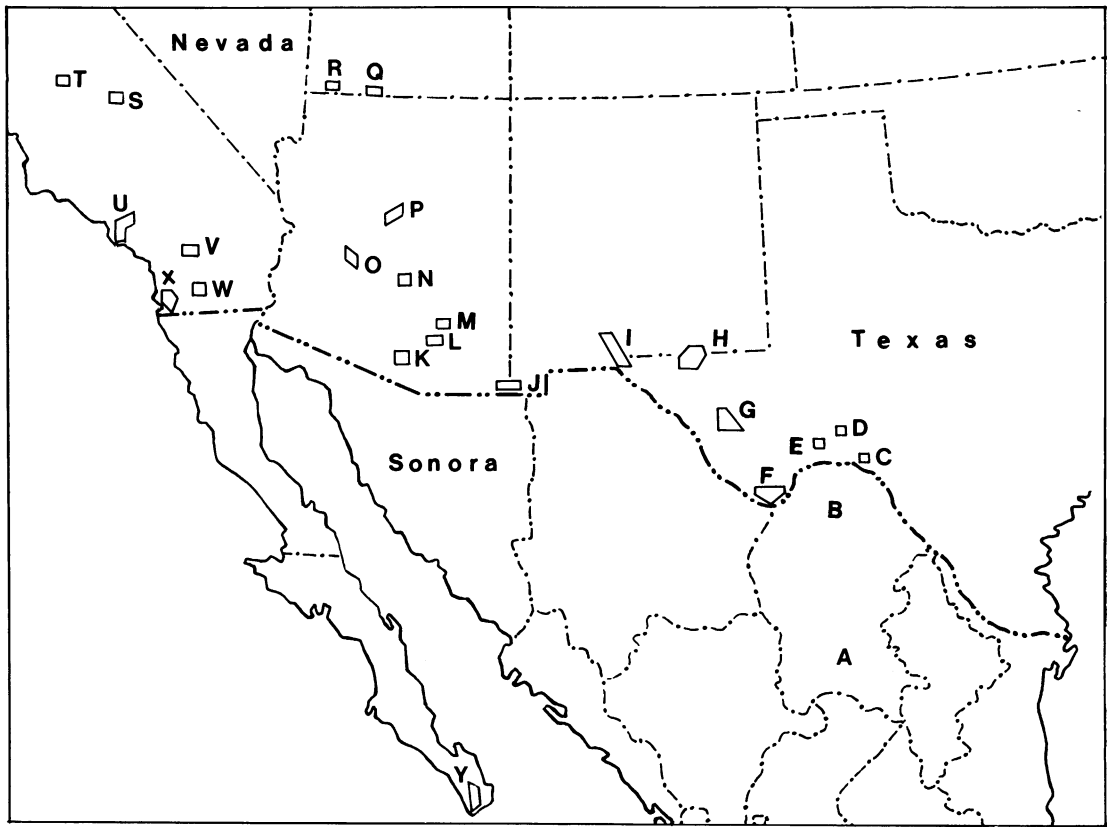
FIG. 15.   Geographic location of populations represented in samples A through Y (table 5).

more similar to some samples of *T. hobart-smithi* than to northern populations of *T. planiceps*; and in this feature *T. atriceps* is similar to *T. hobartsmithi* as is *T. yaquia* (cf. McDiarmid, 1968, p. 167), which typically has the sixth supralabial entirely (100%) light in color (fig. 1C).

PERCENTAGE OF FIFTH SUPRALABIAL THAT IS LIGHT IN COLOR: We recorded this only when the normal number of seven supralabials was present on each side. Variation in this feature is not correlated with that in the other characters of head coloration discussed above. Comparisons (*t*-tests) of the largest samples (more than 10 of each sex; samples F, N, X) failed to indicate sexual dimorphism in *T. hobartsmithi* or *T.*

planiceps. Therefore, we pooled the data for both sexes (table 7; fig. 20). We conclude that there is relatively little geographic variation in this character; frequently there are no differences between samples of *T. hobartsmithi* and *T. planiceps*; the extreme values for the sample means for *T. planiceps* are bracketed by those for *T. hobartsmithi*; *T. atriceps* is similar to both *T. hobartsmithi* and *T. planiceps* in this feature (figs. 1E–H); and *T. yaquia* is distinctive (cf. McDiarmid, 1968, p. 167), typically having the fifth supralabial entirely (100%) light (fig. 1C).

POSTERIOR EXTENSION OF HEAD CAP: The dark, dorsal head coloration extends from one-half to three dorsal scale lengths past the posterior end of the suture between

TABLE 6
Variation in Ventrolateral Extension of Head Cap[a] and in Percentage of Anterior Temporal that is Light in Color in Three Species of *Tantilla*

Sample[b]	Head cap			Anterior temporal		
	Mean ± std. error	(Range)	N	Mean ± std. error	(Range)	N
A	0.0 ± 0.000	(0.0–0.0)	10	16.0 ± 4.971	(0.0–50.0)	10
B	0.0	(0.0–0.0)	4	19.2	(5.0–30.0)	4
C	—	—	—	12.3	(1.0–25.0)	7
D	0.0 ± 0.000	(0.0–0.0)	20	20.3 ± 3.044	(1.0–45.0)	21
F	0.0 ± 0.000	(0.0–0.0)	40	6.7 ± 1.466	(0.0–40.0)	41
G	0.0 ± 0.000	(0.0–0.0)	11	2.2	(0.0–10.0)	9
H	0.0 ± 0.000	(0.0–0.0)	13	6.2 ± 2.493	(0.0–25.0)	13
J	0.1 ± 0.071	(0.0–1.0)	14	7.2 ± 1.997	(0.0–20.0)	14
L	—	—	—	6.4 ± 2.761	(0.0–25.0)	11
N	0.0 ± 0.000	(0.0–0.0)	50	13.0 ± 1.286	(0.0–33.0)	50
O	0.0 ± 0.000	(0.0–0.0)	17	1.5 ± 0.761	(0.0–10.0)	15
R	0.0	(0.0–0.0)	5	7.4	(0.0–13.0)	5
T	1.2	(1.0–1.5)	6	0.0	(0.0–0.0)	6
U	1.2	(1.0–2.0)	6	1.7	(0.0–10.0)	6
V	1.5 ± 0.098	(1.0–2.0)	13	0.0 ± 0.000	(0.0–0.0)	13
W	0.6	(0.0–1.5)	5	—	—	—
X ♂♂	1.4 ± 0.082	(0.5–2.0)	23	—	—	—
X ♀♀	1.7 ± 0.112	(1.0–3.0)	22	—	—	—
X (all)	1.5 ± 0.072	(0.5–3.0)	46	1.2 ± 0.897	(0.0–40.0)	45
Y	1.2	(0.0–2.5)	5	4.0	(0.0–20.0)	5

[a] Number of scales below angle of mouth; [b] A, *T. atriceps*; B–R, *T. hobartsmithi*; T–Y, *T. planiceps*.

the parietal scales on most specimens of *T. atriceps* and *T. hobartsmithi* (figs. 1G, H). It extends from two to three and one-half scales beyond the suture in *T. planiceps* (figs. 1E, F). Comparisons (*t*-tests) of the largest samples (more than 10 of each sex; samples D, F, H, L, N, X) failed to indicate sexual dimorphism in any population of *T. hobartsmithi* or *T. planiceps*. Therefore, we pooled the data for both sexes (table 8; fig. 21). We conclude that there is geographic variation in this character in *T. hobartsmithi*; most samples of *T. hobartsmithi* are significantly different from those of *T. planiceps*; the mean for each sample of *T. hobartsmithi* is less than or equal to the lowest extreme in the range of any sample of *T. planiceps*; the westernmost samples of *T. hobartsmithi* are not significantly different from other samples of the same species, whereas they differ significantly from the samples of *T. planiceps*;

T. atriceps is similar to *T. hobartsmithi* (fig. 21); and *T. planiceps* is similar to *T. yaquia* (cf. McDiarmid, 1968, p. 164, and our figs. 1C, E, F).

SHAPE OF POSTERIOR EDGE OF DARK HEAD CAP: We recorded this because it is distinctive in some species of *Tantilla*. Nearly all the specimens we examined had dark caps with posterior edges that could be recognized as one of the types illustrated in figure 22; a few had irregular head caps that were recorded as such. Data for the four largest population samples (three of *T. hobartsmithi*; one of *T. planiceps*) are summarized in table 9. The head caps of most specimens were either convex or straight. We analyzed each sample separately for association between sex and shape of head cap, using χ^2 tests with contingency tables. For samples F, L, and N we used shape categories of "convex," "straight," or "oth-
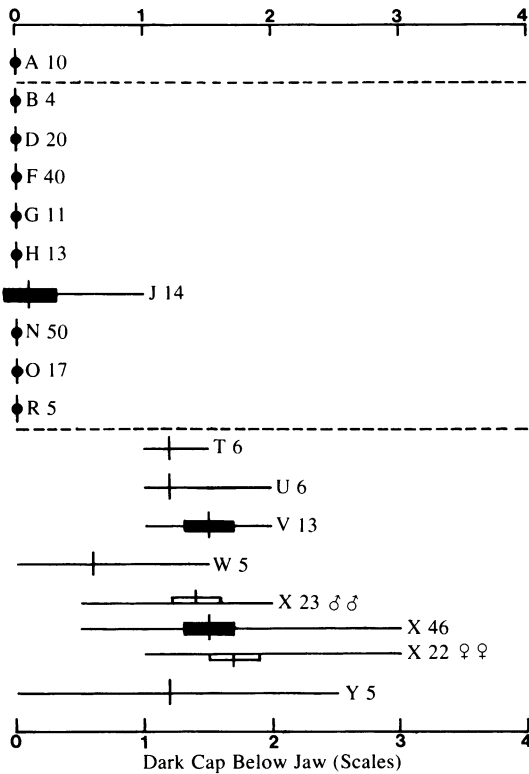
FIG. 16. Variation in ventrolateral extension of dark head cap in samples of three species of *Tantilla* (separated by dashed lines; top to bottom, *T. atriceps, T. hobartsmithi, T. planiceps*). Horizontal line indicates range, vertical line indicates mean, rectangle indicates 95% confidence interval (solid = sexes pooled; open, above range = males only; open, below range = females only). Letter beside range is sample (table 5), number is sample size.

marized in table 10. A χ^2 test for association between *T. hobartsmithi* and *T. planiceps* (using three shape categories; "convex," "straight," and "other") suggests these species are distinctly different ($P < 0.05$), which should be viewed cautiously because of the geographic variation in *T. hobartsmithi*. Inspection of table 10 suggests that *T. atriceps* (excluded from analysis because of small sample size) is more similar to *T. planiceps* than to *T. hobartsmithi*, but this is in part an artifact from lumping samples within species. In this regard it is pertinent to note that of the Coahuilan *T. hobartsmithi* in sample B (N = 8), three have the head cap straight, three have it pointed, and two (25%) have it convex, although a convex head cap is found most frequently in *T. atriceps* (85.7%; table 10). McDiarmid (1968, p. 164) stated that the posterior edge of the dark head cap usually is straight in *T. yaquia*. This character is most useful in comparison with *T. nigriceps*, on nearly all specimens of which the posterior

er," lumping rare categories due to their small representation in the samples; for sample X, of course, we used only the shape categories of "convex" and "straight." The tests failed to indicate sexual dimorphism in any sample. Therefore, we pooled the data for both sexes for subsequent analyses. Analysis of the three largest samples of *T. hobartsmithi* with a 3 × 3 contingency table (samples F, L, and N; shape categories "convex," "straight," and "other") revealed significant geographic variation ($P < 0.05$). The data for three species are sum-

FIG. 17. Variation in percentage of anterior temporal that is light in color in samples of three species of *Tantilla*; interpretation as in figure 16.

TABLE 7

Variation in Percentage of Seventh, Sixth, and Fifth Supralabial that is Light in Color in Samples of Three Species of *Tantilla*

Sam-ple[a]	Seventh			Sixth			Fifth		
	Mean ± std. error	(Range)	N	Mean ± std. error	(Range)	N	Mean ± std. error	(Range)	N
A	68.4 ± 6.322	(33.0–100.0)	11	96.2 ± 2.665	(70.0–100.0)	11	82.1 ± 4.315	(57.0–100.0)	11
B	55.0	(20.0–75.0)	3	99.0	(97.0–100.0)	3	93.7	(90.0–96.0)	3
C	60.4	(23.0–88.0)	7	98.1	(96.0–100.0)	7	85.6	(75.0–98.0)	7
D	68.0 ± 3.876	(40.0–97.0)	20	98.6 ± 0.498	(92.0–100.0)	20	87.6 ± 1.651	(70.0–98.0)	20
F	47.9 ± 3.106	(5.0–90.0)	45	87.1 ± 2.760	(0.0–100.0)	45	68.4 ± 2.499	(37.0–100.0)	45
G	33.0 ± 4.592	(12.0–50.0)	10	82.1 ± 5.743	(40.0–99.0)	10	65.5 ± 4.310	(45.0–85.0)	10
H	53.8 ± 4.806	(22.0–72.0)	13	96.2 ± 1.836	(75.0–100.0)	13	82.8 ± 3.320	(55.0–97.0)	13
J	39.6 ± 4.661	(17.0–75.0)	14	97.5 ± 0.970	(90.0–100.0)	14	68.1 ± 2.889	(50.0–90.0)	14
L	53.4 ± 3.498	(35.0–80.0)	13	80.0 ± 10.167	(0.0–100.0)	13	79.8 ± 4.806	(40.0–99.0)	13
N	57.0 ± 1.476	(39.0–75.0)	46	94.9 ± 2.252	(0.0–100.0)	45	85.2 ± 1.394	(60.0–99.0)	46
O	52.0 ± 3.003	(20.0–70.0)	17	93.9 ± 1.950	(75.0–100.0)	17	72.6 ± 3.268	(50.0–90.0)	17
P	50.0	(40.0–60.0)	5	98.2	(95.0–100.0)	5	74.0	(60.0–80.0)	5
R	53.4	(45.0–67.0)	5	97.2	(95.0–99.0)	5	78.4	(67.0–95.0)	5
T	21.3	(18.0–25.0)	6	74.2	(67.0–83.0)	6	86.7	(75.0–95.0)	6
U	21.8	(14.0–40.0)	6	75.8	(50.0–95.0)	6	86.7	(70.0–95.0)	6
V	13.0 ± 1.543	(5.0–20.0)	11	65.2 ± 4.105	(35.0–85.0)	11	76.5 ± 4.081	(55.0–97.0)	11
W	23.6	(20.0–33.0)	5	76.0	(70.0–80.0)	5	77.0	(70.0–95.0)	5
X	21.1 ± 1.071	(5.0–40.0)	42	72.0 ± 2.125	(16.0–97.0)	42	82.9 ± 1.820	(40.0–100.0)	42
Y	43.6	(15.0–75.0)	5	85.0	(60.0–100.0)	5	79.6	(65.0–99.0)	5

[a] A, *T. atriceps*; B–R, *T. hobartsmithi*; T–Y, *T. planiceps*.

edge of the dark head cap is either angular or pointed (fig. 1D).

PRESENCE OF LIGHT NUCHAL COLLAR: Many species of *Tantilla* characteristically have a distinct light (white, cream, gray) collar bordering the posterior edge of the dark head cap (e.g., *T. wilcoxi,* fig. 1B); in some species this collar is absent (e.g., *T. nigriceps,* fig. 1D). Presence or absence of the light collar among our six largest population samples (five of *T. hobartsmithi;* one of *T. planiceps*) are summarized in table 11. Most specimens have a distinct light collar. We analyzed each sample separately for association between sex and presence or absence of collar, using χ^2 tests with 2 × 2 contingency tables. The tests failed to indicate sexual dimorphism in any sample. Therefore, we pooled the data for both sexes for subsequent analyses. Analysis of the five largest samples of *T. hobartsmithi* with a 5 × 2 contingency table revealed significant geograph-

ic variation ($P < 0.05$); inspection of table 11 suggests there is a disproportionate number of specimens lacking the collar in sample L. The data for three species are summarized in table 12. A χ^2 test for association between *T. hobartsmithi* and *T. planiceps* suggests these species are distinctly different ($P < 0.05$), which should be viewed cautiously because of the geographic variation in *T. hobartsmithi*. Indeed, inspection of table 11 indicates that some samples of *T. hobartsmithi* (e.g., sample H) and of *T. planiceps* (e.g., sample X) are indistinguishable in this character. Table 12 reveals that usually the collar is present in *T. atriceps,* as in *T. hobartsmithi* and *T. planiceps*. McDiarmid (1968, p. 164) stated that in *T. yaquia* "the head cap always is bordered by a light nuchal collar." This character is most useful in comparison with *T. nigriceps,* nearly all specimens of which lack a light nuchal collar.
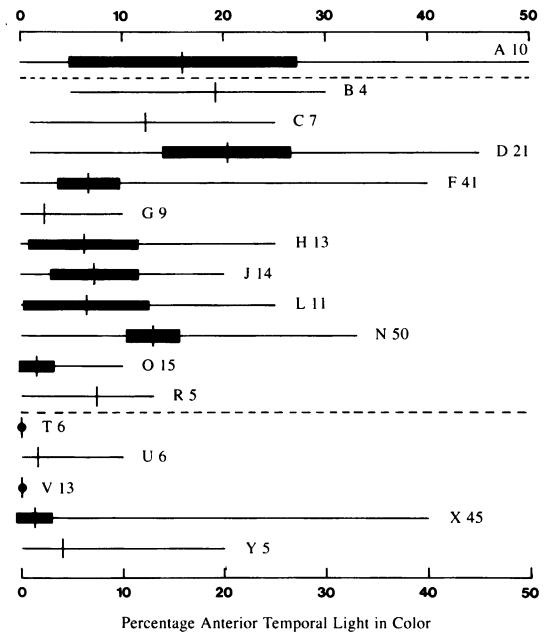
WIDTH OF LIGHT NUCHAL COLLAR: On

FIG. 18. Variation in percentage of seventh supralabial that is light in color in samples of three species of *Tantilla*; interpretation as in figure 16.

spots on the nape immediately behind the light nuchal collar; observations for the four largest population samples (more than 20; three samples of *T. hobartsmithi*; one of *T. planiceps*) are summarized in table 13. We analyzed each sample separately for association between sex and presence or absence of dark nuchal spots, using χ^2 tests with 2 × 2 contingency tables. The tests failed to indicate sexual dimorphism in any sample. Therefore, we pooled the data for both sexes for subsequent analyses. Analysis of the three largest samples of *T. hobartsmithi* with a 3 × 2 contingency table failed to indicate geographic variation. The data for three species are summarized in table 14. A χ^2 test for association between *T. hobartsmithi* and *T. planiceps* suggests these species are distinctly different from each other ($P < 0.05$), whereas a test between *T. atriceps* and *T. hobartsmithi* did not. The results of these tests are not surprising since inspection of

specimens for which the nuchal collar was present, we noted its width (number of scale-lengths spanned middorsally). Comparisons (*t*-tests) of the largest samples (more than 10 of each sex; samples D, F, H, L, N, X) failed to indicate sexual dimorphism in any population of *T. hobartsmithi* or *T. planiceps*. Therefore, we pooled the data for both sexes (table 8; fig. 23). We conclude that there is relatively little geographic variation in this character; frequently there are no differences between samples of *T. hobartsmithi* and *T. planiceps*; the extreme values for the sample means for *T. planiceps* are bracketed by those for *T. hobartsmithi*; and *T. atriceps* is similar to both *T. hobartsmithi* and *T. planiceps* in this feature, as is *T. yaquia* (cf. McDiarmid, 1968, p. 164).

PRESENCE OF DISTINCT BROWN SPOTS POSTERIOR TO NUCHAL COLLAR: We recorded the presence or absence of distinct brown

FIG. 19. Variation in percentage of sixth supralabial that is light in color in samples of three species of *Tantilla*; interpretation as in figure 16.

TABLE 8

Variation in Posterior Extension of Dark Head Cap[a] and in Width[b] of Light Nuchal Collar in Samples of Three Species of *Tantilla*

Sample[c]	Cap extension			Collar width		
	Mean ± std. error	(Range)	N	Mean ± std. error	(Range)	N
A	1.5 ± 0.133	(1.0–2.0)	14	0.8 ± 0.120	(0.0–1.2)	11
B	1.2	(0.0–2.0)	8	0.8	(0.0–1.0)	8
C	1.8	(1.0–3.0)	7	0.8	(0.5–1.0)	7
D	1.1 ± 0.068	(1.0–2.5)	27	1.1 ± 0.043	(0.5–1.5)	27
E	1.1 ± 0.139	(0.5–2.0)	12	0.9 ± 0.148	(0.0–1.5)	12
F	1.4 ± 0.064	(0.5–3.0)	70	0.9 ± 0.034	(0.0–1.5)	67
G	1.2 ± 0.117	(0.8–2.0)	12	0.8 ± 0.143	(0.0–1.5)	12
H	1.0 ± 0.074	(0.0–2.0)	32	1.0 ± 0.058	(0.5–2.0)	32
I	1.1 ± 0.118	(0.5–2.0)	11	0.8 ± 0.123	(0.0–1.0)	11
J	1.4 ± 0.110	(1.0–2.3)	15	0.6 ± 0.126	(0.0–1.5)	16
K	2.0	(1.5–3.0)	7	0.4	(0.0–1.0)	7
L	2.0 ± 0.074	(1.0–3.0)	53	0.6 ± 0.057	(0.0–1.5)	49
M	1.8 ± 0.110	(1.0–2.5)	22	0.4 ± 0.082	(0.0–1.0)	22
N	1.5 ± 0.065	(0.5–2.5)	60	0.8 ± 0.040	(0.0–1.5)	60
O	1.8 ± 0.106	(1.0–2.5)	17	1.0 ± 0.042	(0.5–1.5)	17
P	1.9	(1.0–3.0)	7	0.6	(0.0–1.0)	7
Q	2.0 ± 0.080	(1.0–2.5)	20	0.7 ± 0.090	(0.0–1.0)	20
R	1.8 ± 0.086	(1.5–2.5)	14	0.8 ± 0.097	(0.0–1.0)	12
S	2.0	(2.0–2.0)	5	—	—	—
T	2.8	(2.0–3.0)	6	1.0	(1.0–1.0)	6
U	2.8	(2.0–3.5)	6	0.9	(0.5–1.0)	6
V	2.7 ± 0.087	(2.0–3.0)	13	0.9 ± 0.052	(0.5–1.0)	13
W	2.3	(2.0–2.5)	5	0.8	(0.0–1.0)	5
X	2.4 ± 0.056	(2.0–3.0)	47	1.0 ± 0.021	(0.5–1.5)	46
Y	3.1	(2.5–3.5)	5	1.0	(1.0–1.0)	5

[a] Number of scales beyond posterior end of suture between parietals; [b] number of scales; [c] A, *T. atriceps*; B–S, *T. hobartsmithi*; T–Y, *T. planiceps*.

the data (tables 13, 14) reveals that the presence of dark nuchal spots posterior to the light nuchal collar is common in *T. planiceps* and rather uncommon in *T. atriceps* and *T. hobartsmithi*. Indeed, spots were present on at least one specimen of *T. planiceps* in all samples of five or more snakes. Dark nuchal spots vary from being present in 0% to 100% of the specimens of *T. yaquia* from different samples (McDiarmid, 1968, pp. 164–165).

SCUTELLATION

Most features of scutellation show rather limited variation within a population sample. A few characters are sexually dimorphic and

a few demonstrate considerable geographic variation. In general, the variation in scutellation of *Tantilla planiceps* and its closest relatives is such that it is not used easily in diagnosing species or identifying specimens.

CHARACTERS SHOWING NO SIGNIFICANT VARIATION IN LARGER SAMPLES (10 or more for each sex within a sample): Comparisons (*t*-tests) within the six larger samples (D, F, H, L, N, X; table 5; fig. 15) representing two species (*T. hobartsmithi* [D–N] and *T. planiceps* [X]), failed to indicate sexual dimorphism in any of the following 15 features (usual trait in parentheses): number of right supralabials (7); number of left supralabials
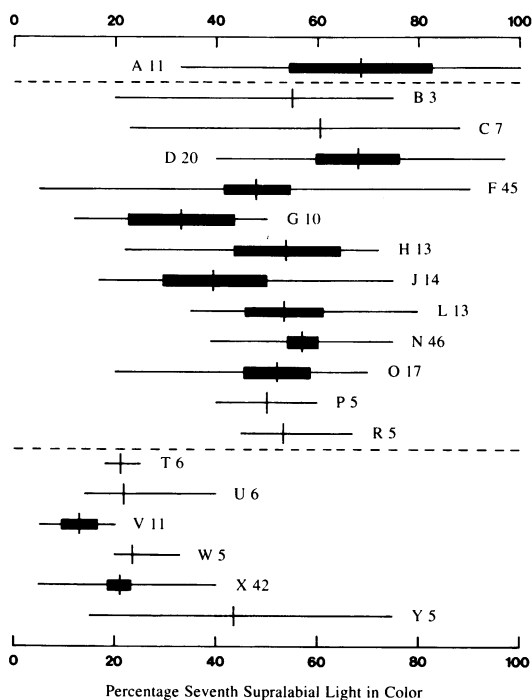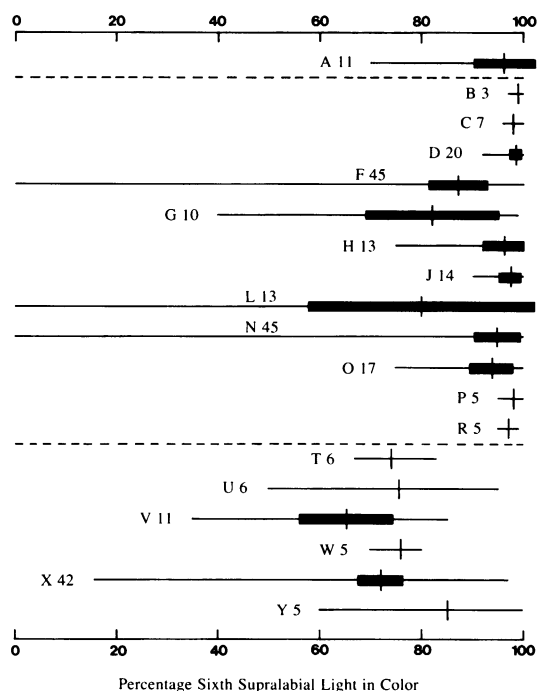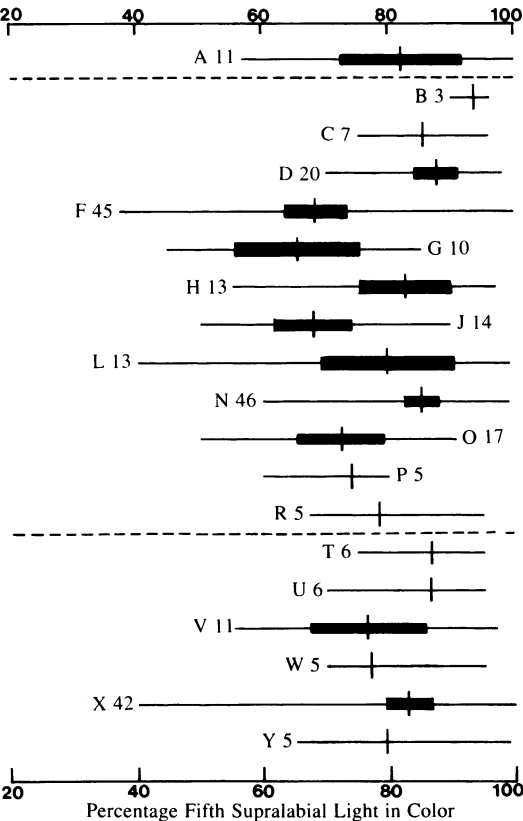
FIG. 20. Variation in percentage of fifth supralabial that is light in color in samples of three species of *Tantilla*; interpretation as in figure 16.

(7); number of right infralabials (6); number of left infralabials (6); number of right preoculars (1); number of left preoculars (1); number of right primary temporals (1); number of left primary temporals (1); number of right secondary temporals (1); number of left secondary temporals (1); and number of dorsal scale rows counted in five places along the body (15). Comparison of the same 15 characters among the same six samples but with the sexes pooled also failed to indicate any significant differences. *Tantilla atriceps* is similar to *T. hobartsmithi* and *T. planiceps* in all these features, as is *T. yaquia*.

CHARACTERS SHOWING NO SIGNIFICANT VARIATION IN SMALLER SAMPLES (10 or more specimens with sexes pooled): Since

no sexual dimorphism was found within the larger samples, the same 15 features discussed immediately above were analyzed for geographic variation by comparing them in additional smaller samples with the sexes pooled. Comparisons within nine smaller samples (E, G, I, J, M, O, Q, R, V) representing two species (*T. hobartsmithi* [E–R]
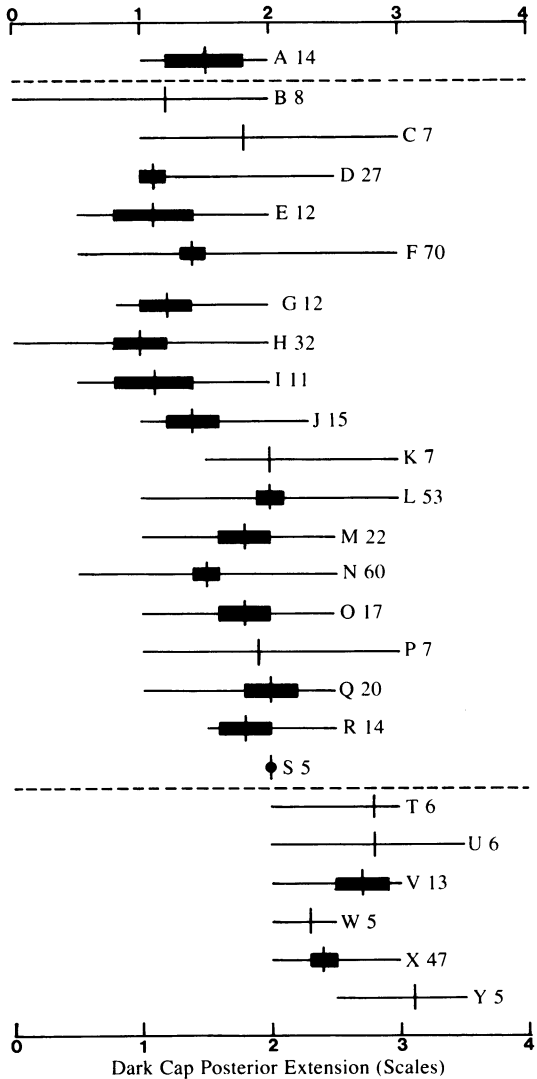
FIG. 21. Variation in posterior extension (number of scales) of dark head cap in samples of three species of *Tantilla*; interpretation as in figure 16.

TABLE 9
Variation in Shape of Posterior Edge of Dark Head Cap in Samples of Two Species of *Tantilla*

Sample[a]		Convex	Straight	Pointed	Angular	Concave	Irregular	N
F	Males	14	11	8	3	0	0	36
	Females	8	8	9	4	0	2	31
L	Males	16	3	1	4	0	0	24
	Females	16	4	4	4	0	0	28
N	Males	18	10	3	1	0	0	32
	Females	14	6	2	3	1	0	26
X	Males	18	5	0	0	0	0	23
	Females	13	10	0	0	0	0	23

[a] F–N, *T. hobartsmithi*; X, *T. planiceps*.

and *T. planiceps* [V]) failed to indicate any significant differences.

NUMBER OF VENTRAL SCALES: There is more variation in this character than in any others of scutellation. Variation in ventrals must be examined carefully, however, lest erroneous conclusions be reached concerning its taxonomic significance. Comparisons (*t*-tests) within the largest samples (10 or more of each sex) indicate significant sexual dimorphism within each population. Also, there is considerable geographic variation (table 15; fig. 24). A glance at figure 24 may cause one to wonder whether the sample of *T. planiceps* from southern Baja California Sur (Y) should be considered specifically distinct from the samples from California (U–X) because the differences appear so abrupt, graphically. However, considerable geographic variation within *T. hobartsmithi* from northern Mexico and southwestern Texas (B, D) to southern Utah (R) is also

demonstrated (fig. 24), and consideration of the latitudinal distribution of the populations suggests that intraspecific variation in *T. planiceps* is reasonably comparable to that in *T. hobartsmithi* (fig. 25). *Tantilla atriceps* is most similar to nearby populations of *T. hobartsmithi* in this character, but also similar to samples of *T. planiceps* from Baja California Sur. McDiarmid (1968) demonstrated that number of ventrals decreases with latitude in *T. yaquia* also, but that specimens from southern Arizona and northern Sonora have considerably more ventrals than have the local *T. hobartsmithi* (near sample L; table 15). These males of *T. yaquia* have 145–157 ventrals ($\bar{x} = 151.4$, N = 5) and the females have 155–165 ($\bar{x} = 159.1$, N = 8; McDiarmid, 1968, p. 160). This local difference in number of ventrals is consistent with recognizing *T. yaquia* and *T. hobartsmithi* as different species, particularly considering their differences in hemipenes and

TABLE 10
Variation in Shape of Posterior Edge of Dark Head Cap in Three Species of *Tantilla*

Species	Convex	Straight	Pointed	Angular	Concave	Irregular	N
T. atriceps	12 (85.7%)	2 (14.3%)	0	0	0	0	14
T. hobartsmithi	280 (48.5%)	120 (20.8%)	94 (16.3%)	69 (12.0%)	9 (1.6%)	5 (0.9%)	577
T. planiceps	90 (64.8%)	46 (33.1%)	2 (1.4%)	0	1 (0.7%)	0	139

| Straight | Convex | Concave | Angular | Point |
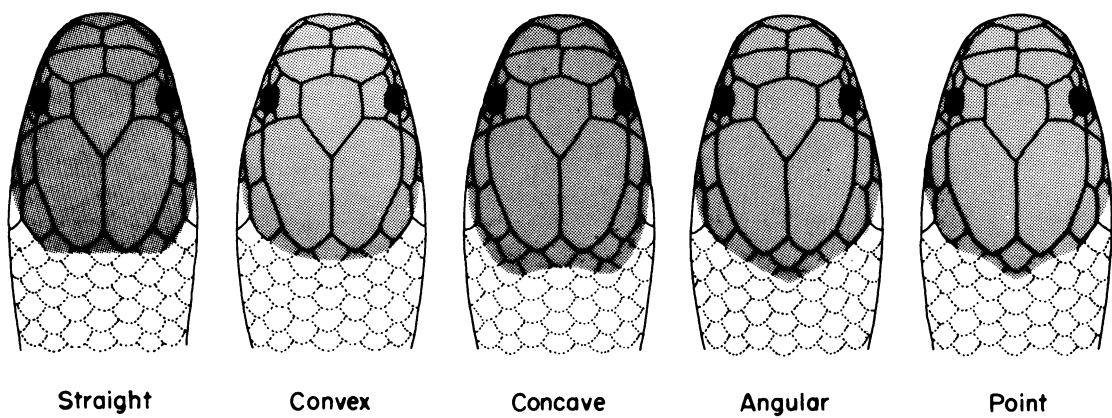
FIG. 22.   Shapes of posterior edge of dark head cap of snakes related to *Tantilla planiceps*. Outline and scutellation based on *T. hobartsmithi*, AMNH 107377.

head coloration. Because of the clinal nature of the variation in number of ventrals we conclude that this character is not satisfactory for distinguishing subspecies among these snakes.

NUMBER OF SUBCAUDAL SCALES: There are fewer samples to compare in subcaudals than in ventrals because there are considerably more specimens with the tail incomplete than with the body incomplete. Neverthe-

less, comparisons (*t*-tests) within the largest samples (10 or more of each sex) indicate significant sexual dimorphism in each population. Geographic variation is not as pronounced as in number of ventrals (table 15; fig. 26). *Tantilla atriceps* is similar to nearby populations of *T. hobartsmithi* in this feature. The data for *T. yaquia* from southern Arizona and northern Sonora are few (McDiarmid, 1968, p. 160), males and females both having 62–75 subcaudals with means of 66.0 (N = 4) and 68.5 (N = 6), respectively. This sample of *T. yaquia* appears more similar in subcaudals to the samples of *T. planiceps* from Riverside County, California (V) and *T. hobartsmithi* from Big Bend National Park, Texas (F) than to the geographically nearest sample of *T. hobartsmithi* from Tucson, Arizona (L), which also

TABLE 11

Variation in Presence or Absence of a Light Nuchal Collar in Samples of Two Species of *Tantilla*

Sample[a]		Present	Absent	N
D	Males	14	0	14
	Females	13	0	13
F	Males	34	2	36
	Females	29	1	30
H	Males	12	0	12
	Females	20	0	20
L	Males	19	4	23
	Females	22	6	28
N	Males	30	2	32
	Females	24	2	26
X	Males	23	0	23
	Females	23	0	23

[a] D–N, *T. hobartsmithi*; X, *T. planiceps*.

TABLE 12

Variation in Presence or Absence of a Light Nuchal Collar in Three Species of *Tantilla*

| Species	Present	Absent	N
T. atriceps	10	3	13
	(76.9%)	(23.1%)	
T. hobartsmithi	502	70	572
	(87.8%)	(12.2%)	
T. planiceps	137	1	138
	(99.3%)	(0.7%)	
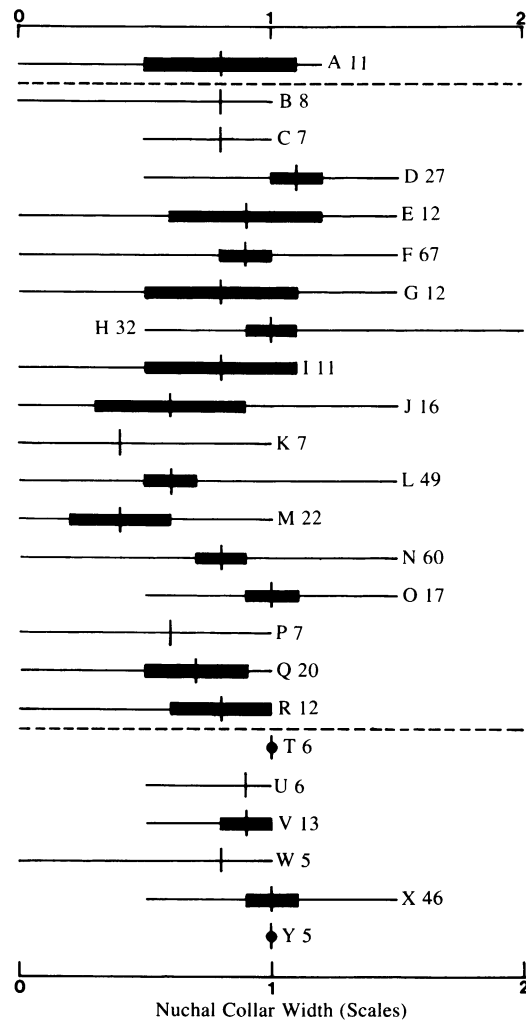
FIG. 23. Variation in width (number of scales) of light nuchal collar in samples of three species of *Tantilla*; interpretation as in figure 16.

TABLE 13
Variation in Presence or Absence of Distinct Brown Spots Posterior to Nuchal Collar in Samples of Two Species of *Tantilla*

Sample[a]		Present	Absent	N
D	Males	1	9	10
	Females	0	11	11
F	Males	4	17	21
	Females	2	16	18
N	Males	2	27	29
	Females	2	17	19
X	Males	12	11	23
	Females	10	12	22

[a] D–N, *T. hobartsmithi*; X, *T. planiceps*.

we pooled the data for both sexes for additional comparisons (fig. 27), which indicate that the pattern of geographic variation in this character is basically the same as in number of ventrals (fig. 24). Similarly, McDiarmid's (1968, p. 165, fig. 2) data indicate that populations of *T. yaquia* in southern Arizona and northern Sonora ($\bar{x}$ = about 220) differ significantly in this feature from the nearest populations of *T. hobartsmithi* (J, L; table 15).

NUMBER OF POSTOCULARS: Comparisons (*t*-tests) of the largest samples (more than 10 of each sex; samples D, F, H, L, N, X) failed to indicate sexual dimorphism in any population of *T. hobartsmithi* or *T. planiceps*. Therefore, we pooled data for both sexes (table 16; figs. 28, 29). We conclude that populations of *T. hobartsmithi* and *T. planiceps*

is consistent with considering *T. yaquia* and *T. hobartsmithi* as different species.

NUMBER OF VENTRALS PLUS SUBCAUDALS (TOTAL): Only four samples were sufficiently large (10 or more of each sex) to test (*t*-tests) for sexual dimorphism: three of them (F, L, N; all *T. hobartsmithi*) showed no dimorphism and one (X; *T. planiceps*) showed a marginally significant difference (*t* = 2.1919; *n* = 33). Nevertheless, the difference between the means of the two sexes in sample X is only 3.4 scales (table 15), so

TABLE 14
Variation in Presence or Absence of Distinct Brown Spots Posterior to Nuchal Collar in Three Species of *Tantilla*

Species	Present	Absent	N
T. atriceps	1 (9.1%)	10 (90.9%)	11
T. hobartsmithi	27 (8.2%)	304 (91.8%)	331
T. planiceps	78 (60.5%)	51 (39.5%)	129

TABLE 15

Variation in Number of Ventral Scales, Number of Subcaucal Scales, and Number of Ventrals Plus Number of Subcaudals (Total) in Samples of Three Species of *Tantilla*

Sample[a]	Ventrals Mean ± std. error	(Range)	N	Subcaudals Mean ± std. error	(Range)	N	Ventrals + Subcaudals Mean ± std. error	(Range)	N
A ♂♂	129.2 ± 1.213	(123–140)	13	57.4	(45–66)	9	186.1	(179–194)	8
B ♂♂	134.0	(124–157)	8	57.1	(54–59)	7	187.8	(180–194)	7
D ♂♂	133.3 ± 0.879	(129–139)	14	59.6	(57–63)	7	193.3	(188–200)	7
D ♀♀	139.4 ± 1.123	(130–144)	13	51.1	(49–54)	8	191.2	(187–196)	8
D (all)	—	—	—	—	—	—	192.2 ± 1.019	(187–200)	15
F ♂♂	138.8 ± 0.578	(129–145)	36	66.9 ± 0.660	(62–74)	24	206.5 ± 1.149	(193–218)	24
F ♀♀	146.2 ± 0.534	(141–153)	31	58.0 ± 0.725	(53–65)	18	204.3 ± 1.173	(196–212)	18
F (all)	—	—	—	—	—	—	205.2 ± 0.865	(191–218)	44
H ♂♂	137.2 ± 0.604	(134–142)	12	61.8	(60–63)	6	200.0	(197–203)	6
H ♀♀	144.2 ± 0.623	(138–150)	20	54.7 ± 0.637	(50–58)	15	199.3	(195–204)	15
H (all)	—	—	—	—	—	—	199.5 ± 0.604	(195–204)	21
I ♂♂	—	—	—	—	—	—	195.6	(194–200)	5
I ♀♀	—	—	—	—	—	—	206.0	(202–210)	2
I (all)	—	—	—	—	—	—	199.6	(194–210)	9
J ♂♂	—	—	—	—	—	—	193.3	(189–197)	6
J ♀♀	—	—	—	—	—	—	197.2	(186–204)	4
J (all)	—	—	—	—	—	—	194.9 ± 1.728	(186–204)	10
L ♂♂	141.3 ± 0.750	(135–151)	23	60.6 ± 1.045	(48–69)	21	201.5 ± 0.898	(194–211)	21
L ♀♀	148.7 ± 0.590	(142–157)	28	53.8 ± 0.658	(47–61)	20	201.8 ± 1.112	(189–212)	20
L (all)	—	—	—	—	—	—	201.7 ± 0.688	(189–212)	42
M ♂♂	141.0 ± 0.540	(137–145)	16	—	—	—	200.3	(194–207)	9
M ♀♀	152.0	(150–156)	6	—	—	—	207.7	(204–210)	3
M (all)	—	—	—	—	—	—	202.2 ± 1.465	(194–210)	12
N ♂♂	141.6 ± 0.403	(136–147)	31	61.1 ± 0.388	(56–64)	27	203.0 ± 0.509	(197–208)	26
N ♀♀	149.9 ± 0.709	(141–156)	25	54.6 ± 0.844	(47–63)	18	204.1 ± 1.084	(191–211)	17
N (all)	—	—	—	—	—	—	203.4 ± 0.527	(191–211)	43
O ♂♂	144.6	(140–150)	8	—	—	—	208.4	(203–213)	5
O ♀♀	151.9	(144–157)	9	—	—	—	207.5	(200–212)	6
O (all)	—	—	—	—	—	—	207.9 ± 1.224	(200–213)	11
Q ♂♂	155.8	(153–162)	8	64.2	(61–66)	8	220.1	(216–226)	8
Q ♀♀	165.7 ± 0.541	(164–169)	12	58.3 ± 0.448	(56–61)	10	223.9 ± 0.604	(221–227)	10
Q (all)	—	—	—	—	—	—	222.2 ± 0.798	(216–227)	18
R ♂♂	157.4	(155–160)	8	68.3	(65–73)	6	225.8	(222–230)	6
R ♀♀	166.6	(162–169)	5	60.2	(60–61)	4	228.0	(227–229)	3
R (all)	—	—	—	—	—	—	226.6	(222–230)	9
S ♂♂	—	—	—	—	—	—	218.5	(218–219)	2
S ♀♀	—	—	—	—	—	—	220.0	(220)	1
S (all)	—	—	—	—	—	—	218.8	(217–220)	5
U ♂♂	167.5	(166–169)	2	66.0	(65–67)	2	—	—	—
U ♀♀	178.7	(177–180)	3	60.0	(60)	2	—	—	—
V ♂♂	178.1 ± 1.090	(172–184)	11	66.4 ± 1.127	(58–71)	10	244.7 ± 1.826	(235–251)	10
V ♀♀	194.0	(193–195)	2	64.0	(63–65)	2	258.0	(256–260)	2
V (all)	—	—	—	—	—	—	246.9 ± 2.137	(235–260)	12
X ♂♂	169.0 ± 0.672	(163–176)	22	66.0 ± 0.585	(60–69)	18	234.6 ± 1.067	(226–244)	18
X ♀♀	177.8 ± 0.831	(167–185)	22	60.9 ± 1.019	(52–70)	17	238.0 ± 1.156	(230–247)	17
X (all)	—	—	—	—	—	—	236.2 ± 0.828	(226–247)	35
Y ♂♂	137.5	(134–140)	4	59.5	(59–60)	2	197.5	(197–198)	2
Y ♀♀	148.0	(148)	1	—	—	—	—	—	—

[a] A, *T. atriceps*; B–S, *T. hobartsmithi*; U–Y, *T. planiceps*.
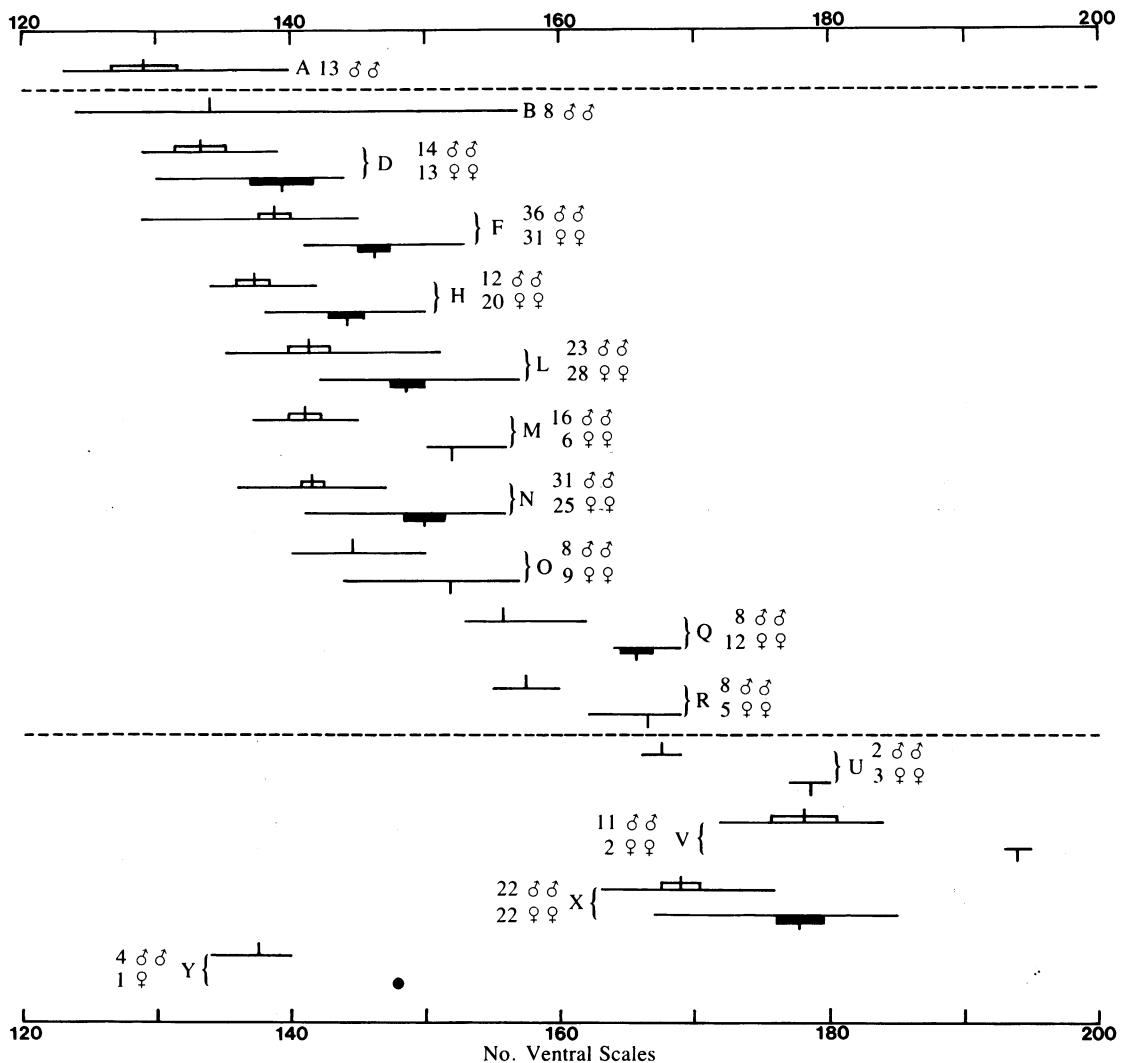
FIG. 24.   Variation in number of ventral scales in samples of three species of *Tantilla*; interpretation as in figure 16, except open rectangle = males only, solid = females only.

are similar to each other, having a mean closer to two scales than to one; and *T. atriceps* appears distinctive in having a mean closer to one scale. Indeed, of the 14 specimens of *T. atriceps* comprising sample A, nine had 1-1 postoculars and five had 2-2. Thus, this feature of cephalic scutellation tends to support the recognition of *T. atriceps* and *T. hobartsmithi* as different species. *Tantilla yaquia* is similar to *T. hobartsmithi* and *T.*

planiceps in this character, as McDiarmid (1968, p. 161) found two postoculars on all specimens examined.

CONTACT OF MENTAL WITH ANTERIOR GENIALS: The mental may be in contact with the anterior genial on both sides of the chin, on only one side, or on neither side due to midventral mutual contact of the first pair of infralabials. Observations for the six largest population samples (five of *T. hobartsmithi*;
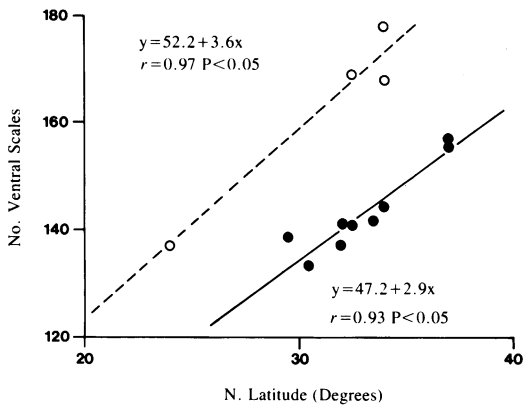
FIG. 25.   Correlation between degrees north lat-
itude of sample locality and number of ventral
scales (sample mean) in males of two species of
Tantilla. Dashed line represents *T. planiceps*; solid
line, *T. hobartsmithi*.

one of *T. planiceps*) are summarized in table
17. Only two samples (L, N) are sufficiently
large to test for association between sex and
mental-genial contact, using χ^2 tests with
contingency tables in which specimens with
the contact on only one side were pooled
with those having no contact and using cor-
rection for small samples; sexual dimor-
phism is not indicated. Therefore, we pooled
the data for both sexes for subsequent com-
parisons. Five samples of *T. hobartsmithi*
(table 17) were analyzed with a 5 × 2 contin-
gency table (contact categories "one side
only" and "neither side" pooled again),
which indicated significant geographic vari-
ation within *T. hobartsmithi* ($P < 0.05$). The
data for three species are summarized in ta-
ble 18 (samples within each species pooled).
A χ^2 test for association between *T. ho-
bartsmithi* and *T. planiceps* (still pooling
"one side only" and "neither side") indi-
cated no significant difference. However, a
similar test (but with correction for small
samples) with *T. hobartsmithi* and *T. atri-
ceps* indicated they are different ($P < 0.05$).
One may hesitate to attach much significance
to this because of the geographic variation
occurring within *T. hobartsmithi*, but in-
spection of tables 17 and 18 shows that most
specimens of *T. atriceps* (71.4%) lack con-

tact between the mental and either anterior
genial, whereas in all samples of *T. hobart-
smithi* and *T. planiceps*, most specimens have
the mental in contact with both anterior ge-
nials; the latter applies also (62.5%) to the
sample (B) of *T. hobartsmithi* from Coahui-
la. *Tantilla yaquia* is similar to *T. atriceps*
in this character, the vast majority of speci-
mens having the mental separated from the
anterior genials by the first pair of infralabi-
als (McDiarmid, 1968, p. 161).

SUPRALABIALS ENTERING ORBIT: Consid-
ering the largest population samples (D, F,
H, L, N, X; N = 25 or more) or all samples
pooled for each of the species, *T. atriceps*,
T. hobartsmithi, and *T. planiceps*, all have
the third and fourth supralabials entering the
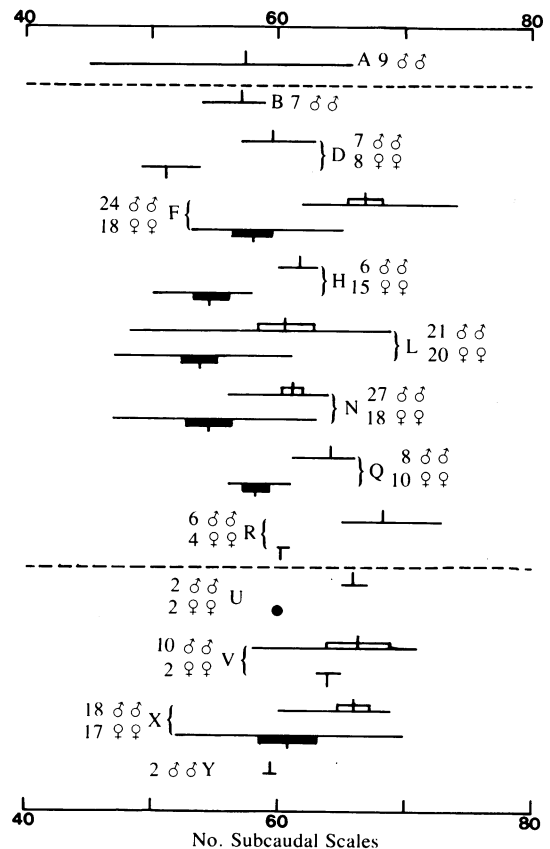
FIG. 26.   Variation in number of subcaudal
scales in samples of three species of *Tantilla*; in-
terpretation as in figure 24.

TABLE 16
Variation in Number of Postoculars in Samples of Three Species of *Tantilla*

Sample[a]	Right postoculars			Left postoculars		
	Mean ± std. error	(Range)	N	Mean ± std. error	(Range)	N
A ♂♂	1.4 ± 0.133	(1–2)	14	1.4 ± 0.133	(1–2)	14
B ♂♂	2.0	(2)	8	2.0	(2)	8
D ♂♂	1.8 ± 0.097	(1–2)	14	1.8 ± 0.113	(1–2)	14
D ♀♀	1.8 ± 0.104	(1–2)	13	1.8 ± 0.104	(1–2)	13
D (all)	1.8 ± 0.069	(1–2)	27	1.8 ± 0.076	(1–2)	27
E (all)	1.9 ± 0.083	(1–2)	12	2.0	(2)	12
F ♂♂	1.6 ± 0.082	(1–2)	36	1.8 ± 0.073	(1–2)	36
F ♀♀	1.6 ± 0.087	(1–2)	31	1.6 ± 0.087	(1–2)	31
F (all)	1.6 ± 0.058	(1–2)	70	1.7 ± 0.055	(1–2)	70
G (all)	1.9 ± 0.083	(1–2)	12	2.0	(2)	12
H ♂♂	1.8 ± 0.130	(1–2)	12	1.8 ± 0.112	(1–2)	12
H ♀♀	1.8 ± 0.091	(1–2)	20	1.8 ± 0.091	(1–2)	20
H (all)	1.8 ± 0.074	(1–2)	32	1.8 ± 0.070	(1–2)	32
I (all)	1.8 ± 0.121	(1–2)	11	1.6 ± 0.152	(1–2)	11
J (all)	2.0	(2)	16	1.9 ± 0.062	(1–2)	16
L ♂♂	2.0 ± 0.041	(1–2)	24	2.0 ± 0.043	(1–2)	23
L ♀♀	1.9 ± 0.061	(1–2)	27	1.9 ± 0.061	(1–2)	27
L (all)	1.9 ± 0.037	(1–2)	52	1.9 ± 0.038	(1–2)	51
M (all)	1.9 ± 0.062	(1–2)	22	1.9 ± 0.062	(1–2)	22
N ♂♂	2.0 ± 0.031	(1–2)	32	2.0 ± 0.031	(2–3)	32
N ♀♀	1.9 ± 0.053	(1–2)	26	2.0 ± 0.038	(1–2)	26
N (all)	2.0 ± 0.028	(1–2)	60	2.0 ± 0.023	(1–3)	60
O (all)	2.0	(2)	16	1.8 ± 0.095	(1–2)	17
Q (all)	2.0 ± 0.050	(1–2)	20	1.9 ± 0.068	(1–2)	20
R (all)	2.0	(2)	14	2.0	(2)	14
V (all)	2.0	(2)	13	1.9 ± 0.076	(1–2)	13
X ♂♂	2.0 ± 0.043	(1–2)	23	2.0	(2)	23
X ♀♀	1.9 ± 0.086	(1–2)	23	1.9 ± 0.060	(1–2)	23
X (all)	1.9 ± 0.047	(1–2)	47	2.0 ± 0.029	(1–2)	47
Y (all)	1.8	(1–2)	5	1.6	(1–2)	5

[a] A, *T. atriceps*; B–R, *T. hobartsmithi*; V–Y, *T. planiceps*.

eye on either one or both sides in more than 90% of the specimens. The following supralabials or combinations thereof were also seen entering the orbit on a few individuals: number 3 only; 3–5; and 4+5. *Tantilla yaquia* is similar to these species in this character (McDiarmid, 1968, p. 162).

CONTACT OF PREFRONTAL WITH SUPRALABIALS: In many specimens the prefrontal is in contact with one or more supralabials on either one or both sides of the head; usually such contact is lacking due to contact between the nasal and preocular. Observations for the six largest samples (five of *T.*

hobartsmithi, one of *T. planiceps*) are summarized in table 19. Four samples (F, L, N, X) are sufficiently large to test for association between sex and prefrontal-supralabial contact, using χ^2 tests with contingency tables in which specimens with the contact on only one side were pooled with those having contact on both sides. Sexual dimorphism is not indicated, analyzing with correction for small samples. Therefore, we pooled data for both sexes for subsequent comparisons. Five samples of *T. hobartsmithi* (table 19) were analyzed with a 5 × 2 contingency table (contact categories "one side only" and
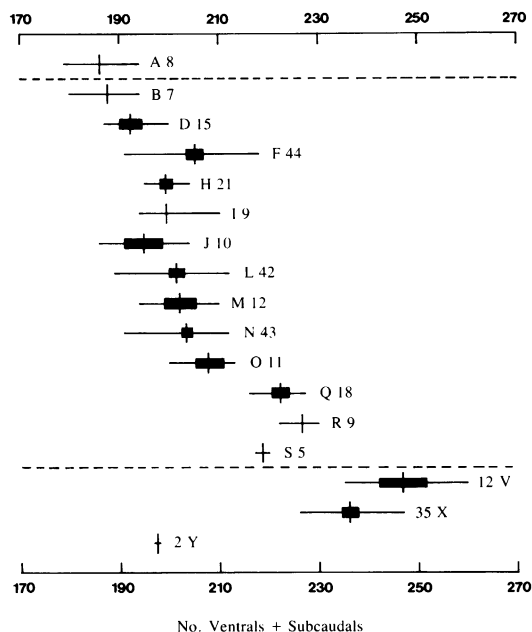
FIG. 27. Variation in the sum of the number of ventrals plus subcaudals in samples of three species of *Tantilla*; interpretation as in figure 16.

with both the second and third supralabials or only the third.

DIVISION OF NASAL SCALE: In most specimens of *T. atriceps, T. hobartsmithi,* and *T. planiceps* the nasal is divided below the naris but not above it (tables 21, 22). Inspection of the data suggests that there is no sexual dimorphism in division of the nasal, there is little if any geographic variation in this character, and in *T. planiceps* the nasal is divided both above and below the naris more frequently (ca. 25%; table 22) than in the other species. Four of seven AMNH specimens of *T. yaquia* examined have the nasal divided below the naris and grooved above, on both sides, which occurred rarely in the other three species.

POSITION OF NARIS IN NASAL SCALE: In most specimens of *T. hobartsmithi* the naris is located within the upper half of the nasal, although often it is medial in position (tables 23, 24). Inspection of the data suggests that

"both sides" pooled again), which indicated significant geographic variation within *T. hobartsmithi* ($P < 0.05$). The data for three species are summarized in table 20 (samples within each species pooled). A χ^2 test for association between *T. hobartsmithi* and *T. planiceps* (2 × 2 contingency table, pooling as above) indicated a significant difference ($P < 0.05$) between these two species, whereas a test with *T. hobartsmithi* and *T. atriceps* failed to indicate a difference. One must be cautious in attaching too much significance to this, however, because the differences are not very sharp and because of the geographic variation occurring within *T. hobartsmithi*. In *T. yaquia* also, most specimens have neither prefrontal in contact with any supralabials (McDiarmid, 1968, p. 161). If the prefrontal is in contact with any supralabials in *T. atriceps, T. hobartsmithi,* or *T. planiceps,* in at least 80% of the specimens it is in contact with only the second supralabial; in other specimens, contact was
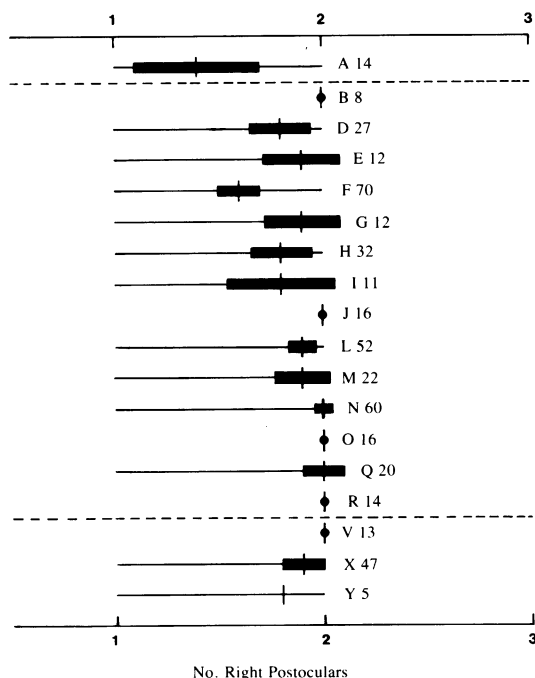

FIG. 28. Variation in number of right postoculars in samples of three species of *Tantilla*; interpretation as in figure 16.

TABLE 17
Variation in Contact of Mental Scale with
Anterior Genials in Largest Population Samples

Sample[a]		Both sides	One only	Neither side	N
D	Males	11	1	2	14
	Females	11	0	2	13
F	Males	32	0	4	36
	Females	30	0	1	31
H	Males	9	0	2	11
	Females	17	1	2	20
L	Males	22	0	2	24
	Females	21	2	5	28
N	Males	16	3	13	32
	Females	19	2	5	26
X	Males	22	0	1	23
	Females	20	2	1	23

[a] D–N, *T. hobartsmithi*; X, *T. planiceps*.

TABLE 19
Variation in Contact of Prefrontal with
Supralabials in Largest Population Samples

Sample[a]		Both sides	One only	Neither side	N
D	Males	4	3	7	14
	Females	3	2	8	13
F	Males	21	3	10	34
	Females	12	5	14	31
H	Males	4	2	6	12
	Females	8	1	10	19
L	Males	4	4	16	24
	Females	2	2	23	27
N	Males	7	8	17	32
	Females	7	2	17	26
X	Males	2	4	17	23
	Females	3	1	19	23

[a] D–N, *T. hobartsmithi*; X, *T. planiceps*.

there is no sexual dimorphism in this character and there might be geographic variation of frequencies within *T. hobartsmithi* (table 23). *Tantilla atriceps* is similar to *T. hobartsmithi*, whereas *T. planiceps* is rather different, having the naris in a medial position in the vast majority of specimens and sometimes even in the lower half of the nasal (tables 23, 24). *Tantilla yaquia* appears to be most similar to *T. atriceps* and *T. hobartsmithi* in this character, as eight AMNH specimens examined have the naris high in the upper half of the nasal.

DIVISION OF ANAL PLATE: We did not re-

cord this, but we casually examined it in counting ventrals on almost all, if not literally all, specimens. In no instance did we notice an undivided or partly divided anal plate.

SCALE ANOMALIES: Of the few anomalies observed, essentially all, and those noted here, were on the species for which we examined the most specimens, *T. hobartsmithi*. Perhaps extra half-ventrals (one to several) were the most frequently observed anomalies, such as on UAZ 26420 (last ventral, left side; not counted as a ventral). On ASU 10307 the last ventral is divided ap-

TABLE 18
Variation in Contact of Mental Scale with
Anterior Genials in Three Species of *Tantilla*

Species	Both sides	One only	Neither side	N
T. atriceps	2 (14.3%)	2 (14.3%)	10 (71.4%)	14
T. hobartsmithi	449 (78.2%)	19 (3.3%)	106 (18.5%)	574
T. planiceps	109 (78.4%)	13 (9.4%)	17 (12.2%)	139

TABLE 20
Variation in Contact of Prefrontal with
Supralabials in Three Species of Tantilla

Species	Both sides	One only	Neither side	N
T. atriceps	5 (35.7%)	1 (7.1%)	8 (57.1%)	14
T. hobartsmithi	167 (29.5%)	72 (12.7%)	327 (57.8%)	566
T. planiceps	15 (10.8%)	17 (12.2%)	107 (77.0%)	139

TABLE 21
Variation in Division of Nasal Scale in Largest Population Samples

Sample[a]		Below naris only[b]	Below, and grooved above[c]	Below only (one side), above also (other)	Above and below[b]	N
D	Males	8	0	1	0	9
	Females	9	0	2	0	11
F	Males	22	0	0	0	22
	Females	18	2	0	0	20
N	Males	21	5	1	1	28
	Females	13	4	2	0	19
X	Males	20	3	0	0	23
	Females	18	0	0	3	21

[a] D–N, *T. hobartsmithi*; X, *T. planiceps*; [b] on both sides of the head; [c] grooved on either one or both sides of the head.

FIG. 29. Variation in number of left postoculars in samples of three species of *Tantilla*; interpretation as in figure 16.

proximately across the midline similar to division of the anal plate. Undivided subcaudals were seen also, as on RSF 3420, with "pairs" two through five fused at midline. One snake (AMNH 73567) has very complicated reductions and additions of dorsal scale rows, and another (MCZ 32393) has the left eye missing and the entire left side of the head covered with an otherwise essentially normal complement of cephalic scutes. One

specimen (ASDM 53) has a small extra scale on both sides of the head; the scale is in contact with the postnasal, prefrontal, preocular, and the second and third supralabials, thus constituting a small loreal.

TABLE 22
Variation in Division of Nasal Scale in Three Species of *Tantilla*

Species	Below naris only[a]	Below, and grooved above[b]	Below only (one side), above also (other)	Above and below[a]	N
T. atriceps	9 (81.8%)	2 (18.2%)	0	0	11
T. hobartsmithi	253 (79.6%)	31 (9.7%)	14 (4.4%)	20 (6.3%)	318
T. planiceps	85 (64.9%)	12 (9.2%)	1 (0.8%)	33 (25.2%)	131

[a] On both sides of the head; [b] grooved on either one or both sides of the head.

TABLE 23

Variation in Position of Naris in Nasal Scale in Largest Population Samples

Sample[a]		Upper half	Medial	Lower half	N
D	Males	5	5	0	10
	Females	8	3	0	11
F	Males	13	9	0	22
	Females	16	4	0	20
N	Males	28	1	0	29
	Females	19	1	0	20
X	Males	0	22	1	23
	Females	0	20	1	21

[a] D–N, *T. hobartsmithi*; X, *T. planiceps*.

TABLE 24

Variation in Position of Naris in Nasal Scale in Three Species of *Tantilla*

Species	Upper half	Medial	Lower half	N
T. atriceps	8 (72.7%)	3 (27.3%)	0	11
T. hobartsmithi	272 (82.9%)	56 (17.1%)	0	328
T. planiceps	17 (13.0%)	109 (83.2%)	5 (3.8%)	131

SIZE AND PROPORTIONS

Some analyses of data on body length (snout-vent), tail length, and total length (table 25) produce ambiguous results. Comparisons (*t*-tests) of body length of the two sexes within four large samples (F, L, N, X), representing two species (*T. hobartsmithi* [F–N] and *T. planiceps* [X]), failed to indicate sexual dimorphism, except in sample L. Comparisons of tail length within the same four samples failed to indicate sexual dimorphism also, except in sample X. And comparisons of total length within the same four samples failed to indicate sexual dimorphism also, except in sample L. Figures 30 and 31 suggest that there is a small degree of sexual dimorphism in tail length of *T. hobartsmithi* and *T. planiceps*.

Considering that some population samples include more juveniles than others, we attempted to compare lengths of only the adults. By examining gonads on AMNH specimens of *T. hobartsmithi*, we concluded that males mature at about 130 millimeters in body length, whereas females mature at about 145. Nevertheless, tests for sexual dimorphism among the adults in the largest samples still produced ambiguous results.

It is difficult to draw useful conclusions from the data on body, tail, and total lengths (table 25; figs. 30, 31, 32), but the following

are clear: (1) In *T. hobartsmithi* and *T. planiceps*, males of a given size generally have a somewhat longer tail than females of the same size; (2) for females of *T. hobartsmithi*, the relationship of tail length to total length is essentially identical to that for males of *T. planiceps*; (3) the relationship of tail length to total length in males of *T. atriceps* is unclear, as the few data points are rather scattered; (4) there may be geographic variation in body, tail, and total lengths within *T. hobartsmithi*; (5) the largest *T. planiceps* exceed 370 mm. in total length, whereas no specimen of *T. hobartsmithi* measures more than 320 mm.; (6) the smallest *T. hobartsmithi* are shorter than 100 mm. in total length, whereas no specimen of *T. planiceps* is shorter than 125 mm.; (7) measurements for *T. atriceps* are similar to those for many samples of *T. hobartsmithi*; and (8) McDiarmid's (1968, pp. 167, 169) data for *T. yaquia* suggest its measurements are more similar to those of *T. hobartsmithi* than to those of *T. planiceps*.

MAXILLARY BONES

We examined the maxillary characters described and illustrated for *Tantilla gracilis* by Hardy and Cole (1968, pp. 624, 625). None of these, however, proved to be taxonomically useful within the *T. planiceps* complex. Maxillae of *T. hobartsmithi* are illustrated in figure 33.

NUMBER OF MAXILLARY TEETH ANTERIOR TO FANGS: The number of ungrooved

TABLE 25
Variation in Lengths (in Millimeters) in Samples of Three Species of *Tantilla*

Sample[a]	Body Mean ± std. error	Body (Range)	Body N	Tail Mean ± std. error	Tail (Range)	Tail N	Total Mean ± std. error	Total (Range)	Total N	Tail/total × 100 Mean ± std. error	Tail/total (Range)	Tail/total N
A ♂♂	140.0 ± 5.592	(117–183)	14	50.2 ± 1.846	(44–59)	9	192.6 ± 8.144	(168–230)	9	26.3 ± 1.005	(20.4–30.6)	9
B ♂♂	143.6	(117–205)	8	49.3	(39–57)	7	184.1	(156–201)	7	26.7	(25.0–28.6)	7
D ♂♂	133.3 ± 4.044	(91–152)	14	48.3	(29–60)	7	176.1	(120–209)	7	27.2	(24.2–28.7)	7
D ♀♀	144.5 ± 5.007	(107–173)	13	44.0	(31–51)	8	187.5	(138–209)	8	23.4	(21.7–25.1)	8
D (all)	138.7 ± 3.320	(91–173)	27	46.0 ± 2.077	(29–60)	15	182.2 ± 6.447	(120–209)	15	25.2 ± 0.618	(21.7–28.7)	15
F ♂♂	133.4 ± 4.822	(72–168)	35	49.3 ± 3.380	(24–75)	23	175.1 ± 9.926	(96–241)	23	27.7 ± 0.446	(23.8–31.1)	23
F ♀♀	143.0 ± 4.809	(85–188)	31	45.2 ± 3.282	(23–67)	17	183.2 ± 11.214	(108–255)	17	24.3 ± 0.419	(21.3–26.4)	17
F (all)	136.3 ± 3.525	(72–188)	68	46.6 ± 2.375	(23–75)	42	175.4 ± 7.385	(95–255)	42	26.1 ± 0.392	(21.3–31.1)	42
H ♂♂	122.2 ± 10.093	(70–159)	12	34.3	(23–56)	6	133.2	(93–202)	6	25.3	(23.8–27.7)	6
H ♀♀	128.5 ± 8.313	(78–180)	20	40.6 ± 3.786	(20–58)	16	168.5 ± 13.089	(101–234)	16	23.6 ± 0.566	(18.3–26.2)	16
H (all)	126.2 ± 6.350	(70–180)	32	38.9 ± 3.189	(20–58)	22	158.9 ± 11.228	(93–234)	22	24.0 ± 0.471	(18.3–27.7)	22
L ♂♂	124.4 ± 6.024	(80–163)	24	41.1 ± 3.180	(21–62)	22	163.7 ± 9.485	(102–225)	22	24.5 ± 0.559	(19.6–27.9)	22
L ♀♀	162.1 ± 7.793	(86–214)	26	45.5 ± 3.328	(22–63)	19	198.2 ± 12.662	(108–263)	19	22.6 ± 0.370	(19.6–25.1)	19
L (all)	142.9 ± 5.611	(80–214)	51	42.7 ± 2.284	(21–63)	42	178.1 ± 8.096	(102–263)	42	23.6 ± 0.363	(19.6–27.9)	42
M ♂♂	153.4 ± 5.888	(90–188)	16	49.9 ± 4.877	(22–72)	9	196.6 ± 14.868	(112–260)	9	25.0 ± 0.767	(19.6–27.7)	9
M ♀♀	167.5	(130–184)	6	47.7	(43–52)	3	217.0	(190–235)	3	22.0	(21.2–22.6)	3
M (all)	157.2 ± 5.071	(90–188)	22	49.3 ± 3.656	(22–72)	12	201.7 ± 11.674	(112–260)	12	24.2 ± 0.691	(19.6–27.7)	12
N ♂♂	134.8 ± 6.287	(85–190)	32	44.0 ± 3.004	(25–71)	27	172.2 ± 9.640	(110–256)	27	25.0 ± 0.371	(22.1–28.1)	27
N ♀♀	149.0 ± 7.919	(84–213)	26	38.7 ± 3.120	(21–57)	18	171.8 ± 11.772	(107–250)	18	22.2 ± 0.381	(19.6–24.6)	18
N (all)	140.5 ± 4.966	(84–213)	59	41.6 ± 2.168	(21–71)	46	171.2 ± 7.261	(107–256)	46	23.9 ± 0.333	(19.6–28.1)	46
O ♂♂	159.0	(138–173)	8	56.8	(52–62)	5	210.8	(190–235)	5	27.0	(26.4–27.4)	5
O ♀♀	133.0 ± 12.364	(88–180)	9	35.8	(26–55)	6	157.3	(114–235)	6	22.6	(21.4–23.4)	6
O (all)	145.2 ± 7.397	(88–180)	17	45.4 ± 4.374	(26–62)	11	181.6 ± 14.497	(114–235)	11	24.6 ± 0.708	(21.4–27.4)	11
Q ♂♂	158.6	(107–199)	8	51.8	(30–68)	8	210.4	(137–267)	8	24.2	(21.9–26.0)	8
Q ♀♀	185.6 ± 11.423	(105–221)	12	52.0 ± 4.611	(25–65)	10	232.0 ± 17.610	(130–284)	10	22.1 ± 0.522	(19.1–23.8)	10
Q (all)	174.8 ± 8.954	(105–221)	20	51.9 ± 3.442	(25–68)	18	222.4 ± 12.727	(130–284)	18	23.1 ± 0.459	(19.1–26.0)	18
R ♂♂	180.7	(154–202)	7	66.0	(54–80)	5	244.8	(208–274)	5	26.9	(25.8–29.2)	5
R ♀♀	166.7	(108–238)	6	41.8	(28–75)	4	191.0	(136–313)	4	21.3	(19.6–24.0)	4
R (all)	174.2 ± 10.603	(108–238)	13	55.2 ± 6.659	(28–80)	9	220.9 ± 20.184	(136–313)	9	24.4 ± 1.100	(19.6–29.2)	9
V ♂♂	223.3 ± 8.943	(158–272)	11	68.6 ± 3.063	(47–79)	10	294.1 ± 12.481	(205–351)	10	23.3 ± 0.280	(21.7–24.8)	10
V ♀♀	200.5	(173–228)	2	56.5	(47–66)	2	257.0	(220–294)	2	21.9	(21.4–22.4)	2
V (all)	219.8 ± 8.468	(158–272)	13	66.6 ± 3.100	(47–79)	12	287.9 ± 12.014	(205–351)	12	23.1 ± 0.288	(21.4–24.8)	12
X ♂♂	211.8 ± 9.420	(127–276)	23	67.4 ± 3.879	(36–91)	19	277.0 ± 14.060	(163–367)	19	24.1 ± 0.293	(21.2–25.6)	19
X ♀♀	193.2 ± 12.935	(113–293)	23	50.1 ± 4.810	(27–82)	17	232.9 ± 19.655	(143–374)	17	21.2 ± 0.403	(18.1–23.5)	17
X (all)	203.2 ± 7.891	(113–293)	47	59.2 ± 3.346	(27–91)	36	256.2 ± 12.284	(143–374)	36	22.7 ± 0.347	(18.1–25.6)	36
Y ♂♂	136.5	(102–161)	4	49.0	(40–58)	2	190.5	(165–216)	2	25.5	(24.2–26.8)	2
Y ♀♀	200.0	(200)	1	—	—	—	—	—	—	—	—	—
Y (all)	149.2	(102–200)	5	49.0	(40–58)	2	190.5	(165–216)	2	25.5	(24.2–26.8)	2

[a] A, *T. atriceps*; B–R, *T. hobartsmithi*; V–Y, *T. planiceps*.
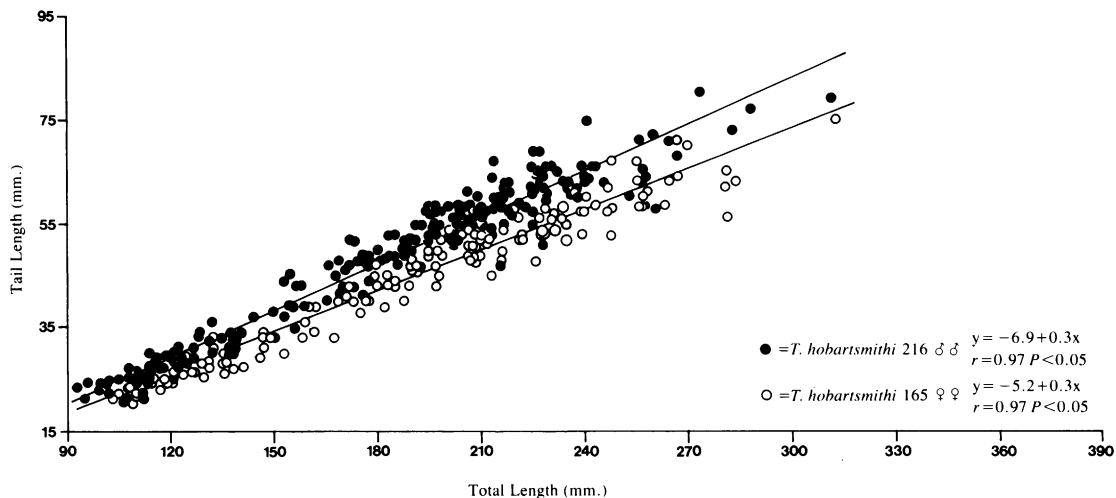
FIG. 30.   Correlation between total length and tail length in *Tantilla hobartsmithi*. Crowding of symbols in places precluded plotting each individual, but all known extremes are shown.

maxillary teeth ranges from 10 to 14 (table 26). Although no sample is sufficiently large to test for sexual dimorphism with confidence, a *t*-test within sample X (10 males, eight females; $t = 0.7828$, $P > 0.05$) suggested the sexes could be pooled to compare different samples (fig. 34). We conclude that

there are no consistent differences between *T. hobartsmithi* and *T. planiceps*, and *T. atriceps* is similar to them in this character.

NUMBER OF FANGS: There are two (rarely three) functional, grooved fangs on the maxilla of *T. atriceps, T. hobartsmithi,* and *T. planiceps,* with no indication of either sexual
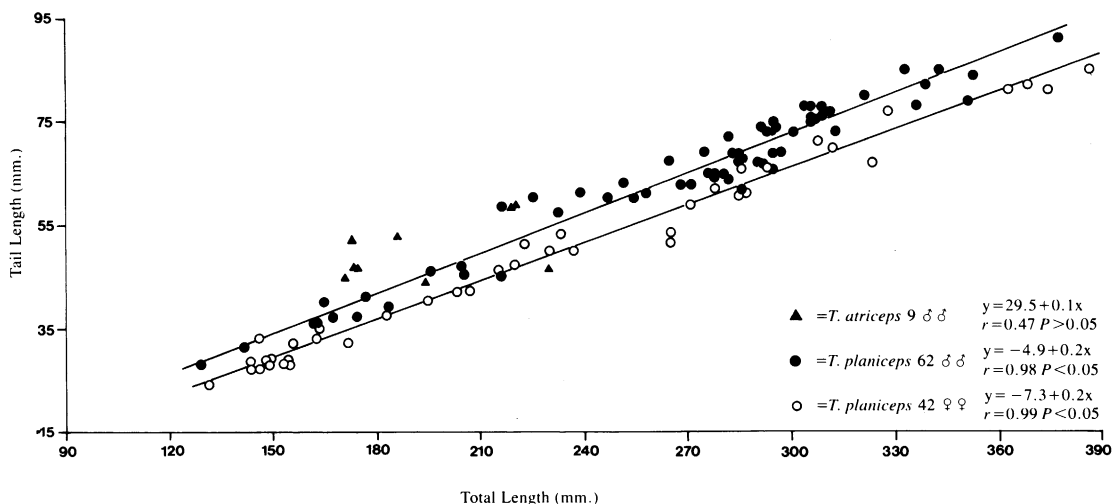

FIG. 31.   Correlation between total length and tail length in *Tantilla planiceps* and *T. atriceps*. Crowding of symbols in places precluded plotting each individual, but all known extremes are shown.

dimorphism or geographic variation (table 26). Usually a diastema is present between the posteriormost ungrooved tooth and the anteriormost fang.

LATERAL ANTERIOR FORAMINA: These range in number from one to three (table 27). Although no sample is sufficiently large to test for sexual dimorphism with confidence, a *t*-test within sample X (10 males, eight females; $t = 0.8164$, $P > 0.05$) suggested the sexes could be pooled to compare different samples. Comparisons of five samples (F, L, N, Q, X) containing 10 or more specimens, including representatives of two species (*T. hobartsmithi* [F–Q], *T. planiceps* [X]), failed to indicate significant differences between any samples. *Tantilla atriceps* is similar to both *T. hobartsmithi* and *T. planiceps* in usually having two lateral anterior foramina (table 27). When the usual number of two of these foramina are present on the maxilla, more than 90% of the specimens each of *T. atriceps, T. hobartsmithi,* and *T. planiceps* have the anterior foramen distinctly larger than the posterior one, and usually it is two to three times as large in diameter.

TOOTH BELOW POSTERIOR FORAMEN: When the usual number of two lateral anterior foramina were present, we determined which tooth or socket occurred directly below the center of the posterior foramen; this varied from six to 10 (table 27). No sample
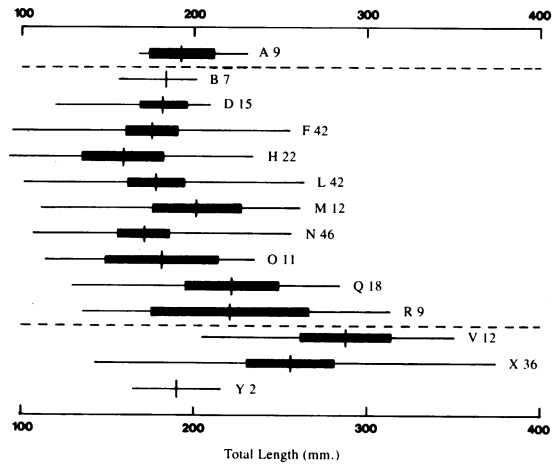
FIG. 32. Variation in total length in samples of three species of *Tantilla*; interpretation as in figure 16.

is sufficiently large to test for sexual dimorphism, but the apparent lack of such dimorphism in other maxillary characters suggested that the sexes could be pooled to compare different samples. Comparisons (*t*-tests) of four samples (F, L, Q, X) containing more than 10 specimens, including representatives of two species (*T. hobartsmithi* [F–Q], *T. planiceps* [X]), suggest there is geographic variation within *T. hobartsmithi* and no con-
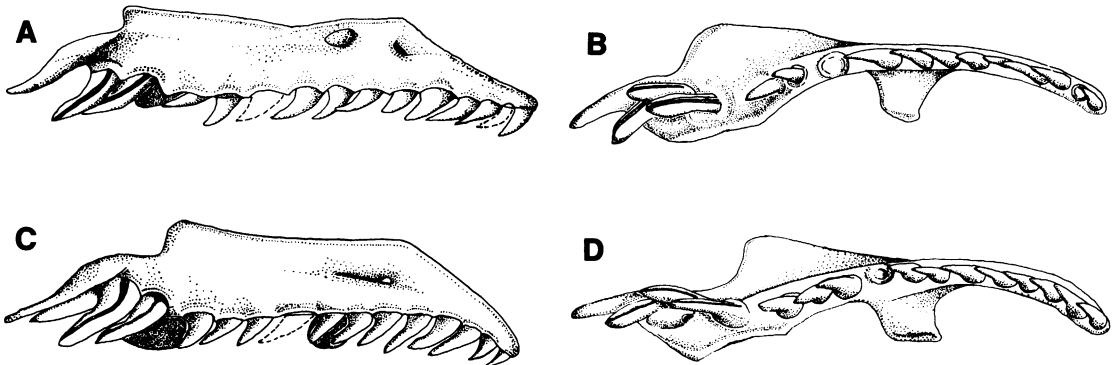
FIG. 33. Right maxillary bones from two specimens of *T. hobartsmithi*. A. Lateral view, BYU 11278, ♂. B. Ventral view, BYU 11278. C. Lateral view, BYU 11316, ♀. D. Ventral view, BYU 11316.

TABLE 26
Variation in Maxillary Dentition in Samples of Three Species of *Tantilla*

Sample[a]	No. maxillary teeth anterior to fangs			No. fangs			Tooth opposite suborbital process		
	Mean ± std. error	(Range)	N	Mean ± std. error	(Range)	N	Mean ± std. error	(Range)	N
A ♂♂	11.4	(10–12)	5	2.0	(2)	6	7.9	(7–8.5)	5
B ♂♂	11.8	(11–12)	5	2.0	(2)	5	7.5	(7–8)	5
F ♂♂	10.8 ± 0.179	(10–12)	12	2.0 ± 0.000	(2)	13	6.8 ± 0.139	(6–8)	12
F ♀♀	11.0	(10–12)	3	2.0	(2)	4	7.2	(7–7.5)	3
F (all)	10.8 ± 0.174	(10–12)	15	2.0 ± 0.000	(2)	17	6.9 ± 0.118	(6–8)	15
I (all)	11.8	(11–12)	5	2.0	(2)	5	7.7	(7–8)	5
J (all)	12.0	(11–13)	7	2.0 ± 0.000	(2)	9	7.3	(7–8)	6
L ♂♂	11.4	(11–12)	5	2.0	(2)	5	6.9	(6.5–7)	5
L ♀♀	11.7 ± 0.140	(11–12)	11	2.0 ± 0.000	(2)	12	7.2 ± 0.121	(6.5–8)	11
L (all)	11.6 ± 0.125	(11–12)	16	2.0 ± 0.000	(2)	17	7.1 ± 0.093	(6.8–8)	16
M (all)	11.6	(11–12)	5	2.0	(2)	5	7.3	(6–8)	5
N (all)	11.8 ± 0.133	(11–12)	10	2.0 ± 0.000	(2)	10	7.2 ± 0.134	(7–8)	10
Q ♂♂	11.8	(11–12)	6	2.0	(2)	7	7.8	(7.5–8)	4
Q ♀♀	12.0 ± 0.288	(11–14)	9	2.1 ± 0.111	(2–3)	9	7.6 ± 0.182	(7–8.5)	9
Q (all)	11.9 ± 0.181	(11–14)	15	2.1 ± 0.062	(2–3)	16	7.6 ± 0.131	(7–8.5)	13
V (all)	11.8	(11–12)	4	2.0	(2)	4	8.1	(8–8.5)	4
X ♂♂	11.9 ± 0.233	(10–13)	10	2.0 ± 0.000	(2)	10	8.4 ± 0.157	(7.5–9)	10
X ♀♀	11.6	(11–13)	8	2.0	(2)	8	8.1	(7–10)	8
X (all)	11.8 ± 0.172	(10–13)	18	2.0 ± 0.000	(2)	18	8.3 ± 0.172	(7–10)	18
Y (all)	10.7	(10–11)	3	2.0	(2)	3	7.0	(6–7.5)	3

[a] A, *T. atriceps*; B–Q, *T. hobartsmithi*; V–Y, *T. planiceps*.
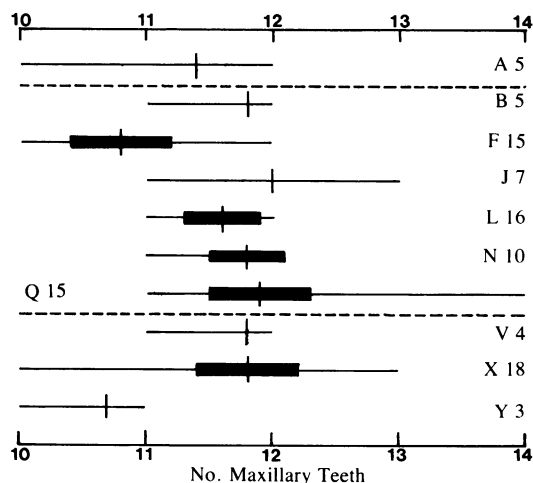

FIG. 34. Variation in number of maxillary teeth anterior to the fangs in samples of three species of *Tantilla*; interpretation as in figure 16.
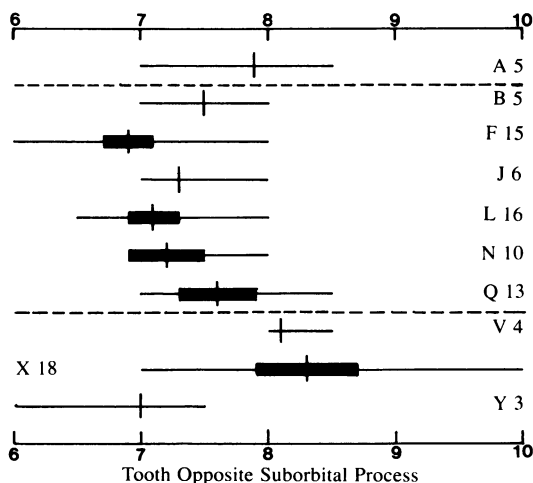

FIG. 35. Variation in which tooth is opposite to the suborbital process on the maxilla in samples of three species of *Tantilla*; interpretation as in figure 16.

TABLE 27
Variation in Lateral Anterior Foramina in Maxillae in Samples of Three Species of *Tantilla*

Sample[a]	No. foramina			Tooth below posterior foramen[b]		
	Mean ± std. error	(Range)	N	Mean ± std. error	(Range)	N
A ♂♂	1.8	(1–3)	6	7.5	(7–8)	3
B ♂♂	2.0	(1–3)	5	7.0	(7)	3
F ♂♂	2.1 ± 0.136	(1–3)	13	6.7 ± 0.121	(6–7)	9
F ♀♀	2.0	(2)	3	6.8	(6.5–7)	3
F (all)	2.1 ± 0.110	(1–3)	16	6.8 ± 0.097	(6–7)	12
I (all)	2.0	(2)	5	7.4	(7–8)	5
J (all)	1.9 ± 0.111	(1–2)	9	7.4	(6.5–8)	7
L ♂♂	2.0	(1–3)	5	7.0	(7)	3
L ♀♀	1.9 ± 0.148	(1–3)	12	6.8	(6–7)	8
L (all)	1.9 ± 0.134	(1–3)	17	6.8 ± 0.121	(6–7)	11
M (all)	2.2	(2–3)	5	7.0	(7)	4
N (all)	1.9 ± 0.100	(1–2)	10	7.2 ± 0.166	(6.5–8)	9
Q ♂♂	2.0	(2)	7	8.0	(8)	5
Q ♀♀	1.7 ± 0.166	(1–2)	9	7.8	(7–9)	6
Q (all)	1.8 ± 0.100	(1–2)	16	7.9 ± 0.147	(7–9)	11
V (all)	2.0	(2)	4	8.2	(8–9)	4
X ♂♂	1.9 ± 0.100	(1–2)	10	8.3 ± 0.290	(7–10)	9
X ♀♀	1.8	(1–2)	8	7.7	(7–9.5)	6
X (all)	1.8 ± 0.090	(1–2)	18	8.0 ± 0.251	(7–10)	15
Y (all)	2.3	(2–3)	3	7.3	(6–8)	3

[a] A, *T. atriceps*; B–Q, *T. hobartsmithi*; V–Y, *T. planiceps*; [b] data recorded only when normal number (two) of foramina were present.

sistent difference between *T. hobartsmithi* and *T. planiceps* (table 27). *Tantilla atriceps* is similar to *T. hobartsmithi* and *T. planiceps* in this character (table 27), which has a pattern of geographic variation similar to that illustrated in figure 35.

SUBORBITAL PROCESS: Counting posteriad, tooth (or socket) number six to 10 occurs directly opposite the distal tip of the suborbital process (table 26). Although no sample is sufficiently large to test for sexual dimorphism with confidence, a t-test within sample X (10 males, eight females; $t = 1.1245$, $P > 0.05$) suggested the sexes could be pooled to compare different samples. There appear to be no consistent differences among *T. hobartsmithi*, *T. planiceps*, and *T. atriceps* in this character (table 26; fig. 35). Usually the anterior and posterior edges of the suborbital process are not parallel in *T. atriceps* (100% of four specimens), *T. hobartsmithi* (60% of 86 specimens), and *T. plani-*

ceps (80% of 50 specimens), although there appears to be geographic variation in this feature (the edges were not parallel in 90% of 10 specimens each in samples F and N of *T. hobartsmithi*).

LATERAL FLANGE: Usually the posterior edge of the lateral flange forms an obtuse angle in *T. atriceps* (100% of four specimens), *T. hobartsmithi* (96% of 103 specimens), and *T. planiceps* (98% of 50 specimens).

SEX RATIO AND ANOMALIES

Using the number of males and number of females in population samples listed in table 5, we calculated χ^2 for all samples of at least 20 specimens for which sex was determined. Eight samples (D, F, H, L, M, N, Q, X), representing two species (*T. hobartsmithi* [D–Q], *T. planiceps* [X]), were involved. The tests are consistent with the hypothesis that there is a 50:50 sex ratio in each popu-
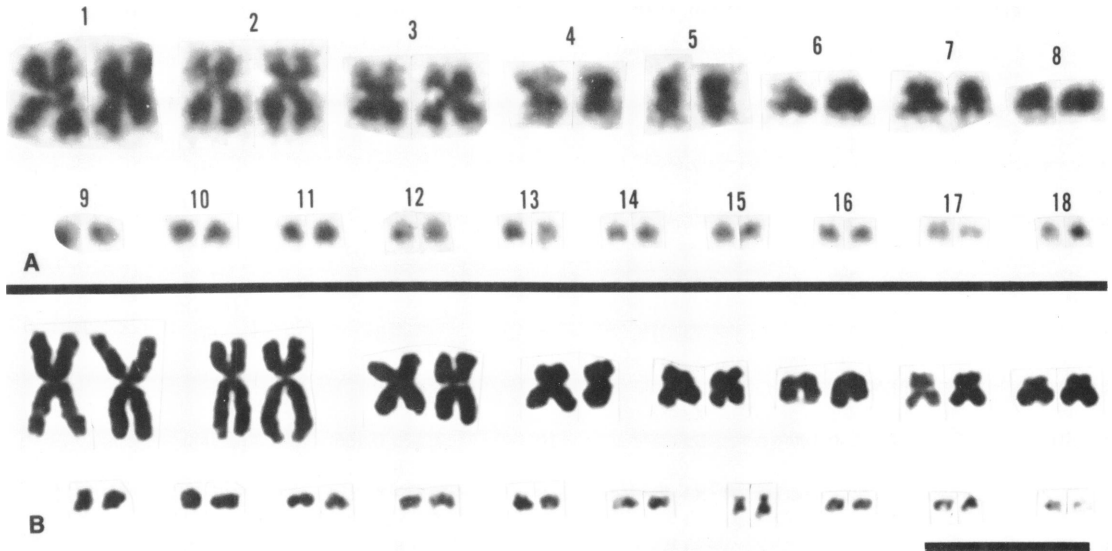
FIG. 36. Karyotypes of two species of *Tantilla*. A. *T. hobartsmithi*, $2n = 36$, AMNH 108915, δ. B. *T. coronata*, $2n = 36$, AMMH 116350, $\female$; line represents 10 microns.

lation, except for sample M, which did, however, conform in using Yates's correction.

No instances of intersexuality (e.g., Hardy, 1970) were found, but two adult males had anomalous hemipenes. A *T. hobartsmithi* (DEH 1895), with a body length of 152 mm., had no spines on the left organ but a normal, spinose right organ. A *T. planiceps* (SDSNH [L. M. Klauber specimen] 35283), with a body length of 241 mm. and testes measuring 10 mm. × 3 mm. had no visible ornamentation whatsoever on either of its partly everted hemipenes.

CHROMOSOMES

Since living *Tantilla* of most species are obtained infrequently, few opportunities arise to study their karyotypes. Van Devender and Cole (1977) presented the only chromosome data yet published for the genus (*T. vermiformis* from Costa Rica). Using the same methods, we obtained data from two North American specimens: A *T. hobartsmithi* (AMNH 108915, male from Arizona); and a *T. coronata* (AMNH 116350, female

from Tennessee). We examined chromosomes from a total of 19 dividing cells (nine mitotic, 10 meiotic, including six primary and four secondary spermatocytes) from bone marrow and testes.

For *T. hobartsmithi*, preparations were unclear but definitely the diploid number is 36, of which 16 are macrochromosomes and 20 are microchromosomes (fig. 36A). Considering the macrochromosomes in order of decreasing size, numbers 1 and 3 appeared metacentric, number 5 appeared metacentric to submetacentric, numbers 2, 4, and 7 appeared submetacentric, number 8 appeared submetacentric to subtelocentric, and number 6 appeared telocentric. Shape of the microchromosomes usually could not be resolved, but in one cell one clearly was metacentric. No satellites, secondary constrictions, or heteromorphic pairs were observed. The haploid number is 18, with 8 bivalents of macrochromosomes and 10 bivalents of microchromosomes (fig. 37).

Preparations for *T. coronata* were clearer and showed basically the same karyotype

(fig. 36B), with 36 chromosomes (16 macro-chromosomes + 20 microchromosomes). Considering the macrochromosomes in order of decreasing size, numbers 1, 3, and 4 are metacentric, numbers 2, 5, and 7 are sub-metacentric, number 8 is subtelocentric, and number 6 is telocentric (numbers 5 and 6 are similar in size). Shape of the microchromo-somes usually could not be resolved, but at least two were bi-armed. No satellites, sec-ondary constrictions, or heteromorphic pairs were observed. Thus, the only sharp differ-ence indicated in the karyotypes of *T. ho-bartsmithi* and *T. coronata* is a slight differ-ence in centromere position in chromosome number 4, which might not be upheld when better preparations of *T. hobartsmithi* are available. In addition, these karyotypes are exceedingly similar to that of *T. vermiformis* from Costa Rica (Van Devender and Cole, 1977).
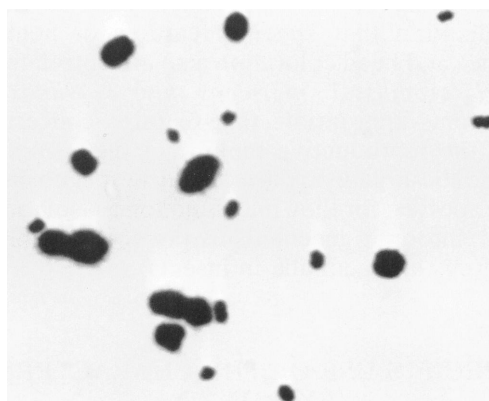

FIG. 37. Chromosomes of *T. hobartsmithi* (AMNH 108915, ♂) at meiotic metaphase I ($n = 18$).

TAXONOMIC JUDGMENTS

Having examined variation, we must de-cide which characters are best for identifying and diagnosing species within the *T. plani-ceps* group.

SPECIES CONCEPTS

We accept Wiley's (1978, p. 18) revision of Simpson's (1961) definition of species: "A species is a single lineage of ancestral de-scendant populations of organisms which maintains its identity from other such lin-eages and which has its own evolutionary tendencies and historical fate." The question remains, how does one recognize whether two (or more) population samples represent different species, particularly if the popula-tions are allopatric? If bisexual (gonocho-ristic) organisms are involved, as in *Tantilla,* we accept reproductive data for distinguish-ing between lineages if there are indications of an inability to interbreed and produce fer-tile F_1 or F_2 offspring (i.e., a biological species concept, excepting circular overlap [Mayr, 1963, pp. 339, 507–512]).

Since there are no direct data on inter-breeding among different populations of *Tantilla,* we use a morphological species concept, occasionally indulging in guess-work about interbreeding, based on patterns of variation and distribution. Initially, all populations sampled are considered as rep-resenting one species unless there are indi-cations that certain samples represent dis-tinctly different lineages.

We examined classical features of color-ation, scutellation, and body measurements, and we examined some details of dentition and maxillary bones plus male genitalia, in an effort to clarify the specific status of the populations Tanner (1966) included in *Tan-tilla planiceps*. Based on the variation and distribution observed in these characters (chromosome data were too few to be useful) we conclude that male genitalia (hemipenes) are more useful than any other features for distinguishing among these snakes. Variation in major hemipenial characters often is correlated with variation in head col-oration, and our use of hemipenes in char-

acterizing species is supported by the realization that specific features of hemipenes and head coloration also are correlated in *T. gracilis, T. nigriceps,* and *T. wilcoxi.* It seems appropriate that features concerning the reproductive biology of these gonochoristic organisms are useful in diagnosing the species, for they may function as isolating or reinforcing mechanisms (as vocalizations in frogs and genitalia in insects).

SPECIFIC USE OF THE CHARACTERS EXAMINED

Many of the characters examined are not useful for distinguishing among the species previously assigned to *T. planiceps,* for two principal reasons: (1) Absence of significant variation (e.g., number of supralabials); or (2) variation present and possibly extensive, but mosaic or otherwise not geographically cohesive (e.g., percentage of anterior temporal that is light in color). Although some of these features are quite useful in comparison with other species of *Tantilla,* we do not further consider most of them in this paper, as our primary concern is to sort out the species previously assigned to *T. planiceps.*

The characters most indicative that Tanner's (1966) concept of *Tantilla planiceps* included four species (*T. atriceps, T. hobartsmithi, T. yaquia,* and *T. planiceps*) are presented in table 28, with the species listed in general arrangement from east to west. Although no single feature will unequivocally identify every specimen, most of these 14 characters in combination will identify almost any pertinent specimen, without resorting to identification based simply on provenance. There are additional characters that vary geographically so that adjacent populations of two species are less similar than distantly separated populations, which is consistent with the hypothesis that the species do not interbreed. These characters are included in the following justification for our recognition of each species.

Tantilla planiceps vs. *Tantilla yaquia:* Although these species are similar in all three

important features of head coloration, they differ in two of the three characters of scutellation and in size, as well as differing in all six hemipenial features (table 28). Most significantly: There is no overlap in data pertaining to origin of the hemipenial retractor muscle; the hemipenis of *planiceps* is noncapitate, whereas that of *yaquia* is semicapitate; and the basal hemipenial spines on *planiceps* are smaller (when present) than the very large ones on *yaquia.* In addition, there is hardly any overlap in data pertaining to length of the retracted hemipenis (table 3; fig. 8).

Tantilla planiceps vs. *Tantilla hobartsmithi:* Although these species are nearly sympatric in places in California, they maintain their distinctness in 12 of the 14 important characters (table 28), being rather similar only in the number of postoculars and contact of the mental with the anterior pair of genials. Most significantly: There is no overlap in the number of spines in the spinose midsection of the hemipenis; there is hardly any overlap in the minimum number of rows of these spines; the hemipenis of *planiceps* is noncapitate, whereas that of *hobartsmithi* is distinctly capitate; and these species differ in all three features of head coloration. In addition, all large samples of *hobartsmithi* differ significantly from those of *planiceps* in the percentage of the seventh supralabial that is light in color (table 7; figs. 1, 18), the specimens of *planiceps* from southern Baja California Sur being the ones most similar to *hobartsmithi.*

Tantilla planiceps vs. *Tantilla atriceps:* These species differ in·10 of the 12 important characters for which there are data on *atriceps* (table 28), being rather similar only in the general shape of the hemipenis and in having its apex noncapitate. Most significantly: There is no overlap in the number of spines in the spinose midsection of the hemipenis; there is hardly any overlap in the number of rows of these spines; they differ in all three features of head coloration; and they differ in all three features of scutellation. In addition, these species differ significantly in length of retracted hemipenis (table 3; fig. 8);

TABLE 28
Summary of Taxonomically Useful Characters of Four Species of *Tantilla*

Character	*T. atriceps*	*T. hobartsmithi*	*T. yaquia*	*T. planiceps*
Hemipenes:				
Origin of retractor muscle[a] (fig. 7)	27.6 (25–32) 14[b]	26.2 (20–34) 128	23.4 (22–24) 5	33.7 (30–38) 62
General shape (fig. 6)	Subcylindrical	Subcylindrical to clavate	Subcylindrical to clavate	Subcylindrical to bulbous
Number of spines in spinose midsection (fig. 9)	32.4 (26–40) 14	23.8 (16–37) 52	46.3 (37–58) 3	57 (45–73) 30
Minimum number of rows of spines approximately encircling spinose midsection (fig. 12)	2.6 (2–3) 14	1.2 (1–3) 66	2.8 (2–4) 4	4.1 (3–5) 34
Condition of apex (fig. 6)	Not capitate	Capitate	Semicapitate	Not capitate
Relative size of the two basal spines (fig. 6)	Medium-large	Medium-large	Very large	Small-large[c]
Head coloration:				
Ventrolateral extension of dark head cap (figs. 1, 16)	No	No	Yes	Yes
Posterior extension of dark head cap[d] (figs. 1, 21; table 8)	1.5	1.0–2.0	Similar to *T. planiceps*	2.3–3.1
Presence of distinct brown spots posterior to light nuchal collar (tables 12, 13)	Rarely (10%)	Rarely (8%)	Often	Often (60%)
Scutellation:				
Number of postoculars (figs. 28, 29)	Usually 1-1	Usually 2-2	2-2	Usually 2-2
Contact of mental with anterior pair of genials (tables 17, 18)	Usually not	Usually so	Usually not	Usually so
Position of naris in nasal scale (tables 23, 24)	Usually in upper half	Usually in upper half	Usually in upper half	Usually medial
Size (mm):				
Minimum total length (figs. 30, 31)	?	ca. 93	ca. 104	ca. 129
Maximum total length (figs. 30–32)	?	ca. 313	ca. 325	ca. 386

[a] Number of subcaudals posterior to vent; [b] data presented thusly are: $\bar{x}$ (range) N; [c] often one is, and sometimes both are, missing; [d] sample means; number of scales beyond posterior end of suture between parietals.

percentage of the seventh supralabial that is light in color (table 7; figs. 1, 18); and there is no overlap in number of ventral scales for *atriceps* and *planiceps,* excepting specimens of *planiceps* from southern Baja California Sur (table 15; fig. 24).

Tantilla yaquia vs. *Tantilla hobartsmithi:* Although these species are literally or very nearly sympatric in southern Arizona, they maintain their distinctness in eight of the 14 important characters (table 28). Most significantly: There is hardly any overlap in the number of spines in the spinose midsection of the hemipenis; the hemipenis of *yaquia* is semicapitate, whereas that of *hobartsmithi* is distinctly capitate; the basal hemipenial spines of *yaquia* are distinctly larger than those of *hobartsmithi*; and these species differ in all three features of head coloration. In addition, samples of *yaquia* from the north-

ern part of its range (Arizona) differ significantly in the following characters from samples of *hobartsmithi* from Arizona, although far more distantly derived samples are similar in them: Length of retracted hemipenis (table 3; fig. 8); and number of ventrals plus subcaudals (compare our table 15 and fig. 27 with data in McDiarmid, 1968, pp. 161, 165). Indeed, in comparing number of ventrals plus subcaudals, sample L of *hobartsmithi* (from the vicinity of Tucson) is more similar to the southernmost sample of *yaquia* (from southern Sinaloa and Nayarit) than to the northernmost sample (which includes Arizona).

Tantilla yaquia vs. *Tantilla atriceps*: These species differ in nine of the 12 important characters for which there are data on *atriceps* (table 28). Most significantly: The hemipenis of *yaquia* is semicapitate, whereas that of *atriceps* is noncapitate; the basal hemipenial spines of *yaquia* are distinctly larger than those of *atriceps*; and these species differ in all three features of head coloration. In addition, there is hardly any overlap in length of the retracted hemipenis (table 3; fig. 8); and these species generally differ in number of ventral scales, the greatest similarity occurring in comparing males of *atriceps* with males of the southernmost sample of *yaquia* (from southern Sinaloa and Nayarit), in which, nevertheless, the mean for *yaquia* is outside the observed range for *atriceps* (compare our table 15 and fig. 24 with data in McDiarmid, 1968, p. 160).

Tantilla hobartsmithi vs. *Tantilla atriceps*: Although these species are sympatric in Coahuila and do not differ in any of the three important characters of head coloration, they differ in four of the six hemipenial features and two of the three characters of scutellation (table 28). Most significantly: The hemipenis of *hobartsmithi* is distinctly capitate, whereas that of *atriceps* is noncapitate. In addition, although *hobartsmithi* and *atriceps* do not differ significantly in any characters of head coloration that we analyzed, the following aspects of hemipenial morphology are significant: (1) In general comparison (table 28) these species appear

similar in origin of the retractor muscle, but there is geographic variation in *hobartsmithi* and the geographically closest samples of it and *atriceps* (Coahuila and Texas) appear to be the most different in this character (hardly any overlap; table 3; fig. 7); (2) apparently there is geographic variation in *hobartsmithi* in length of retracted hemipenis, and, again, the geographically closest samples of it and *atriceps* (Coahuila) appear to be the most different (table 3; fig. 8); (3) *hobartsmithi* shows geographic variation in number of spines in the spinose midsection, and, again, the geographically closest samples of it and *atriceps* (Coahuila, Texas) appear to be the most different (table 4; fig. 9); and (4) *hobartsmithi* shows geographic variation in number of rows of spines in the spinose midsection, and, again, the geographically closest samples of it and *atriceps* (Coahuila, Texas) appear to be the most different, with no overlap in this character in Coahuila and hardly any overlap in Texas (table 4; fig. 12).

Furthermore, there is a geographic continuity (basically separate distributions) to the occurrence of the two kinds of snakes having distinctly different hemipenes, but sympatry is demonstrated by TNHC 33891 and TNHC 33892, two males collected on August 16, 1962 at 10 miles W, 7 miles N Ocampo, Coahuila, Mexico. TNHC 33891 (*hobartsmithi*) has a distinctly capitate hemipenis with 21 spines in the spinose midsection, arranged with only one row around the organ; TNHC 33892 (*atriceps*) has no indication of capitation of the hemipenis, and has 37 spines in the spinose midsection, arranged with a minimum of three rows approximately encircling the organ. In addition to the two specimens that document sympatry in Coahuila, we have found the distinctly different hemipenes among 41 specimens from Texas, which also do not show signs of intergradation: Three *atriceps*, two from Duval County (BM 92.10.39–40) and one from Kleberg County (AIM 931); and 38 *hobartsmithi* from 10 counties (Brewster, Culberson, Jeff Davis, Loving, Maverick, Presidio, Reagan, Reeves, Terrell, and Val Verde).

The striking differences in hemipenial

morphology correlated with geographic distribution and somewhat correlated with aspects of scutellation, indicate that these snakes represent different species. Thus, we reject an obvious alternative hypothesis, that the lack of conspicuous differences in head coloration suggests these snakes represent one species. By recognizing these species primarily on the basis of hemipenial morphology plus variable features of scutellation, we are left with the problem of trying to identify females with certainty. As the ranges of *hobartsmithi* and *atriceps* are narrowly sympatric, the females presently can best be identified based on the identity of the males within whose range they were found. Indeed, we recognize the irony of this conclusion, considering that we initiated this investigation because of our dissatisfaction with identifying specimens in part on the basis of geography! Hardy is studying morphology of the cloaca and lower reproductive tracts in females, attempting to solve this problem.

Thus, we regard *T. planiceps, T. yaquia, T. hobartsmithi,* and *T. atriceps* as separate species, based primarily on the anatomy of male copulatory organs, with supporting evidence from features of head coloration, scutellation, and size (table 28). Tanner (1966, p. 144), in discussing why he treated these forms as subspecies of *T. planiceps* (but with *hobartsmithi* treated as a junior synonym of *atriceps*), stated: "Perhaps the most general and interrelating character in the species is the fine middorsal stripe. In spite of its variation in width and faintness or absence in some specimens, the stripe is the one character which ties the entire subspecies assemblage together." As did McDiarmid (1968, p. 172) with *T. yaquia,* we dissected several specimens of *T. hobartsmithi* and determined that this "stripe" is in fact a middorsal blood vessel, which often is visible through the translucent skin of these snakes.

SUBSPECIES

In addition to the forms discussed immediately above, Tanner (1966) recognized four

other subspecies of "*Tantilla planiceps,*" three of which had been regarded as distinct species by previous authors.

Tantilla planiceps eiseni: Stejneger "1895" [1896] recognized that specimens of *Tantilla* from Fresno, California were specifically distinct from *Tantilla nigriceps* from farther east in the United States, and thus he described *T. eiseni,* although he did not compare the specimens with *T. planiceps.* Tanner (1966) considered *eiseni* and *planiceps* to be conspecific, with which we agree, but he recognized them as different subspecies, based on differences in number of ventral scales and number of ventrals plus subcaudals. The specimens we examined include the holotype of *T. eiseni* (USNM 11766; ♀) and five paratypes, including a male (USNM 55387) whose hemipenis we dissected; these specimens are included in sample T (table 5). We also examined the holotype of *Coluber planiceps* Blainville, 1835 (MNHN 818; ♂), whose hemipenis also was examined. Characters of hemipenes, head coloration, scutellation, and dentition are exceedingly similar in *planiceps* and *eiseni.* The differences in number of ventral scales (table 15; fig. 24) and number of ventrals plus subcaudals (table 15; fig. 27; which probably is not independent from number of ventrals), and in dentition (tables 26, 27; figs. 34, 35) are readily interpreted as geographic variation within one species; some of this variation may represent gradual clines such as occur within *T. hobartsmithi* in the same characters (see especially fig. 25). Therefore, we do not recognize *eiseni* as a subspecies of *Tantilla planiceps.* We consider *T. eiseni* Stejneger "1895" [1896] as a junior synonym of *Tantilla planiceps* (Blainville, 1835), which we regard as monotypic. In comparing the type-series of *T. eiseni* with Stejneger's "1895" [1896] (pp. 117–118) original description, we found two discrepancies worth mentioning: (1) The specimens have six infralabials on each side (instead of "sublabials 7"); and (2) contact of the mental with the anterior pair of genials is rather variable within the type-series (instead of "first pair of sublabials not

in contact behind mental''; which he had included in the diagnosis).

Tantilla planiceps transmontana: Klauber (1943) named this subspecies based primarily on its extremely high number of ventral scales, and also on a reportedly shorter tail and lighter dorsal color than occurs on the nominate form. At the time of the description of this subspecies, there was no overlap known in number of ventrals on specimens from the inland deserts of southern California and specimens from the Pacific coast, but more recently available specimens demonstrate that overlap exists (table 15; fig. 24); nevertheless, a distinctly high number of ventrals occurs on specimens referred to *transmontana* (table 15). Considering the wide extent of geographic variation in ventrals in both *T. planiceps* and *T. hobartsmithi* (e.g., figs. 24, 25), and considering that the number of ventrals is affected, at least in some snakes, by embryonic incubation temperatures (Fox, Gordon, and Fox, 1961), we do not advocate recognizing subspecies solely on the basis of different ventral counts. Such a practice would require naming new subspecies within some clines (e.g., fig. 24), and we are reluctant to do this without compelling reason. In addition, the specimens we examined that previously were referred to *transmontana* did not consistently have a distinctively shorter tail than other specimens of *planiceps,* nor did we recognize any aspects of coloration among the preserved specimens that warranted subspecific recognition, although the specimens we examined included all six paratypes of *transmontana.* Finally, the male paratype (LMK 2633) whose hemipenis we examined was typical of *planiceps* in hemipenial characters. Thus, we do not recognize the subspecies *T. p. transmontana.* We consider *T. eiseni transmontana* Klauber, 1943 as a junior synonym of *Tantilla planiceps* (Blainville, 1835), which we regard as monotypic.

Tantilla planiceps utahensis: Blanchard (1938, pp. 372–373) considered specimens of *Tantilla* from Utah and the Sierra Nevada of California as specifically distinct from *T. atriceps* (our *T. hobartsmithi*), based on the

former being "a larger and more elongate species with more ventrals and with a relatively short tail." Tanner (1966, p. 146) reported no significant difference between these forms in the ratio of tail length to total length, but maintained them as separate subspecies of *T. planiceps,* reporting no overlap in number of ventral scales and stating: "Only the ventrals (Table 2) provide a useful key character." The specimens we examined include at least eight of the paratypes of *utahensis,* and although we did not examine hemipenes of any of the paratypes, we examined them on 15 other specimens. We assign the populations of *utahensis* to *T. hobartsmithi* on the basis of their similarities in hemipenes and other important characters (table 28), in which they differ strikingly from *T. planiceps* (see above). The question remains, should *utahensis* be recognized as a subspecies of *T. hobartsmithi* based on body size and number of ventrals? Although the largest specimens of *T. hobartsmithi* and those with the highest number of ventrals are in the samples previously referred to *utahensis,* there is geographic variation in both features, including a gradual cline in ventrals, and the geographically nearest populations of these two nominal forms are among the most similar in length (table 25; fig. 32) and number of ventrals (table 15; fig. 24); we predict that additional samples from western populations will reveal an overlap in number of ventrals. Thus, we consider *T. utahensis* Blanchard, 1938 as a junior synonym of *Tantilla hobartsmithi* Taylor, "1936" [1937], which we regard as monotypic.

Tantilla planiceps bogerti: Hartweg (1944, p. 1) named *Tantilla bogerti* and diagnosed it as being similar in color pattern to *T. yaquia,* but with "subcaudal scales fewer." McDiarmid (1968) justified considering *T. bogerti* as a junior synonym of *Tantilla yaquia* Smith, 1942, which he regarded as monotypic. We fully concur with that decision.

Considering all the additional population samples we examined within the four species of the *Tantilla planiceps* complex, we do not
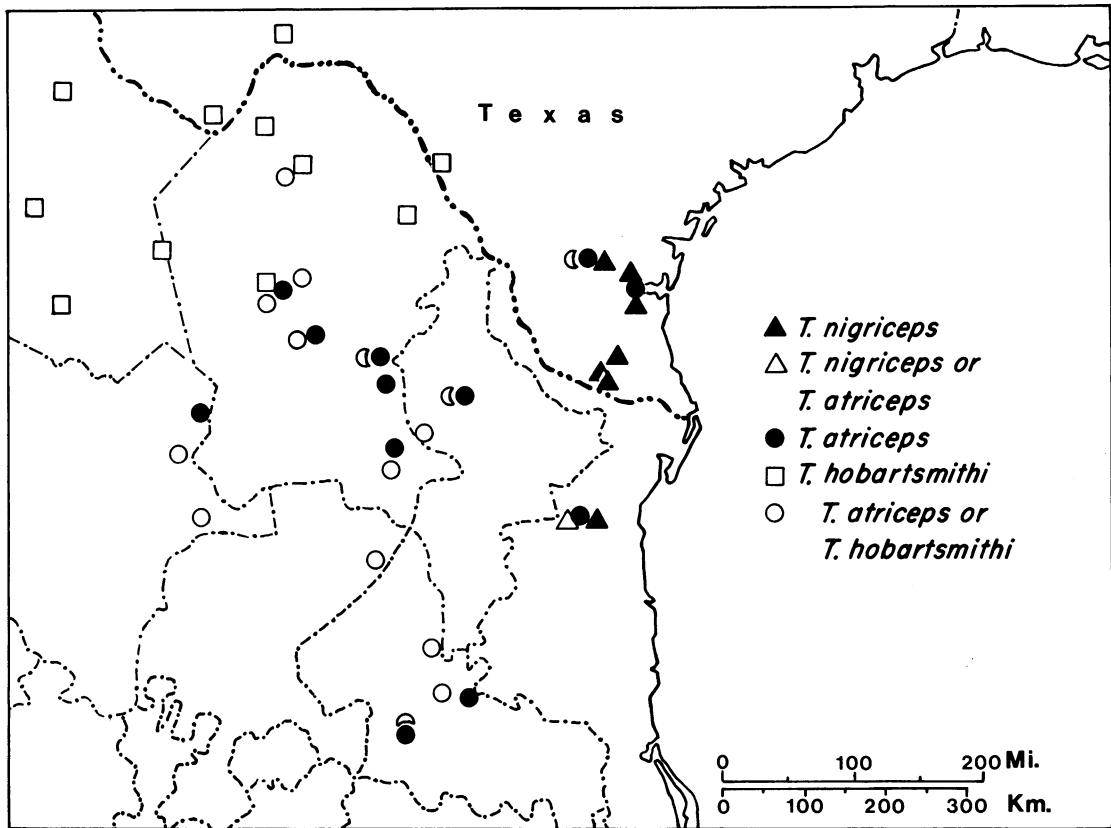
FIG. 38.   Geographic distribution of *Tantilla atriceps* and related species (including problematical specimens) in southern Texas and northern Mexico. Open circles represent specimens for which identification cannot be based on hemipenial morphology (females, juvenile males, or males for which we did not examine hemipenes).

recognize any as sufficiently distinctive to warrant recognition of subspecies. Thus, we regard the following forms as four distinct, monotypic species: *T. planiceps, T. yaquia, T. hobartsmithi,* and *T. atriceps.*

ADDITIONAL PROBLEMS

DISTINGUISHING BETWEEN *Tantilla atriceps* AND *Tantilla hobartsmithi*: Although *T. atriceps* and *T. hobartsmithi* are sibling species, males can be identified by examining hemipenes. But how do we identify females, juveniles, and adult males whose hemipenes we have not examined?

Specimens taken well outside the distri-

butional range of *T. atriceps* but within the range of *T. hobartsmithi* can be assumed to be *T. hobartsmithi,* but those from southern Texas (especially Duval County and southward) and from certain states in Mexico (Coahuila, Durango, Nuevo León, San Luis Potosí, and Zacatecas) are problematical. Geographic distribution of problematical specimens is shown in figure 38.

While Hardy strives to alleviate the problem by investigating new characters, which are promising, there are only three features of scutellation with which to try identifying problematical specimens now: (1) Number of postoculars, which usually are 2-2 in *hobartsmithi* but are 1-1 in nine of 14 males

TABLE 29
Problematical Specimens: *Tantilla atriceps* or *Tantilla hobartsmithi*?

Collection	Specimen	General locality	No. of postocu- lars (r-l)	Mental contacts anterior genials?	No. of ventrals	Sex	Tentative I.D.[a]
KU	67721	San Luis Potosí	2-2	No	126	♀	*atriceps*[b]
FWMSH	7254	San Luis Potosí	2-2	No	137	♀	*atriceps*
FMNH	105096	San Luis Potosí	2-2	No	138	♀	*atriceps*[c]
RGW	4980	Zacatecas	2-2	No	143	♀	*atriceps*[b]
FSM	39627	Nuevo León	1-1	Yes	130	♀	*atriceps*[c]
LSU	14524	Coahuila, S	2-1	No	141	♀	*atriceps*[d]
CM	48158	Coahuila, central	1-1	No	135	♀	*atriceps*[c]
KU	38200	Coahuila, central	1-2	Yes	140	♀	?
EAL	3403	Coahuila, central	2-2	Yes	137	♀	*hobartsmithi*
TNHC	33890	Coahuila, central	2-2	Yes	139	♀	*hobartsmithi*[e]
SRSU	1494	Coahuila, N	2-2	Yes	139	♀	*hobartsmithi*
RGW	5404	Durango	1-1	Yes	136	♂	*atriceps*[d]
IPN	2879	Durango	2-2	No	143	♂	?
LSU	14523	Nuevo León	1-1	Yes	133	♂	*atriceps*
ASU	11497	Coahuila, central	1-1	No	126	♂	*atriceps*[c]

[a] Listed accordingly in Specimens Examined; [b] found far south (>300 km.) of any records for *T. hobartsmithi*; [c] collected with a male *T. atriceps*; [d] found south of any records for *T. hobartsmithi*; [e] collected with a male each of *T. atriceps* and *T. hobartsmithi*.

(64%) of *atriceps* (table 16; figs. 28, 29); (2) contact of the mental with the anterior pair of genials (both scales), which usually is present in *hobartsmithi* (78%) but not in *atriceps* (contact lacking in 71%; table 18); and (3) possibly a lower number of ventrals in *atriceps* than in *hobartsmithi* (table 15; fig. 24).

Selected characters, tentative identification, and remarks concerning the 15 problematical specimens of which we are aware are presented in table 29. Although some specimens (e.g., KU 38200) might be regarded as hybrids or intergrades, the absence of convergence in hemipenial characters in males from pertinent localities seems to warrant greater significance than variation in features of scutellation that are somewhat variable anyway. Surely, better characters are needed to identify problematical specimens with confidence, and additional collecting is needed throughout the range of *T. atriceps*, especially at localities where it coexists with *T. hobartsmithi*. For additional details on the geographic ranges of these species, see the species accounts.

DISTINGUISHING BETWEEN *Tantilla atriceps* AND *Tantilla nigriceps*: While *T. atriceps* has been treated incorrectly as conspecific with *T. planiceps* and we have been addressing that issue, generally it has been accepted without question that *T. atriceps* and *T. nigriceps* (which occurs primarily in grasslands in the midwestern and southwestern United States) are specifically distinct. These species usually are distinguished on the basis of head coloration. In *T. nigriceps* (fig. 1D), the dark cap is "V-shaped, its apex extending three to five scale lengths posterior to parietals on middorsal line; no nuchal collar"; and in *T. atriceps* (fig. 1H), the dark cap usually extends one to three scales posterior to the parietals and has "a straight or slightly convex posterior margin; a nuchal collar at least faintly visible" (Smith, 1942, p. 42). In both species, however, shape of the dark head cap is somewhat variable, and this is particularly so on specimens we have

TABLE 30

Comparison of *Tantilla nigriceps* and *Tantilla atriceps* from Southern Texas and Northeastern Mexico

Specimen	General locality	Head cap length[a]	Head cap shape	Light collar?	No. of post-oculars	No. of ven-trals	No. of cau-dals	Sex	Origin, hemi-penial retrac-tor mus-cle	Rows of hemi-penial spines	Species
TCWC 38061	Texas	3½	Angular	No	2-2	135	48	♂	31	3	*nigriceps*
TCWC 38062	Texas	3	Point[b]	No	2-2	133	50	♂	31	—	*nigriceps*
TCWC 38073	Texas	3	Point[c]	No	2-2	130	—	♂	32	3	*nigriceps*
TCWC 33981	Texas	3	Point	—	—	—	54	♂	32	—	*nigriceps*
TCWC 18374	Texas	3	Point	—	—	—	50	♂	32	3	*nigriceps*
TCWC 33980	Texas	3	Point	—	—	—	50	♂	29	1	*nigriceps*
AIM 500.3	Texas	3½	Point[d]	No	1-1	130	51	♂	—	—	*nigriceps*
TCWC 48204	Tamaulipas	3	Point	No	1-1	123	52	♂	33	2	*nigriceps*
AIM 3202	Texas	2	Point[d]	Yes	1-1	135	39	♀	—	—	*nigriceps*
TCWC 38060	Texas	2½	Point[b]	No	2-2	144	42	♀	—	—	*nigriceps*
TCWC 33982	Texas	3	Point[e]	—	—	—	39	♀	—	—	*nigriceps*
TCWC 18373	Texas	3	Point	—	—	—	39	♀	—	—	*nigriceps*
BM 87.1.4.25	Texas	3	Point[c]	No	1-1	151	—	♀	—	—	*nigriceps*
TCWC 48205	Tamaulipas	1½	Point[f]	No	1-1	136	42	♀	—	—	??
TCWC 48206	Tamaulipas	2	Point[g]	No	1-1	119	56	♂	34	2	??
TCWC 48207	Tamaulipas	1	Convex[h]	No	2-2	127	49	♂	31	2	*atriceps*
TCWC 44013	Coahuila	1½	Point	Yes	2-2	132	67	♂	29	3	*atriceps*
FSM 39626	Nuevo León	3	Straight	No	1-1	122	54	♂	29	2	*atriceps*
BM 92.10.29.41	Texas	2	Convex	Yes	2-1	120	60	♂	29	—	*atriceps*
BM 92.10.29.40	Texas	2	Convex	Yes	1-1	127	—	♂	26	2	*atriceps*
BM 92.10.29.39	Texas	1	Convex	Yes	1-1	125	—	♂	31	2	*atriceps*
AIM 931	Texas	2	Convex[h]	No	2-2	135	45	♂	32	3	*atriceps*

[a] Number of scales beyond posterior end of suture between parietals; [b] irregular, long, and narrow; [c] long and narrow; [d] elongate; [e] truncate; [f] angular to point; [g] convex to point; [h] irregular.

seen from southern Texas and northeastern Mexico. Perhaps most significantly, the hemipenes of *T. atriceps* and *T. nigriceps* are exceedingly similar in all characters examined; and, as in *T. atriceps*, *T. nigriceps* usually has the mental separated from the anterior pair of genials and a relatively low number of ventrals.

Selected characters that illustrate the difficulty in distinguishing between *T. atriceps* and *T. nigriceps* among specimens from southern Texas and northeastern Mexico are presented in table 30. Presently it appears that the best features for identifying these specimens are those of head and nape col-

oration. The specimens from the British Museum come close to documenting sympatry between these species in Texas, but their data are complete only to county; and, since they were sent to the British Museum in the last century, it is not unreasonable to question whether the locality data more accurately reflect the point of shipment than the place of capture. Nevertheless, three specimens more recently collected in Kleberg County, Texas (AIM 931; AIM 500.3; AIM 3202) nearly demonstrate sympatry. The series of four snakes from Tamaulipas (TCWC 48204–48207) may be most important. These were all collected at one locality and include one

specimen that is readily referred to *atriceps*, one readily referred to *nigriceps*, and two that are questionable.

A careful analysis of geographic variation in *Tantilla nigriceps*, yet to be carried out, will provide the data necessary to conclude whether *T. atriceps* and *T. nigriceps* are sympatric at some localities, whether they interbreed at others, and how this should best be reflected taxonomically. If future work indicates that these forms are interbreeding geographic variants of one species, the name *Tantilla nigriceps* Kennicott, 1860, has precedence over *Homalocranium atriceps* Günther, 1895. If these species should become synonymized, this will not affect the specific status of *Tantilla hobartsmithi*, as there is no indication of interbreeding between *T. atriceps* and *T. hobartsmithi*, which are sympatric (discussed above), nor between *T. nigriceps* and *T. hobartsmithi*. The geographic ranges of *nigriceps* and *hobartsmithi* broadly overlap in Texas, Chihuahua, and Arizona, without signs of the two forms interbreeding; and specimens of *nigriceps* (e.g., ASDM 2239; ASDM 2247) and *hobartsmithi* (CAS-SU[4] 7615) from the vicinity of Willcox, Cochise County, Arizona, virtually document sympatry.

One additional alternative should be addressed concerning our taxonomic treatment of these taxa. Is it reasonably possible that "*T. hobartsmithi*" and "*T. nigriceps*" are western and eastern subspecies, respectively, of one species, while the intergrades constitute "*T. atriceps*"? We do not consider it likely because *T. hobartsmithi* and *T. nigriceps* broadly approach each other geographically without indications of interbreeding in New Mexico, Arizona, and Chihuahua, and apparently they are sympatric at least in southeastern Arizona (discussed above).

THE STATUS OF *Tantilla praeoculum* (Bocourt, 1883 [1870–1909]): Smith and Larsen (1975) reviewed the status of this name, which previously had been relegated to the synonymy of both *T. planiceps* and *T. nigriceps* (also see Taylor, "1936" [1937]). Since *praeoculum* was reported from Colo-

[4] CAS specimen, formerly of Stanford University.

rado, and had a low number of ventrals, Smith and Larsen were concerned that it might represent *T. planiceps atriceps* as applied by Tanner (1966), in which case *praeoculum* would have priority. However, Smith and Larsen also realized that prior to 1883 the term "Colorado" might have been used more broadly than it is today, and thus they thought the type-specimen could have been found almost anywhere in the southwestern United States. Thinking that the holotype was lost or destroyed, Smith and Larsen based their review on a translation of Bocourt's original description of *Homalocranion praeoculum*. They concluded that *praeoculum* should be retained as a junior synonym of *T. nigriceps fumiceps* (Cope, 1861), "until conclusive evidence for some other disposition becomes available" (Smith and Larsen, 1975, p. 239).

As we, too, were concerned that the name *praeoculum* could be involved with the *planiceps* group, in 1974 one of us examined the still-existing holotype (ZMB 80 13). The data recorded from this specimen follow, with comments in two places where there are important differences between our observations and Smith and Larsen's (1975) translation of Bocourt's (1883 [1870–1909]) description: Body length 132 mm. (perhaps documenting shrinkage); tail incomplete; dark head cap not extending below angle of mouth; dark head cap extending on nape three scales beyond posterior end of suture between parietals, angular at posterior edge, followed neither by light collar nor distinct brown spots; 30% anterior temporal light in color; 95% seventh supralabial light in color; supralabials 7-7 (numbers 3+4 entering each orbit); infralabials 6-6; preoculars 2-2 (lower right one a horizontally elongate sliver); postoculars 2-2; temporals 1+1 each side; all dorsal scale counts 15; ventrals 140 (not 130); anal divided; mental contacts both anterior genials; prefrontals separated from supralabials; nasal divided below naris only (not entirely divided); naris medial in nasal.

The holotype is a male with retracted hemipenes. Although its brittle condition negated a thorough examination, dissection of the

wilcoxi   *planiceps*   *yaquia*   *nigriceps*   *atriceps*   *hobartsmithi*   *gracilis*

Light collar lost

Hemipenis semi-capitate;
Mental/genial contact lost

1 postocular

Hemipenis capitate

Dark cap lost;
Light collar lost;
1 postocular;
6 supralabials;
Hemipenial spines less numerous ($\bar{x}<20$)

Mental/genial contact lost

Hemipenis semi-capitate;
Hemipenial spines less numerous ($\bar{x}<30$)

Hemipenial spines less numerous ($\bar{x}<40$)

Hemipenial spines less numerous ($\bar{x}<60$)

Hemipenis not capitate;
Hemipenial spines numerous ($\bar{x}>60$)
Dark head cap present;
Light collar on nape;
Mental contacts anterior genials
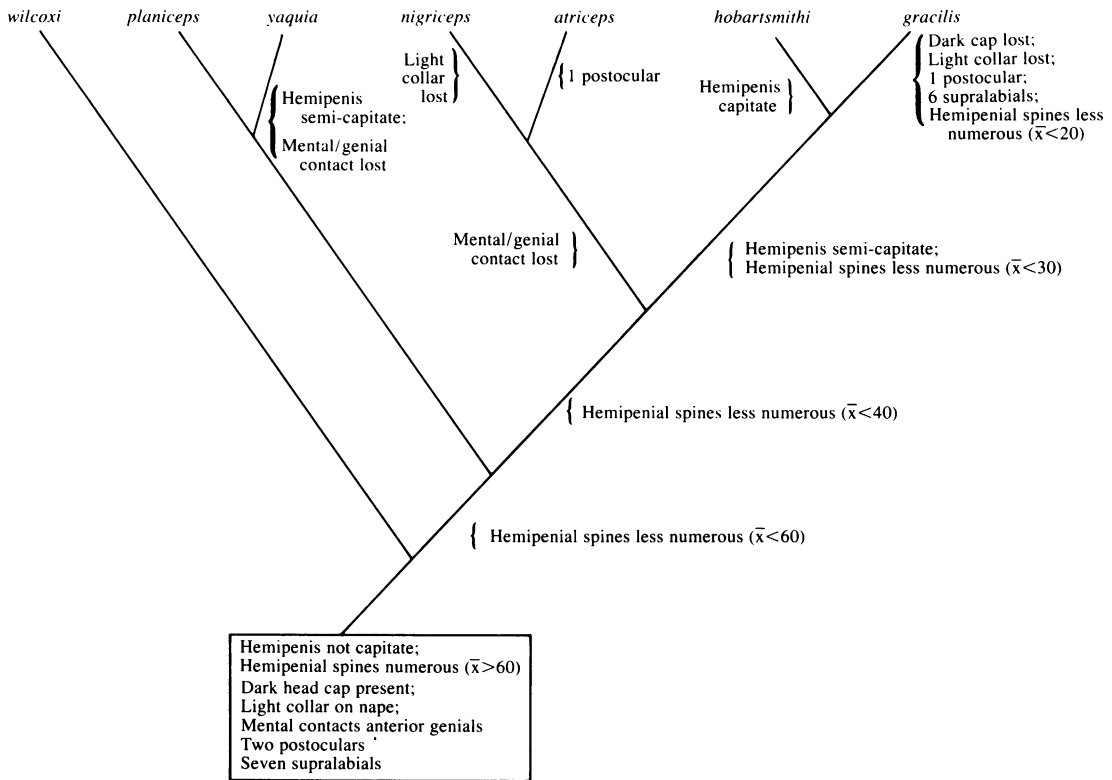Two postoculars
Seven supralabials

FIG. 39. Proposed phylogenetic relationships of seven species of *Tantilla*.

right hemipenis revealed the following: Basal spine large, with another (somewhat smaller) on opposite side; spinose midsection with at least 30 small to large spines, in three rows (minimum); apex calyculate, with proximal calyces spinulate, some spinules difficult to distinguish from small spines in spinose midsection; not capitate. The hemipenis is strikingly different from that of *T. hobartsmithi* (=Tanner's [1966] *T. planiceps atriceps*) and perfectly consistent with that of *Tantilla nigriceps*.

All features of the holotype of *H. praeoculum* are typical of *Tantilla nigriceps,* excepting the anomalous preoculars and the contact of the mental with the anterior pair of genials. Smith and Larsen (1975) thought the specimen represented the southern subspecies, *T. n. fumiceps,* because of the low

number of ventrals reported (originally given in error as 130), and thus they questioned the locality data. However, the locality data sent to us along with the holotype read: "Denver, Colorado." Since the correct number of ventrals is 140, the specimen probably was collected farther north than Smith and Larsen surmised, perhaps even in eastern Colorado. We conclude that *Homalocranion praeoculum* Bocourt, 1883 (1870–1909), is a junior synonym of *Tantilla nigriceps* Kennicott, 1860.

RELATIONSHIPS

A thorough discussion of relationships within *Tantilla* awaits completion of more revisionary work, particularly including investigation of hemipenial morphology.

Nevertheless, we present hypotheses on the relationships of the seven species whose hemipenes we described herein, which includes all species occurring in the United States except *T. rubra* of southern Texas and *T. coronata* and its allies east of the Mississippi River.

We proceeded by reviewing and listing the diagnostic characters of the seven species under consideration, but ignoring such traits as number of ventrals, which can be highly variable intraspecifically. Next we checked the state of these characters as best we could in about 20 additional species of *Tantilla* (including most Mexican species and some Central American species), by reviewing the literature and our unpublished observations on hemipenial morphology of additional species. Then we simply regarded the most frequently occurring state of a character as representing the condition probably present in the common ancestor of the seven species being considered; deviations from this ancestral state were regarded as derived. Finally, we chose to illustrate (fig. 39) the one diagram (of several alternatives) that we think most reasonably indicates the phylo-genetic relationships of these snakes, based on shared-derived characters.

The relationships illustrated (fig. 39) indicate a few instances of convergence: development of a semicapitate hemipenis (*T. yaquia* and the *hobartsmithi-gracilis* ancestor); mental-genial contact lost (*T. yaquia* and the *nigriceps-atriceps* ancestor); light collar lost (*T. nigriceps* and *T. gracilis*); and one postocular (*T. atriceps* and *T. gracilis*). Since individual variation occurs somewhat frequently in the two scale characters, this does not seem unacceptable. We are satisfied with the arrangement as it includes the following: grouping the similar *T. planiceps* and *T. yaquia* as sister taxa; grouping the highly similar (and possibly interbreeding) *T. nigriceps* and *T. atriceps* as sister taxa; and grouping the sibling species *T. atriceps* and *T. hobartsmithi* close together, although their hemipenes are strikingly different. The illustrated relationships make geographic sense also, considering distribution of the species, but elaboration of scenarios on biogeography and evolution, so far as we are concerned, will await additional investigations with additional species.

SPECIMENS EXAMINED

The following localities for 847 specimens are arranged alphabetically, except specimens with unspecified localities are listed first. Localities are listed essentially as we found the data on specimen tags, in museum catalogues, or on loan invoices, with the following exceptions: the wording of some localities was rearranged in order to maintain a consistent format; some obvious misspellings are followed by the correct spelling in brackets; some localities that are geographically close were pooled into one statement [identified in brackets]; and elevations, if stated, follow the locality.

The 494 specimens from the population samples (A–Y) that were compared and analyzed statistically (table 5; fig. 15) are each identified by the appropriate italicized letter immediately preceding the pertinent catalogue numbers.

Many specimens from Laurence M. Klauber's (LMK) private collection are now in the collection of the San Diego Society of Natural History (SDSNH). Some of them bear an SDSNH number, but some do not; those that do not are listed as (LMK [SDSNH] . . .). The same procedure is used for some Joseph F. Copp (JFC) specimens in the Museum of Vertebrate Zoology (MVZ). Although specimens from the Arizona-Sonora Desert Museum (ASDM) have been incorporated into the University of Arizona collections (UAZ), they still can be individually recognized at UAZ by their ASDM numbers.

Tantilla atriceps (N = 17♂♂)

U.S.A.: TEXAS: *Duval Co.:* A (BMNH 92.10.29.39, and 92.10.29.40). *Kleberg Co.:* 8.4 mi. E Riviera, 97°40′44″W, 27°18′N, A (AIM 931).

MEXICO: COAHUILA: 19.1 mi. E Casas Colorados, 4000 ft. (TCWC 44013); Cuatro Cienegas de Carranza, A (CM 42823); 1–3 km. E Cuatro Cienegas de Carranza, A (CM 48156–7); 10 mi. W, 7 mi. N Ocampo, A (TNHC 33892); 4 mi. N Saltillo, A (FMNH 105319); 95 mi. N Saltillo, 27 mi. S Monclova, on rt. 57, A (UAZ 23763).

MEXICO: DURANGO: 25.6 mi. S Tlahualilo, A (UIMNH 48787).

MEXICO: NUEVO LEON: A (BMNH 1946.1.8-81, and 1946.1.8-82 [syntypes of *Homalocranium atriceps*]); 12.2 mi. NNE Cienega de Flores (FSM 39626).

MEXICO: SAN LUIS POTOSI: 10 mi. NW El Tepeyac, A (UMMZ 120225); N San Luis Potosí at Chano Longa, A (FMNH 105097 [=E. H. Taylor–H. M. Smith no. 23475, reported by Smith (1942, p. 34) as being from 102 km. N San Luis Potosí]).

MEXICO: TAMAULIPAS: 2.6 mi. WNW San Carlos, 1600 ft. (TCWC 48207).

Tantilla hobartsmithi (N = 583)

U.S.A.: ARIZONA: *Cochise Co.:* Aston Draw on San Bernardino Ranch, 18 mi. E Douglas, J (CM 40413–8; UCM 19198–203); Benson (BYU 2941); 3 mi. E Benson (MCZ 62407); Empire Mts., E slope Silton Ranch Canyon (FMNH 142238); S Leadville (near Courtland) (ASDM 2244); St. David (UAZ 26411, 26415); 5 mi. W St. David on U.S. 80 (ASDM 138); Wilcox (CAS 7615). *Coconino Co.:* Grand Canyon Natl. Park, North Rim (GCNPM 8905); Morse's Canyon, ½ mi. S Sedona on U.S. 179, P (UAZ 28041–2); Schnebly Hill Rd., 1.1 air mi. NE jct. Ariz. Hwy. 179 (34°52′10″N, 111°44′35″W), 4600–4700 ft., P (RSF 3443); 2 mi. S, 3 mi. E Sedona, P (MNA 310); 3 mi. S Sedona, P (ASU 10138). *Gila Co.:* Christmas (ASU 1871–2); 28 mi. E Globe, 3000 ft. (CA 10841); Miami (CU 2404); 8 mi. N Roosevelt Dam (UU 677, ♀); nr. Roosevelt Dam (USNM 105238; UU 677a, ♂); Sierra Ancha Mts. (SDSNH 27743–4). *Graham Co.:* Ft. Thomas (ASU 1193); 31 mi. S Stafford [Safford] (SDSNH 36329). *Greenlee Co.:* Clifton (ASDM 1231). *Maricopa Co.:* 11.1 mi. N Apache Jct. (Pinal Co.) on Ariz. Hwy. 88 (CM 48622); Bush Hwy. at Salt River bridge (ASU 13204–5; not plotted); Bushnell Sheep Tank rd., nr. Sunflower (CM 47898); Canyon Lake (ASU 1909); McDowell Mts., Reata Pass (AMNH

108915); Phoenix (ASU 1361, 2069, 11286); Scottsdale (ASU 2332); 1–1.5 mi. SSW Sunflower, ca. 41 rd. mi. (U.S. 87) NE Mesa, 3600–3700 ft. (RGW 6019); Sycamore Creek, 8 mi. N Sunflower at Oneida Mine (ASU 13977); Tempe (DEH 4615); 42 mi. N Tempe, Verde River (UCM 6524); Verde River, Ft. McDowell Reservation, N (AMNH 86937; UAZ 26392–8, 26417, 26427; ASU 2971, 3265–9, 4671–8, 9029, 9095, 10281–312; LACM 20472; CAS 85462); Verde River, 10 mi. N Beeline Hwy. (ASU 8801); Wickenburg, O (UIMNH 84238–45, 85845); ¼ mi. W Wickenburg, O (UIMNH 84247); 1 mi. SE Wickenburg, O (UIMNH 84248); 2.5 mi. SE Wickenburg, O (UIMNH 84249); 6 mi. SE Wickenburg, O (UIMNH 84250); U.S. Hwy. 60, 6 mi. SSE Wickenburg, along Hassayampa River, O (LBSC 690417-9 [1 specimen], 690417-10 [1 specimen]; 15 mi. SE Wickenburg, O (UIMNH 84251); nr. Wickenburg, O (UIMNH 84246). *Mohave Co.:* 0.3 mi. W Hackberry, 3650 ft. (UAZ 26437). *Pima Co.:* Bear Canyon, 1.5 mi. E Sabino Canyon Visitor Center, 2800 ft., L (LACM 52610); Box Canyon, Santa Rita Mts., 5000 ft. (UAZ 28510); Brown Canyon, Baboquivari Mts., K (UAZ 26419, 26436); Canada del Oro, W side Catalina Mts., 7 mi. E Oracle Junction, M (ASDM 2240); ¾ mi. S Cuprite Mine, 4100 ft., Santa Rita Mts. (UAZ 26403–4); Kitt Peak Rd., 3800 ft., Baboquivari Mts., K (UAZ 26421); 2.6 mi. below jct. picnic area rd. and Kitt Pk. Rd., on Kitt Pk. Rd., Quinlan Mts., K (UAZ 26431); Organ Pipe Cactus Natl. Mon., Alamo Canyon (UWZ H20131; OPCNM [1 specimen]); Organ Pipe Cactus Natl. Mon., Estes Canyon picnic area, W foot of Ajo Mts. (OPCNM [1 specimen]); 2 mi. W jct. Proctor Ranch rd. and Madera Canyon rd., NW side Santa Rita Mts. (UAZ 26435); Quinlan Mts., 3 mi. S (by Kitt Peak Rd.) Ariz. Hwy. 86, K (RSF 3420); Quinlan Mts., 7.9 mi. from jct. Kitt Peak Rd. and Ajo Rd., on Kitt Peak Rd., K (UAZ 26414); Reddington Pass, 7 mi. (by rd.) E Soldier Rd., 4000 ft., L (UAZ 26445); Reddington Pass, 10.4 mi. E Tanque Rd./Catalina Rd. jct., L (MNA 790); Reddington Pass, 13.2 mi. E Tanque Rd./Catalina Rd. Jct., L (MNA 791, 793); Reddington Pass, 15 mi. E Tanque Rd./Catalina Rd. jct., L (MNA 777, 779, 784, 787); Rillito Wash, 1 mi. W Sabino Canyon Rd., L (UAZ 28552); Rincon Mts., Posta Quemada Canyon, ½ mi. E Brady Residence, L (UAZ 28555); Santa Catalina Mts., Sabino Canyon, L (UAZ 26442); Santa Rita Exp. Station (ASU 5657); Santa Rita Mts., Madera Canyon (USNM 26380); Tanque Verde Valley E of Tucson, ½ mi. W Loop Rd., L (ASDM 2243; UAZ 26424); Tanque Verde Mts., 10.5 mi. E Tanque

Verde P.O., Redington [Reddington] Pass Rd., 6000 ft., *L* (UAZ 26438); 20.6 mi. NE jct. Tanque Verde Rd. and Mt. Lemon Hwy. on Tanque Verde Rd., 4000 ft., *L* (DEH 5613–4); 2.8 mi. S of 10.5 mi. W (via Ajo Rd.) Three Pts. (Robles) Jct., Coyote Mts., 3400 ft., *K* (UAZ 26410); Tucson, *L* [includes several localities within or near the metropolitan area] (AMNH 2546–7; ASDM 52–4, 470, 796, 828, 869, 965, 1074, 1102–3, 1107–9; UAZ 26409, 26412, 26418, 26422, 26428, 26433–4, 28516; MCZ 7787; MVZ 59454; UMMZ 67869, 65104 [3 specimens]); 5 mi. E Tucson, *L* (ASDM 1111); 7.8 mi. N Tucson, at end of Campbell Ave., *L* (UAZ 26426); 11 mi. NE Tucson, *L* (ASDM 582); 17 mi. NE Tucson, Tanque Verde and Reddington Rd., *L* (UAZ 26407–8); 17 mi. E Tucson, Agua Caliente Wash, 1.5 mi. E Soldier Trail, *L* (UAZ 28560); 3 mi. E Vail (UAZ 26425). *Pima Co. or Santa Cruz Co.:* Santa Rita Mts. (LACM 7000). *Pinal Co.:* mouth of Aravaipa Creek (UAZ 26440–1); Black Hills, 41 mi. N Tucson (Pima Co.), 3900 ft. (UAZ 26443–4); 30 mi. E Florence (CA 5943–4); 1 mi. E and 2 mi. S Mammoth, 2400 ft., *M* (UAZ 26430, 26432, 26439); 4 mi. NNW Mammoth, *M* (UCM 14163–4); E 0.8 mi. on Bluebird from jct. with Main St., 4 mi. S (on dirt rd.) Mammouth [Mammoth], *M* (UAZ 26401–2); 9 mi. NNE Mammoth, Aravaipa Creek, *M* (UCM 12302); Oracle, *M* (ASDM 1199; MCZ 16416–7); 0.7 mi. NE Oracle, Cherry Valley Ranch, *M* (UAZ 26399–400); 2 mi. NE Oracle, Cherry Valley Ranch, *M* (UAZ 26416); 3 mi. W, 0.5 mi. N Oracle, 4100 ft., *M* (UAZ 26423); 4 mi. (via Ariz. Hwy. 77) W Oracle, *M* (UAZ 26405–6, 26420, 26429 [2 specimens]); 7 mi. E Oracle Junction, W side Catalina Mts., *M* (ASDM 2241); Ray (ASU 1361, 2905); Superior (MCZ 12051). *Santa Cruz Co.:* Nogales Hwy., 2.2 mi. N Tubac (entrance) (ASDM 2242); 2 mi. SW Tumacacori, Tumacacori Mts. (UIMNH 5990–1). *Yavapai Co.:* 9.2 mi. (by Ariz. Hwy. 93) SE Burro Creek, 3200 ft. (UAZ 26446); Congress Junction (CA 3481); Cottonwood, *P* (DEH 5690); Date Creek (UIMNH 84252); Humbug Gold Mines (ASDM 2246; not plotted); 8 mi. W Santa Maria River, Hwy. 93 (ASU 13203); 5.3 mi. S jct. Hwy. 179 and 89A in Sedona, Bell Rock, *P* (DEH 5729).

U.S.A.: CALIFORNIA: *Inyo Co.:* Panamint Mts., Surprise Canyon (CAS 65378); Saline Valley (CAS 89605). *Kings Co.:* S side Tulare Lake, Kern Delta Farm Ranch (MVZ 83454). *San Bernardino Co.:* Granite Mts. (BYU 32371–2); Horse Spring, Kingston Mts., 4750 ft. (MVZ 28569–70); ½ mi. up trail to 49 Palms Oasis, Joshua Tree Natl. Mon. (LBSC 690717-1 [1 specimen]). *Tulare Co.:* Ash Mt., Sequoia Natl. Park, 1650 ft., *S*

(MVZ 19208, 19332); Flame Truck Trail, Sequoia Natl. Park, 1700 ft., *S* (MVZ 27151); Middle Fork, Kaweah River, above Powerhouse #3, 1800 ft., *S* (MVZ 19331); Springville, *S* (SDSNH 9320).

U.S.A.: COLORADO: *Mesa Co.:* Colorado Natl. Mon. (UCM 19254); 5 mi. W Grand Junction (UCM 19255).

U.S.A.: NEVADA: *Nye Co.:* Cane Spring, N.T.S. (BYU 31288); N.T.S. Mercury (BYU 17922–3); 1.4 mi. N gate 200, N.T.S. (BYU 32312).

U.S.A.: NEW MEXICO: *Doña Ana Co.:* Mesilla Valley, *I* (USNM 22380): *Eddy Co.:* Carlsbad Caverns Natl. Park, *H* (TT 3563–5; TNHC 5146); Carlsbad Caverns Natl. Park, Headquarters area, *H* (CCNP 2070–6, 2419, 3629; UMMZ 121826–7); Carlsbad Caverns Natl. Park, Walnut Canyon, Headquarters area, *H* (UMMZ 123489); Carlsbad Caverns Natl. Park, Rattlesnake Spring, *H* (USNM 147897); 30–34 mi. N Carlsbad, U.S. 285 (UNM 14120); 35 mi. SE Carlsbad, Rattlesnake Canyon (KU 11385); Guadalupe Mts., 3 mi. SSW Sitting Bull Falls, *H* (TNHC 16264, 16281); 2.1 mi. W Malaga (UNM 5969); Washington Camp (KU 16120). *Hidalgo Co.:* Guadalupe Mts., Guadalupe Canyon, *J* (KU 74334; UNM 6873); Guadalupe Canyon, 1 mi. W, ¾ mi. N New Mexico-Arizona-Sonora state line, *J* (LACM 2724–5).

U.S.A.: TEXAS: *Brewster Co.:* Alpine (SRSU 1610, 1612–3; TCWC 27472); 11.2 mi. SW Alpine, Paisano Pass (MVZ 53894); 15 mi. E Alpine (SRSU 2012); 15 mi. S Alpine (hwy. 118) on Woodward Ranch (SFA 4326); 18 mi. S Alpine (SRSU 2004); 20 mi. S Alpine (SRSU 1857, 2002); Big Bend Natl. Park (LSUS 1649); Big Bend Natl. Park, 6.6 mi. E Mailbox Tank (on hwy.) on rd. to Dagger Flat (LSUS 1652); Big Bend Natl. Park, *F* (UNM 9327–8); Big Bend Natl. Park, Chisos Mts., Basin, 5200 ft., *F* (AMNH 71040, 72994 [2 specimens], 73566–7; FMNH 26266, 26607, 26610, 27749, 27751–6, 27758, 75850–1; SM 6436–8; UCM 14161; UMMZ 114214; UNM 8716, 8723–4; USNM 103643; UTA R-2135); Big Bend Natl. Park, Chisos Mts., *F* (CA 12456, FMNH 26609); Big Bend Natl. Park, Chisos Mts., NW slope Casa Grande, 6000 ft., *F* (FMNH 26606); Big Bend Natl. Park, Chisos Mts., Cattail Canyon (upper), 4300 ft., *F* (FMNH 27757); Big Bend Natl. Park, Chisos Mts., Chinese Wall, 5800 ft., *F* (FMNH 27759); Big Bend Natl. Park, Chisos Mts., the Divide, 5800 ft., *F* (FMNH 26608); Big Bend Natl. Park, Chisos Mts., desert slope N Nugent Mt., *F* (CA 12454–5); Big Bend Natl. Park, Chisos Mts., Oak Canyon, *F* (FWMSH 7441–2; UNM 9961); Big Bend Natl. Park, Chisos Mts. S Panther Pass, 5750 ft., *F* (UNM 8720); Big Bend

Natl. Park, Chisos Mts., 12.3 mi. SE Panther Jct., 2150 ft., *F* (UNM 8714); Big Bend Natl. Park, Chisos Mts., Wade (Pine) Canyon, *F* (CA 12460–2); Big Bend Natl. Park, Chisos Mts., Willow Creek, 5200 ft., *F* (FMNH 27750); Big Bend Natl. Park, 3.7 mi. S Govt. Spr. Junct., *F* (UNM 8726); Big Bend Natl. Park, Grape Vine Spring, 3040 ft., *F* (UNM 8715, 8719); Big Bend Natl. Park, Green Gulch [several localities], *F* (UNM 8717–8, 8721–2, 8725, 8727–8, 9970–1; USNM 103653; LSU 10331; CA 12457–9, 12463–6); Black Gap Area (TNHC 12548, 12637, 12716, 12730, 12762); Black Gap, Ranch Rd. 2627 to La Linda, Mexico (DMNH 847); Black Gap Wildlife Area, E base Stairway Mt. (UNM 9029); Black Gap Wildlife Management Area, 3 mi. S Dell Tank (DMNH 230); Calamity Creek (SRSU 2001; not plotted); Chisos Mts., Juniper Canyon, *F* (UMMZ 66021); 54.9 mi. S Marathon, *F* (UIMNH 1592); near Mitre Peak, NW of Alpine (FWMSH 274); 8 mi. S Sierra Blanca (FMNH 75852; not plotted). *Crockett Co.:* 12 mi. S Barnhart (KU 83397). *Culberson Co.:* (FWMSH 2588); Bear Canyon, sec. 24, 5000 ft. (UMMZ 123490); Guadalupe Mts., Pratt's Lodge, *H* (SRSU 2013); Guadalupe Mts., McKittrick Canyon, *H* (TCWC 25980); Guadalupe Mts., McKittrick Canyon, jct. of forks, 5200 ft., *H* (UMMZ 123491, 124554); McKittrick Canyon, sec. 3, *H* (UMMZ 122946 [2 specimens]); McKittrick Canyon, 5200 ft., *H* (UMMZ 123492 [2 specimens]); McKittrick Canyon, Guadalupe Mts. Natl. Park, *H* (CCNP 2645); 2 mi. E Nickel Creek, *H* (TCWC 25904); 2 mi. NE Nickle, *H* (KU 72769–71). *El Paso Co.:* El Paso, *I* (CU 4992; MALB 789; MCZ 22825, 32393; MVZ 71926–7); Franklin Mts., just W Ft. Bliss, *I* (MALB 791, 1722; TT 3562); McKelligon Canyon, Franklin Mts., El Paso, *I* (UAZ 35042). *Jeff Davis Co.:* Davis Mts., *G* (TCWC 38063); Davis Mts., Kingston Ranch, N of Madera Canyon, *G* (CA 12467); Davis Mts., Mt. Locke, *G* (FMNH 29504); Davis Mt. State Park, 5000 ft., *G* (UCM 14162); 7 mi. SSE Fort Davis, 4800 ft., *G* (KU 61159); 11 mi. NE Fort Davis, *G* (BCB 8678–9); 25 mi. NW Ft. Davis, Jones Ranch, *G* (TCWC 25931–3, 25940); Indian Mt. Lodge (SRSU 2007; not plotted); 1 mi. NW Jeff Davis Park, Hwy. 118, *G* (LACM 28770). *Loving Co.:* Mentone (BCB 14954–5); near Mentone (TCWC 23526–8). *Maverick Co.:* 6 mi. W Eagle Pass on Hwy. 277 (AIM 2149); 0.6 mi. E jct. Hwys. 277 and 1665 on 277 (AIM 2155). *Pecos Co.:* 13 mi. E Ft. Stockton (TCWC 25964–7); 10.2 mi. down Hovey Rd. from U.S. 67 (TCWC 26182; not plotted). *Presidio Co.:* 9 mi. S Marfa (SRSU 1600); 24.7 mi. SSW Marfa (DEH 1895–8); 25.8 mi. SSW Marfa (DEH 1969);

27.5 mi. SSW Marfa (DEH 1953); 28.5 mi. SSW Marfa (DEH 1902); 37.2 mi. SSW Marfa, 2810 Ranch Rd., 4650 ft. (TCWC 27470–1); 3 mi. SE Presidio (TCWC 27901); ⅔ mi. S to 6¾ mi. E Ruidosa (FWMSH 7468); 7.4 mi. N Ruidosa (SRSU 1651–6); 11 mi. W Valentine on C. E. Miller Ranch (TNHC 4174); 12 mi. W Valentine, ZH Canyon (TNHC 28408). *Reagan Co.:* Big Lake Area (TCWC 38064–9); 9 mi. W, 12 mi. S Big Lake, 2500 ft. (TCWC 31383, 31386); 12 mi. S Best (SRSU 1589–91); 12.1 mi. S Best (SRSU 1588). *Reeves Co.:* Balmorhea (UMMZ 90636 [4 specimens]); 0.5 mi. N Balmorhea (TCWC 25952–4); 6 mi. N Pecos, Hwy. 17 (SRSU 2011); Toyahuale [?Toyahvale; not plotted] (UMMZ 90637). *Sutton Co.:* 24 mi. W Junction (TNHC 7067). *Terrell Co.:* Chandler Ranch, jct. Pecos River and Independence Creek, *D* (AIM 1999); N edge Dryden, *E* (UNM 9962–9); 12.3 mi. W Dryden, *E* (EAL 3240); 30 mi. NE Dryden, Chandler Ranch, *D* (SRSU 2005–6, 2008–10); NE part Sanderson, *E* (SRSU 1529); 3.3 mi. E Sanderson, *E* (UTA R-1438); 11 mi. E Sanderson on U.S. 90, *E* (TCWC 38059); 12 mi. E Sheffield on S. H. 349, *D* (TCWC 38070–1; UAZ 30915, 30929, 30932); 14 mi. S Sheffield, *D* (TCWC 38051–8); 15 mi. S Sheffield, on Blackstone Ranch, *D* (TNHC 7109); 17 mi. S Sheffield, on Blackstone Ranch, *D* (TNHC 8339); 18 mi. S Sheffield, on Blackstone Ranch, *D* (TNHC 8205); 21 mi. S Sheffield, on Blackstone Ranch, *D* (TNHC 7834, 7966); 22 mi. S Sheffield, *D* (TT 2440). *Terrell Co.: Independence Co.:* [?] Pecos River, *D* (UCM 25049–50 [probably same locality in Terrell Co. as for AIM 1999, above]). *Uvalde Co.:* 2.4 mi. W jct. hwy. 55 on Fm. Rd. 334 (USL 20026). *Val Verde Co.:* 1 mi. N Comstock, *C* (AMNH 108363–6); 1.0 mi. E Comstock on U.S. 90, 101°09'40"W, 29°40'15"N, *C* (AIM 1212, 1212.1); U.S. 90 at the Pecos River, *C* (AIM 1921).

U.S.A.: UTAH: *Garfield Co.:* 1 mi. W Star Spring, Henry Mts. (BYU 11757–8); Starr Springs, Henry Mts. (BYU 31206). *Kane Co.:* 6 mi. E Kanab, *Q* (BYU 14967–8); 8 mi. E Kanab, *Q* (BYU 11355; UIMNH 34774); 17 mi. E Kanab, *Q* (BYU 11250, 11255–6, 11272–9, 11316–20). *Washington Co.:* Beaver Dam Mts., on U.S. 91, 3 mi. W Indian farm on Santa Clara Creek (UU 465); 2 mi. N Castle Cliff Station (LBSC 1115; not plotted); Hurricane, *R* (LBSC 1114); Schwitz [Shivwits] Indian Reservation (BYU 2332, 2878); St. George (CAS 55214 [holotype of *Tantilla utahensis*]), and *R* (BYU 1240, 1518, 1553, 1800, 8669, 22808; CAS 54214; LBSC 1113; UMMZ 88541–2; USNM 163630; UU 8a, 109).

MEXICO: CHIHUAHUA: Coyame (UAZ

35045; EAL 3491); 16.1 mi. SW Jiménez (EAL 2534); 10.3 mi. NW Meoque, Rt. 45 (UNM 9303); Sierra Almagro [Almagre], 12 mi. S Faco [Jaco], 5400 ft. (KU 33984); Sierra Pequis, 18.6 mi. (by rd.) W El Ancon (29.6 mi. by rd. W Ojinaga) (UAZ 35044).

MEXICO: COAHUILA: 15 mi. S Allende, *B* (FMNH 47093); 90 mi. NW Ciudad Melchor Muzquiz at Rancho El Melon, *B* (EAL 2734, 2734–2 [1 specimen]); 10 mi. W, 7 mi. N Ocampo, *B* (TNHC 33891); 5.3 mi. (rd.) E Piedra Blanca, *B* (UAZ 32819–20); Sierra del Carmen, 8 mi. SW Piedra Blanca, *B* (MVZ 58363); Sierra Madre Carmens, *B* (SRSU 1519).

MEXICO: SONORA: El Posa, nr. Guaymas (UIMNH 25066 [holotype of *Tantilla hobartsmithi*]); 1 mi. S Hermosillo (LACM 20473); Sierra Magallanes (31°05′N, 109°55′W) (AMNH 107377); near Sonoita (ASU 4581–2).

Tantilla planiceps (N = 142)

CALIFORNIE: (MNHN 818 [holotype of *Coluber planiceps*]); low ventral count suggests the locality is in Baja California Sur, Mexico.

U.S.A.: CALIFORNIA: *Alameda Co.:* (MVZ 80923); canyon north of Mitchell Ravine Corral Hollow (MVZ 80044). *Fresno Co.:* Fresno, *T* (USNM 11766 [holotype of *Tantilla eiseni*], 55387–91 [paratypes of *Tantilla eiseni*]); flat open flood plain of Silver Creek, just above jct. with Panoche Creek (CAS 23242). *Los Angeles Co.:* Duarte, *U* (BYU 18728); Los Angeles, *U* (CAS 13211–2); Palos Verdes Hills, *U* (LACM 20468); Portuguese Bend, *U* (LACM 20467); San Gabriel Canyon, *U* (KU 74363); ½ mi. S Switzer's Camp, San Gabriel Mts. (LACM 20466). *Orange Co.:* Trabuco Canyon (LBSC 1106). *Riverside Co.:* 1.5 mi. S Cabazon, *V* (SDSNH 44270); 3 mi. NW Elsinore, in canyon divided by Hwy. 71 (LBSC [CSCLB] 3026); 3 mi. NW Elsinore, on Hwy. 71, on rd. to Corona, 0.2 mi. off rd. to W (LACM 52609); Riverside, Box Spring Mts. (AMNH 93381); San Gorgonio Pass, *V* (LACM 22222–3); Snow Creek, *V* (AMNH 60514); Snow Creek, crossing Snow Creek rd. at foothills, San Jacinto Mts., *V* (LACM 20469); Tahquite Canyon approx. 1 mi. WSW Palm Springs, *V* (LBSC [WCW] 680114-1 [1 specimen]; SDSNH 37340; LMK [SDSNH] 33760 [paratype of *Tantilla eiseni transmontana*]); Whitewater Canyon, *V* (LBSC 1109–12; LACM 27914). *San Bernardino Co.:* Cottonwood Canyon (LACM 22221; not plotted); 5–6 mi. N North Ontario, Cucamauga Canyon (USNM 104400). *San Diego Co.:* (LMK [SDSNH] 23869, 26749, 28096); Allied Gardens (SDSNH 44128); Bonita, *X* (FMNH 18421); Borrego Rd., nr. the Narrows, *W* (LACM 20465); Borrego State Park, Tamerisk Grove, *W* (LACM 20464); Borrego Valley, ½ mi. E Borrego jct., *W* (SDSNH 43128); Camp Elliot (SDSNH 41754); Camp Pendleton, Oceanside (BYU 8663); Campo (CAS 40122); Rd. from Carmel Valley to La Jolla Valley, 1 mi. W Black Mt. (ca. 5 mi. SE Rancho Santa Fe), 500 ft. (JFC 410); Deerhorn Flat (SDSNH 11890); Descanso (SDSNH 71); El Cajon, *X* (CAS 66317); El Capitan (LMK [SDSNH] 21291); Encanto, *X* (LACM 20463); Fanita Ranch, *X* (LMK [SDSNH] 7386); Fletcher Hills, *X* (SDSNH 43863); Greenwood Cemetery (SDSNH 204); Grossmont, *X* (LMK [SDSNH] 1954, 27600; SDSNH 13753, 41756); Homeland (SDSNH 40625); 3 mi. NE jct. Hwys. 8 and 5, *X* (UCM 47309); 5.0 mi. E jct. Hwys. S2 and 78, *W* (DEH 3934); Kearney Mesa (SDSNH 42061, 43297); La Jolla, *X* (LMK [SDSNH] 28835; JFC 103); La Jolla, Scripps Inst. Oceanography, *X* (JFC [MVZ] 2 unnumbered specimens); La Jolla Valley, ca. 4½ mi. E Rancho Santa Fe, 400 ft. (JFC 130); La Mesa, *X* (LMK [SDSNH] 4354, 27021; SDSNH 43572); La Puerta (Mason Valley) (SDSNH 11260 [paratype of *Tantilla eiseni transmontana*]); Lake Hodges (LMK [SDSNH] 6587); Lincoln Acres (SDSNH 37404); Lyon's Valley (KU 6664); Miramar, *X* (LMK [SDSNH] 35283); Mission Hills, *X* (SDSNH 43400); Mission Valley, *X* (SDSNH 44132); Mt. Palomar (LMK [SDSNH] 22657); The Narrows, *W* (SDSNH 43135); National City, *X* (LMK [SDSNH] 20412; SDSNH 53145); Otay Valley (SDSNH 39321); Poway (LMK [SDSNH] 29116; SDSNH 15545); San Diego, *X* (CAS 64485; CU 1078, 2680; LMK [SDSNH] 1842, 2006, 31973, 32818, 34382, 34789, 35175, 35190; SDSNH 211, 1031, 1262, 3047, 15985, 39277, 39884, 40290, 41519, 42653, 43089, 43276); San Vicente Dam (LMK [SDSNH] 35555); Sentenac Canyon, 1 mi. SE bridge (LMK [SDSNH] 32419, 33997 [paratypes of *Tantilla eiseni transmontana*]; SDSNH 44268); Spring Valley, *X* (LMK [SDSNH] 2337); State College, *X* (LMK [SDSNH] 35646); Witch Creek (SDSNH 11259); Yaqui Well (LMK [SDSNH] 2633–4 [paratypes of *Tantilla eiseni transmontana*]; SDSNH 42766). *Santa Clara Co.:* San Jose, Silver Creek Hills, nr. Bayshore Hwy. (AMNH 90163). *Ventura Co.:* 7.8 mi. N Piru on Piru Canyon Rd. (CAS 13055); Sesbe [Sespe?] Canyon (LACM 2727); Simi Valley, Las Llejas Ranch (LACM 20470).

MEXICO: BAJA CALIFORNIA NORTE: Arroyo El Tajo (SDSNH 45001); Cerro El Potrero (SDSNH 45138); El Progresso, head of El Tajo Canyon, Sierra Juárez (LACM 2729); Matanuco

(CAS 66419); Punta Banda (LBSC 1107-8); 10 mi. SE San Quentin (LACM 2728); 4 mi. S San Vicente (SDSNH 39714).

MEXICO: BAJA CALIFORNIA SUR: 12 mi. NE Cabo San Lucas, *Y* (AMNH 97174-5); 1.3 mi. N El Triunfo, *Y* (CAS 91477); Isla Carmen, Gulf of California (SDSNH 44388); Los Martires, 5 mi. S Rancho Buena Vista (LACM 20462); Rancho La Burrera (LACM 6999); 12.1 mi. NW San Bartolo, *Y* (CAS 91394); San Ignacio (MNHN 1896-151); San José del Cabo, *Y* (CAS 446); Santa Rosalia, 27°21' (MNHN 1892-425).

Tantilla yaquia (N = 9)

U.S.A.: ARIZONA: *Cochise Co.:* above Cox Ranch, 2 mi. S Portal (AMNH 109531). *Santa Cruz Co.:* Pajarito Mts., Sycamore Canyon (ASDM 2255); Pajarito Mts., first canyon E Sycamore Canyon, 50 yds. N Ruby Rd. (ASDM 2237); California Gulch (ASU 14012).

MEXICO: NAYARIT: Acaponeta (AMNH 62259 [holotype of *Tantilla bogerti*]).

MEXICO: SINALOA: Mex. Hwy. 15, 10.4 rd. mi. N Tropic of Cancer (23°37'N, 106°34'W) (RSF 2958).

MEXICO: SONORA: Alamos (MVZ 78758); 9.7 mi. (by rd. to Alamos) SW Milpillas (Chihuahua) (UAZ 40060); Rancho La Palma, 24 km. (by rd.) NE Baviacora (UAZ 35165). Mex. Hwy. 15, 16.1 rd. mi. N jct. rd. to Ures (29°23'N, 110°58'W) [=ca. 20 air mi. N Hermosillo] (RSF 2960).

Tantilla atriceps or T. hobartsmithi (N = 16)

These specimens are one of the above two species but not definitely assigned to either of them because they are females, juveniles, or males whose hemipenes were not examined in sufficient detail.

U.S.A.: TEXAS: *Duval Co.:* (BMNH 92.10.29. 41, ♂).

MEXICO: COAHUILA: 1-3 km. E Cuatro Cienegas de Carranza (CM 48158, ♀); 4 km. E Cuatro Cienegas (ASU 11497, ♂); 0.5 mi. N Cuesta La Muralla, 38 mi. S Monclova (EAL 3403, ♀); 10 mi. W, 7 mi. N Ocampo (TNHC 33890, ♀); 16 mi. E, 18 mi. N Ocampo (KU 38200, ♀); 10 mi. S Saltillo, Hwy. 57 (LSU 14524, ♀); Sierra Babia (SRSU 1494, ♀).

MEXICO: DURANGO: 3 mi. SSE Sombrertillo (RGW 5404, ♂); Villa Juárez (IPN 2879, ♂).

MEXICO: NUEVO LEON: 12.2 mi. NNE Cienega de Flores (FSM 39627, ♀); 20 mi. W Monterrey (LSU 14523, ♂).

MEXICO: SAN LUIS POTOSI: 23 km. N and

23 km. W Cerritos (FWMSH 7254, ♀); Chano Longa, N of San Luis Potosí (FMNH 105096, ♀ [=E. H. Taylor-H. M. Smith no. 23474, reported by Smith (1942, p. 34) as being from 102 km. N San Luis Potosí]); 14 mi. S Matehuala, 4950 ft. (KU 67721, ♀).

MEXICO: ZACATECAS: 6 mi. N San Tiburcio, 5800 ft. (RGW 4980, ♀).

Tantilla atriceps or T. nigriceps (N = 2)

MEXICO: TAMAULIPAS: 2.6 mi. WNW San Carlos, 1600 ft. (TCWC 48205-6).

Tantilla hobartsmithi or T. planiceps (N = 1)

U.S.A.: CALIFORNIA: *Riverside Co.:* Joshua Tree Natl. Mon., Long Canyon, 3.5 mi. N of S boundary, "Cholla Canyon" (LBSC [HSL] 630525-4 [1 specimen]).

The following specimens of additional species were examined for outgroup comparisons.

Tantilla coronata (N = 2)

U.S.A.: LOUISIANA: *East Feliciana Parish:* 10 mi. SE Clinton (LSU 2678).

U.S.A.: TENNESSEE: *Wilson Co.:* Cedars of Lebanon State Forest (AMNH 116350).

Tantilla gracilis (N = 18)

U.S.A.: KANSAS: (1 preserved hemipenis, uncatalogued, lent by Charles W. Myers).

U.S.A.: LOUISIANA: *De Soto Parish:* 1 mi. W (via Frierson Rd.) jct. Frierson Rd. and Linwood Ave. [Shreveport] (LSUS 1650). *Natchitoches Parish:* ca. 1 mi. NW Natchitoches (AMNH 103799-802, 103804, 103805).

U.S.A.: TEXAS: *Brooks Co.:* (TCWC 38072). *Dallas Co.:* (UTA R-133-4); Dallas (UTA R-1102). *Tarrant Co.:* (UTA R-137); S of Benbrook (UTA R-1273); 2 mi. NE Grapevine (UTA R-612); Lake Worth (UTA R-138); western Tarrant Co. (UTA R-1108). *Val Verde Co.:* 19 mi. N Comstock on S.H. 163 (UAZ 31755).

Tantilla nigriceps (N = 52)

U.S.A.: ARIZONA: *Cochise Co.:* 1 mi. SE Dos Cabezas, 5025 ft. (ASDM 2239, 2247); 6 mi. E Portal, 4200 ft. (AMNH 99353); 7.5 mi. E Portal, 4100 ft. (AMNH 99355). *Graham Co.:* 5 mi. E Bonita (CM 58166-7).

U.S.A.: COLORADO: Denver (ZMB 8013 [holotype of *Homalocranion praeoculum*]).

U.S.A.: NEW MEXICO: *Bernalillo Co.:* Sandia Base pistol range (LSUS 2834). *Hidalgo Co.:* 1 mi. W Rodeo on Arizona/New Mexico state line (AMNH 108917); 2.2 mi. N Rodeo, on Rte. 80, 4100 ft. (AMNH 99351). *Socorro Co.:* 2 mi. E Bernardo on U.S. 60 [26 mi. N Socorro] (AMNH 108918); 44 mi. W Bingham (LSU 24780). *Valencia Co.:* 0.3 mi. S Valencia (by state hwy. 47) (LSUS 3724).

U.S.A.: TEXAS: *Aransas Co.:* Hwy. 881, 6.5 mi. SE Rockport (TCWC 18371–2). *Coleman Co.:* Day Ranch, 22 mi. S. Valera (TCWC 19059–62, 27468). *De Witt Co.:* 12 mi. NW Cuevo (TCWC 8783). *Duval Co.:* (BMNH 87.1.4.25). *Ector Co.:* 25.0 mi. NW Odessa (TCWC 46587). *El Paso Co.:* El Paso (TCWC 27473). *Hemphill Co.:* Canadian (TCWC 13052). *Hidalgo Co.:* 3 mi. W La Joya (TCWC 33980); Farm Rd. 681, 5 mi. N McLook (TCWC 18374). *Hudspeth Co.:* 4.2 mi. SE Acala (TCWC 33979). *Kenedy Co.:* 3 mi. S Riviera (TCWC 38073). *Kinney Co.:* Brackettville, Ft. Clark (TCWC 46586). *Kleberg Co.:* Kingsville (AIM 500.3, 3202). *Midland Co.:* on salt lake road, 12.1 mi. S Midland (TCWC 27467). *Starr Co.:* 10.0 mi. S La Gloria (TCWC 27464–6); 3 mi. W Rincon (TCWC 33981); 14 mi. NNE Rio Grande City (TCWC 33982); 16 mi. NE Rio Grande City (TCWC 18373); 17 mi. NW Rio Grande City on Texas 755 (TCWC 38062); 19 mi. NW Rio Grande City on Texas 755 (TCWC 38061); 30 mi. NW Rio Grande City on Texas 755 (TCWC 38060). *Tom Green Co.:* San Angelo (TCWC 22812). *Victoria Co.:* 17 mi. N Victoria (TCWC 8781–2). *Zapata Co.:* 4.0 mi. N Lopeno (TCWC 36433).

MEXICO: CHIHUAHUA: 11.6 mi. N Galeana on Mex. 10, 4700 ft. (UAZ 34415); 1.1 mi. SW Nuevo Casas Grandes (UAZ 34413); 7.1 mi. SE Nuevo Casas Grandes on Mex. 10 (UAZ 34414); 4.2 mi. by Mex. 45 S Samalayuca (UAZ 35043); 13.4 mi. N Villa Ahumada on Mex. 45 (UAZ 34796).

MEXICO: TAMAULIPAS: 2.6 mi. WNW San Carlos, 1600 ft. (TCWC 48204).

Tantilla relicta (N = 1)

U.S.A.: FLORIDA: *Alachua Co.:* 2 mi. S Gainesville (TCWC 10419).

Tantilla rubra (N = 2)

U.S.A.: TEXAS: *Val Verde Co.:* 2 mi. S Pecos River on Pandale-Langtry Rd. (UTA R-2041).

MEXICO: SAN LUIS POTOSI: Xilitla Reg. (LSU 305).

Tantilla wilcoxi (N = 3)

MEXICO: CHIHUAHUA: vicinity of Sta. Barbara (AMNH 67897).

MEXICO: COAHUILA: Saltillo (FMNH 104547 [paratype of *Tantilla wilcoxi rubricata*]).

MEXICO: ZACATECAS: 12 mi. SE (by hwy. 45), then 2 mi. N Zacatecas (LSUS 1653).

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