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BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 153 : ARTICLE 1 NEW YORK : 1974

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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 153, article 1, pages 1–262, figures 1–51, tables 1–21, maps 1–20

Issued April 11, 1974

Price: $10.75 a copy

ISSN 0003–0090

Printed in Great Britain by Lund Humphries

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ABSTRACT

THE GENUS *Rhadinaea* contains 45 species of small to medium-sized snakes that dwell on the American mainland between latitudes 35° North (Cape Hatteras, North Carolina) and 35° South (east-central Argentina), from sea level to 3200 meters of elevation. Most species seem to be diurnal foragers of the forest floor, although several are probably highly secretive and even semifossorial; they feed principally on amphibians and lizards. The primary habitats and routes of dispersal are pine-oak woodlands and cloud forests of Mexico and upper Central America and humid, tropical broadleaf forests, including montane and lowland rain forests.

The generic limits are vague, in part because characters customarily utilized in distinguishing snake genera break down within single species of *Rhadinaea*. A variety of morphological information is useful in the taxonomy of *Rhadinaea*, but species can largely be identified on the basis of color pattern, and the hemipenis proves to be a particularly important source of clues to intergeneric and intrageneric relationships. Underwood's recent expansion of the Natricidae to include *Rhadinaea* and allied genera is not accepted as a natural arrangement, and the genus is retained in the family Colubridae.

Eight species groups are recognized, primarily on the basis of characteristics of the hemipenis, color pattern, and maxillary dentition. The *godmani* group (11 species) has its ancestral homeland and center of dispersal in Nuclear Central America and is considered closest to the basic stock that gave rise to certain other species groups of *Rhadinaea* and to the genera *Trimetopon* and *Coniophanes*. One evolutionary trend seen within the *godmani* group is the reduction from 21 to 19 to 17 rows of dorsal scales. *Rhadinaea godmani* is shown to be an unexpectedly wide-ranging species with a disjunct distribution; the possibility of genetic interchange between this species and *R. hemsteadae*, on the Meseta Central of Chiapas, needs further investigation. The northern *flavilata* group (two species), perhaps derived from the old *godmani* group, is comprised of peripheral relicts and has been largely replaced by the more modern *decorata* (11 species) and *taeniata* (three species) groups. These three groups are confined to Mexico except for the isolated *Rhadinaea flavilata* in the southeastern United States and for *Rhadinaea decorata*, which ranges from east-central Mexico to northwestern Ecuador. The latter species exhibits remarkable geographic variation in the hemipenis and has acquired keeled scales, a new feature in the genus. The occurrence of secondary hybridization in the *taeniata* group is discussed, and the distinctive *aemula* is placed as a subspecies of *Rhadinaea taeniata*; *R. t. aemula* possibly evolved as a mimic of the opisthoglyphous *Coniophanes piceivittis*. The *calligaster* group includes a single, highly variable species in lower Central America and is of questionable derivation from the *godmani* group. The *vermiculaticeps* group (three species) is confined to lower Central America and is probably derived from the *godmani* group. The hemipenis of species in the *vermiculaticeps* group is strikingly similar to that of the diminutive *Rhadinaea schistosa*, a *godmani*-group relict in Veracruz, Mexico, even to the presence of straight spines that were once thought to characterize the nominal genus *Rhadinella*. The origin of the *lateristriga* group (eight species) is obscure, but this group is possibly ancestral to *Pliocercus*, an evidently specialized genus of poisonous-snake mimics. Some specimens of *Rhadinaea decipiens* show an unexplained resemblance in color and pattern to nearly sympatric *Rhadinaea calligaster*, a species not closely related to the *lateristriga* group. Some specimens of the Central American *Rhadinaea guentheri* have shallow grooves on the posterior fangs; this species is closely related to congeners that lack grooves and represents an initial stage in the evolution of opisthoglyphy; a view that the grooved-fang condition is primitive and being lost in such groups is disputed. The *brevirostris* group (six species) is confined to South America. Hemipenial features and scale-row reduction of *Rhadinaea brevirostris* indicate close relationship between this Amazonian species and the more southern *Rhadinaea occipitalis*, which is unique in the genus in having acquired a color pattern of dark spots and the low number of 15 scale rows. Several species have had their center of evolution in or near the Brazilian highlands and show convergence in aspects of color pattern with species that have evolved in Mexico. The general tendency in modern *Rhadinaea* toward loss of bilobation of the hemipenis is well exemplified by the *brevirostris* group, in which all species have retained a split insertion of the major retractor muscle and in which the primitive bilobed condition still appears in the variational repertory of two species.

There are few strict generic synonyms, because the species are sufficiently generalized to have permitted misassignment to a variety of named genera. The rediscovery of *Calamaria dumerilii* is reported; it was originally thought to be a Cuban species and is the type of the name *Urotheca*. The species is a distinct South American member of the *lateristriga* group, thus confirming Dunn's suggestion that the name *Rhadinaea* Cope, 1863, is a junior synonym of *Urotheca* Bibron "1843" [184–?]. However, *Rhadinaea* is retained in the interest of nomenclatural stability, pending application for conservation to The International Commission on Zoological Nomenclature. The names *Taeniophallus*

Cope, 1895, and *Rhadinella* Smith, 1941, are considered to be junior subjective synonyms of *Rhadinaea*, and the emendation *Rhadinea* Garman, 1883, is a junior objective synonym. Two new species, both in the *decorata* group, are described. Taxonomic innovations and changes in nomenclature are summarized in the concluding chapter.

RESUMEN

El género *Rhadinaea* cuenta con 45 especies de culebras del tamaño pequeño al tamaño mediano que habitan el contiente americano entre las latitudes 35° Norte (Cabo Hatteras, Carolina del Norte) y 35° Sur (Argentina oriente-central), desde el nivel del mar hasta 3200 metros de altitud. La mayor parte de las especies parecen ser activos durante el dia buscando su alimento en el suelo del bosque, aunque otras se esconden y aun son semicavadoras; se alimentan principalmente de anfibios y lagartijas. El habitat primario y rutas de dispersión son los bosques de pino-roble y los bosques nublados de México y alta América Central, y los bosques húmedos, tropicales y caducifolios, incluyendo los bosques en las montañas y los bosques lluviosos.

Los límites genéricos son vagos, en parte porque los caracters que generalmente se utilizan para distinguir los géneros de las culebras se desmienbran en especies individuales de *Rhadinaea*. Una diversidad de información morfológica es útil en la taxonomía de *Rhadinaea*, pero las especies pueden ser generalmente identificadas basándose en el color patrón. Además, el hemipenis ha probado ser una fuente particularmente importante en la indicación de parentescos inter- e intragenéricos. La expansión reciente de Underwood del Natricidae para incluir *Rhadinaea* y géneros relacionados no es aceptable como un arreglo natural, y el género está retenido en la familia Colubridae.

Se reconocen ocho grupos de especies, primeramente sobre la base de las características del hemipenis, el color patrón, y la dentición maxilar. El grupo *godmani* (11 especies) tiene su habitat original y centro de dispersión en la alta América Central y es considerado como el más cercano al tronco básico que dió lugar a ciertos otros grupos de especies de *Rhadinaea* y al géneros *Trimetopon* y *Coniophanes*. Una tendencia evolucionaria que parece estar dentro del grupo *godmani* es la reducción del 21 al 19 al 17 de las escamas dorsales. *Rhadinaea godmani* ha sido mostrada como una especie de sorprendentemente amplia dispersión con distribución discontinua; la posibilidad de intercambio genético entre esta especie y *R. hemsteadae*, en la Meseta Central de Chiapas, requere investigaciónes adicionales. El grupo *flavilata* (dos especies), tal vez derivado del antiguo grupo *godmani*, está constituido de relictos periféricos y ha sido ampliamente reemplazado por los grupos más modernos de *decorata* (11 especies) y *taeniata* (tres especies). Estos tres grupos están confinados a México excepto la *Rhadinaea flavilata* aislada en el sureste de los Estados Unidos y la *Rhadinaea decorata*, cuya distribución se extiende desde el centro oriental de México al noroeste del Ecuador. Estas últimas especies muestran notables variaciones geográficas del hemipenis y han adquirido escamas aquilladas, una nueva característica en el género. La ocurrencia de hibridación secundaria en el grupo *taeniata* es discutido, y la *aemula* distintiva está considerada como una subespecie de *Rhadinaea taeniata*; *R. t. aemula* posiblemente se desarrolló como una mímica de *Coniophanes piceivittis*, una culebra opistoglifa. El grupo *calligaster* incluye una sóla especie, altamente variable, en baja América Central y cuya derivasión del grupo *godmani* es dudosa. El grupo *vermiculaticeps* (tres especies) está confinado a la baja América Central y, probablemente, se deriva del grupo *godmani*. El hemipenis de las especies en el grupo *vermiculaticeps* es notablemente similar al diminuto *Rhadinaea schistosa*, un relicto del grupo *godmani* en Veracruz, México, incluyendo la presencia de las espinas rectas, que es una característica que antes se creyeron ser del género nominal *Rhadinella*. El origen del grupo *lateristriga* (ocho especies) es oscuro, pero este grupo es posiblemente antecesor al *Pliocercus*, evidentemente un género especializado en imitar culebras venenosas. Algunos especímenes de *Rhadinaea decipiens* muestran un parecido inexplicable en la coloración y el patrón a *Rhadinaea calligaster*, una especie casi simpátrica pero no muy relacionada al grupo *lateristriga*. Algunos especímenes de *Rhadinaea guentheri* de América Central tienen surcos poco profundos en los dientes posteriores; esta especie esta intimamente relacionada con congéneres que carecen de surcos en los dientes y representa un paso inicial en la evolución da la opistoglifia; una opinión de que los dientes surcados es una condición primitiva que se está perdiendo en tales grupos es disputada. El grupo *brevirostris* (seis especies) está confinado a la América del Sur. Las características del hemipenis y la reducción en las hileras de escamas de *Rhadinaea brevirostris* indican un parentesco cercano de esta especie amazonica con *Rhadinaea occipitalis* más al sur. Ésta última especie es única en el género por haber desarrollado un patrón de la coloración de manchas oscuras y por el bajo número de 15 hileras de escamas. Varias de las especies han tenido su centro de evolución en o cerca de las altiplanicies brasileñas y

muestran convergencia en aspectos del patrón de la coloración con especies que se han desarrollado en México. La tendencia general en *Rhadinaea* moderna se inclina hacia la pérdida de bilobadación del hemipenis que esta bien demostrado por el grupo *brevirostris*, en el cual todas las especies han retenido una inserción separada del músculo retractor principal y en el cual la condición primitiva del hemipenis bilobado todavía aparece en el repertorio de variación de las dos especies.

Hay pocos sinónimos genéricos estrictos, debido a que las especies son suficientemente generalizados que han inducido su asignación equivocada a una variedad de géneros existentes. El redescubrimiento de *Calamaria dumerilii* ha sido reportado; originalmente se pensó que era una especie cubana y es el tipo del nombre *Urotheca*. La especie es un miembro distinto del grupo *lateristriga* sudamericano, que por consiguiente confirma la sugerencia de Dunn de que el nombre *Rhadinaea* Cope, 1863, es un sinónimo más joven de *Urotheca* Bibron "1843" [184–?]. Sin embargo, *Rhadinaea* está retenido en interés de la estabilidad de la nomenclatura, pendiente de la aplicación de conservación a la Comisión Internacional sobre la Nomenclatura Zoológica. Los nombres *Taeniophallus* Cope, 1895, y *Rhadinella* Smith, 1941, son considerados como sinónimos subjetivos jovenes de *Rhadinaea*, y la enmienda *Rhadinea* Garman, 1883, como sinónimo objetivo joven. Se describe dos nuevas especies, ambas del grupo *decorata*. Todos los cambios de la nomenclatura e innovaciones taxonómicas se resúmen en el capítulo final.

INTRODUCTION

"The genus here called *Rhadinaea*, has afforded me considerable perplexity . . ." Edward Drinker Cope, 1863.

COPE'S CENTURY-OLD ADMISSION is probably expressive of the sentiments of each subsequent student of *Rhadinaea*, a large and taxonomically loose assemblage of little snakes that occur in suitable habitat from the southeastern United States to northern Argentina. I became interested in *Rhadinaea* in 1958, in a flooded pine flatwoods in northern Florida, where I first collected specimens of *Rhadinaea flavilata*—the pine woods snake. My study of this species (Myers, 1967) led to a realization that the entire genus was in need of revision. Many species, I found, were exceedingly difficult to identify with existing literature, and an adequate definition of the genus did not exist. Furthermore, there was evidence of considerable confusion concerning the relationships of *Rhadinaea* with various other genera of Neotropical snakes, including *Coniophanes*, *Leimadophis*, *Liophis*, *Lygophis*, and *Trimetopon*. Indeed, from the literature it seemed that a genus called *Rhadinaea* might not be distinguishable from certain of these groups, with particular problems being evident in the case of the South American *Leimadophis-Liophis* complex. Writing about the South American situation, Parker (1935, p. 521) noted that "the generic situation is extremely involved," and Dunn (1922, p. 219) observed: "There are doubtless several natural groups within this mass of . . . snakes, but until better characters are found it is at least unsafe to describe a snake in one of these genera without carefully considering the species of the others." Such comments touch on the need for detailed generic monographs, the paucity of which is one important reason why consensus has not yet been attained on a natural classification of the colubroid snakes. Well over a hundred valid species are included in the aforementioned genera and *Rhadinaea* combined, but revisions have until now been prepared for only two relatively small groups—*Coniophanes* (Bailey, 1939) and *Trimetopon* (Myers, MS). The present revision of *Rhadinaea*, the largest group (45 species), does not solve all the problems of relationships and generic limits, but hopefully it is a movement in the right direction.

My objectives were several: first to determine the names of, and variation in, the species that seem congeneric with *Taeniophis vermiculaticeps*, the type species of *Rhadinaea*, and to arrange the species in natural groups, thus permitting preliminary speculation about genetic relationships and evolution; secondly, to provide detailed descriptions, illustrations, maps, and keys that will make identification of the species as easy as possible; thirdly, to define the genus and to comment on its possible relationships with certain other groups of Neotropical snakes.

It is worth emphasizing at this point that the generic limits of *Rhadinaea* are vague. A number of characters customarily utilized in distinguishing snake genera break down within *Rhadinaea*. This statement is immediately subject to the interpretation that the genus as recognized

might be polyphyletic. But, although I possibly have included a few species whose real relationships may prove to be elsewhere, this is not the source of difficulty; rather it is that the characters tend to break down within single species. In one species, for example, some specimens have grooves on the enlarged, posterior maxillary teeth, whereas other individuals lack grooves as is normal in the genus. Many individuals of another species have weakly keeled scales rather than the smooth condition that obtains elsewhere in the genus. Individuals of two species, representing different species groups, have apical "pits" on the neck scales, although the presence or absence of such structures is often regarded as of generic significance. Such intraspecific variation is doubtlessly of evolutionary importance, but it makes an unqualified generic definition impossible. The present monograph, then, is about a group of relatively generalized animals that are now evolving in diverse ways. Ancestral stocks of this group seem to have given rise to smaller, more specialized assemblages, distinguishable at the generic level (*Coniophanes*, *Pliocercus*, *Trimetopon*), but in *Rhadinaea* itself there has been neither sufficient innovation nor adequate extinction to create the morphological gaps by which some genera are unequivocally recognized.

MATERIALS AND METHOD OF PRESENTATION

Approximately 1200 specimens of *Rhadinaea* were available for this study. This is not an impressive number, considering the broad geographic range and size of the genus, but it probably represented nearly 90 percent of all specimens present in the museums of the world. I examined holotypes or syntypes of about three-fourths of the recognized species and subspecies, and I also saw the type specimens associated with about half the names that I regard as straight synonyms. Some of the types not seen are lost or of uncertain location, but a majority of those known or thought to be extant are housed in the collections of the British Museum of Natural History and the Natur-Museum und Forschungs-Institut Senckenberg.

Scale counts, measurements, and notes on color pattern were obtained from all specimens, except those in which poor condition limited the amount of data that could be taken. A check was made of selected specimens for the presence or absence of hypapophyses on the posterior vertebrae. Maxillae were examined in about 45 percent of the specimens studied. It was not feasible to undertake a comparative osteological study, and it would not serve present purposes to give data for only one or a few species of such a large genus, but a study of skulls and vertebrae would be practical and useful now that the genus and species groups have been defined on other criteria. The hemipenis is considered of particular taxonomic importance in *Rhadinaea* and all everted organs were examined, but most information about hemipenial morphology was necessarily obtained from uneverted organs, which usually were removed from the snake and pinned flat. Availability of material and, secondarily, the tediousness of dissecting and examining the usually small hemipenes limited the number of organs that was studied, but whenever possible I examined at least several retracted hemipenes of a given species, and often I dissected as many males as were available.

The scant information about coloration in life, behavior, and habitats is due in large part to my field experience with the following eight species: *Rhadinaea calligaster*, *R. decipiens*, *R. decorata*, *R. flavilata*, *R. fulviceps*, *R. godmani*, *R. pulveriventris*, and *R. taeniata aemula*. Also, I have maintained living specimens of a ninth species, *R. fulvivittis*, and have seen recently killed specimens of a tenth, *R. hesperia*. Other information has been gleaned from the communications and field notes of colleagues and from the few published accounts.

The species accounts are the most important part of this monograph. They are arranged under eight species groups that are treated in geographic order from north to south, as determined by the distributions of the majority of species within a group. Thus, the primarily North American groups come first, the Central American groups next, and the South American groups last. This plan was adopted mainly for convenience, but it also is vaguely phylogenetic in that the most primitive (*godmani*) group is centrally placed. Each lot of accounts is headed by a characterization and brief discussion of the group. Aspects of ecology, evolution, and zoogeography are discussed in sections following the species accounts. The species are arranged alphabetically within each group.

The species accounts are subdivided into

sections on synonymy, type specimen(s), diagnosis, distribution, description, geographic variation (when pertinent), and remarks. This sequence is altered only in a few cases, for special purposes.

The synonymy of each species includes the correct name and its rejected synonyms, misapplied names, and the different generic combinations that have been used for the aforesaid names. Misapplied names are names of other species that were wrongly used because of inadequate knowledge of the variational limits of a species; such names are misidentifications in one sense, but they often are of historical importance and frequently lead one to hand-colored illustrations and other elegant engravings of a bygone era. Simple misidentifications are of little importance in the taxonomy of *Rhadinaea*, and those I am aware of usually are mentioned in the remarks section rather than in the synonymies. Included after each name in the synonymy is the first bibliographic reference to that name and, also, subsequent references that seem likely to have influenced past and present concepts of the species. These references include major catalogues, checklists, and faunal studies, and all sources containing illustrations of specimens. Data on the type specimen(s) and type locality are given in the synonymy for each rejected synonym; specimens that I have not examined are so indicated.

Data on the type or types of the correct name are given under the section variously headed "Holotype," "Syntypes," or "Designation of Lectotype." I have designated lectotypes only when I thought such action would serve nomenclatural stability. I usually indicate the condition and sex of the principal type and sometimes point out errors in the original description; I do not mean to quibble over slight discrepancies, such as scale counts, which sometimes are due entirely to different methods of counting, but I believe that published data about type specimens should be as uniformly accurate as possible. I have not "restricted" any type locality, and I have ignored completely any attempts by others to restrict localities by decree. I believe that any species based on a single type, or on a series of types from one place, has but one possible type locality, whether or not this locality is known or agrees with the published locality. It is one thing to correct errors in the published record, or to add known detail, but I think it unreasonable and unscientific to guess at, or invent, a locality unless such action is absolutely necessary for nomenclatural stability, which is rarely the case.

The "Diagnosis" gives ways that a species can be most conveniently distinguished from other species. I have tried to make the diagnoses easy to use and relied on distinct aspects of color pattern when possible. The diagnosis should be used in conjunction with the photographs of heads and the drawings of midbody color patterns.

Under "Distribution" I include the major vegetational zones occupied by a species, when this is known to me. The recorded altitudinal range is based on elevations that are actually part of the specimen data. No attempt was made to subsequently determine elevations for place names given as collection sites, because of the frequent probability that specimens were actually taken above or below the recorded locality. The maps showing the distribution of pine-oak forest in Mexico were adapted from Leopold (1959, fig. 6). For names and definitions of the physiographic regions of Middle America, I depended largely on West (1964), Stuart (especially 1954c, 1966), Duellman (1965), and Myers (1969c). It may be well to mention that the "Mesa del Sur" of West (*op. cit.*, p. 63) is here included as part of the Sierra Madre del Sur.

Under "Description" is first given information on maximum size, relative tail length, and scutellation. Traits common to the genus as a whole are generally not repeated here. Means and standard errors of the means of ventrals, subcaudals, and tail length proportions are of little use when comparing one or a few specimens and so only the ranges are given; other statistics are placed where they are most useful, namely in tables that compare all species of a group. The description of color and pattern is of preserved specimens first, followed by notes on the color in life when available. It should be remembered that a whitish surface on a preserved specimen might have been white, greenish, orange, or red when the specimen was alive. Except for coloration in life, the description to this point has been based on the entire sample. Description of the maxilla, next in order, is in some cases based on all available specimens, but often it is not; the number examined is given in the appropriate table. An account of the hemipenis concludes the description, and specimens whose organs were examined are listed.

I attempted to combine all variations into one description, which should thus be fairly representative of the species depending upon the adequacy of the sample. Variation in *Rhadinaea* is most conveniently thought of in the following terms, as previously indicated (Myers, 1967, pp. 68, 69):

A) Intrapopulational variation
  1) Ontogenetic variation
  2) Sexual dimorphism
  3) Uncorrelated (individual) variation
B) Interpopulational variation
  4) Geographic variation

Sexual and ontogenetic variation are so identified, where possible, but not "individual" variation, which requires relatively rigorous testing before it can be known that there is no correlation with age or sex. Individual variation is a poor term because all variation relates ultimately to the individual, but the expression is well established in the literature. Interpopulational, or geographic, variation is not something apart, but is compounded from any or all the classes of intrapopulational variation,[1] and thus is included ipso facto within the description. But, because of its importance to taxonomy and evolution, geographic variation is identified and more fully discussed under its own heading. Larger samples would doubtlessly reveal much more interpopulational variation than was detected in the present study, and some geographic trends probably were not noticed because it often was impossible to compare at one time all the specimens of a species studied.

The "Remarks" section provides room for a variety of topics. The meager data on times of activity are presented when available, but most of the few other items of natural history are given in the first major section (Ecology) following the species accounts. Included for each species is a statement on the etymology of the specific epithet. Once upon a time, most taxonomists had classical educations and few felt obliged to explain the derivation of names given to new species. Probably there are places where I have demonstrated my ignorance of Latin and Greek grammar, but the meaning of names is interesting and I enjoyed these digressions.

[1]Except in the relatively rare situation where a geographically variable character shows no intrapopulational variation, its frequency being either 0 or 100.

ABOUT SPECIES AND SUBSPECIES

Recent years have seen taxonomists engaged in spirited, sometimes heated debate regarding philosophical themes, not the least of which is the definition and recognition of species and subspecies. The literature indicates a lack of consensus on such matters, even though Mayr (e.g., 1966, p. 15) wrote of "*the* modern species concept." (Italics mine.) It is nevertheless true that Mayr's furtherance of the "biological species concept" has had a tremendous influence on taxonomic thinking of the past several decades. Mayr (1942,[2] p. 120, and subsequent publ.) defined species as "groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups." Probably the most significant effect of this philosophy has been the reduction in the number of recognized monotypic species, in favor of species comprised of geographically discrete subspecies. Even though some authors have gone too far along this line, taxonomy still seems the better for it. Those (e.g., Sokal and Crovello, 1970) who are critical of the above quoted definition miss the point when they complain that it does not contain built-in criteria of recognition. Admittedly, taxonomists in most fields have little or no direct knowledge of reproductive capability of the organisms with which they work (certainly this is true of *Rhadinaea*), but the primary purpose of a definition is to express the essential nature of something or of a class of things. I think that a purely operational definition of species may be impossible, for species are where and how you find them. It probably is possible for a definition to express the essential nature of all the kinds of organisms that we would place in the category of species, but the biological species definition, despite its good attributes, does not succeed in doing this. I reject the aforesaid definition as a broad theoretical concept because: 1) it does not apply to asexually and parthenogenetically reproducing organisms (any suggestion that two or more equivalent kinds of species be recognized, according to method of reproduction, is considered adverse to a broad-based concept); 2) it does not express the evolutionary process; 3) it does not express the actual or potential distinctiveness (morphological, etc.) of species.

[2]The present quotation does not come from Mayr's 1940 publication as stated by some authors (including Mayr, 1966, p. 19).

A much superior definition, in my opinon, is that of Simpson's (1961, p. 153) "evolutionary species," which is "a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies." This definition seems applicable to all species, although to be precise, the phrase "or having evolved" could be inserted behind "evolving"—to account for extinct species and those that have arrived at evolutionary impasses. The evolutionary species definition fits asexual and uniparental organisms, as well as intrabreeding bisexual forms, and it also stresses the evolutionary basis of species and the concept of ecological niche (=role). It includes the concept of reproductive isolation, and, where appropriate, also the concept of interbreeding. Maslin (1968) recently emphasized the applicability of the definition to parthenogenetic vertebrates, which are more common than once thought.

I believe that most of the species of *Rhadinaea* recognized herein fit the definition of the evolutionary species, although lack of information quite likely has resulted in misinterpretation of the limits of at least a few kinds. Individual specimens were assigned to species on the basis of morphological criteria (see Taxonomic Characters); the geographic origin of a specimen often simplified the process, but I tried not to let geography over influence my concept of what comprised a given species. Many species of *Rhadinaea* are quite distinctive and specimens could be assigned at a glance; data on taxonomic characters were tabulated and a species was then described on the basis of the entire available sample. Sometimes, the proper designation of a sample was more complicated, as it was not always simple to judge for or against the conspecificity of allopatric populations (e.g., those of *R. taeniata*; or of *R. fulviceps* as distinct from *R. pachyura*), or, in a few cases, even to distinguish between apparently sympatric or partly sympatric species (e.g., *R. godmani* and *R. serperaster*). The more rigorous procedure followed in the difficult cases was essentially as outlined by Inger and Marx (1965, p. 8): 1) examine all characters practically accessible; 2) analyze variation of characters within sympatric samples; 3) correlate all characters within individuals within samples; 4) establish sympatric taxa on basis of (2) and (3); 5) extend analysis of variation to allopatric samples; 6) on basis of (4) and (5) establish limits of species.

The final decision (6, above) is influenced by the adequacy of the sample and the nature of the variation, which is to say that, in the last analysis, the taxonomic decision is subjective to a greater or lesser extent. Some workers think that modern numerical methods provide the objectivity needed in taxonomy, but, even so, a human decision is involved in the final interpretation or acceptance of computer results.

The recognition of subspecies is an unimportant matter in my estimation, although I realize that some workers still regard subspecies as natural units of great evolutionary importance, rather than the convenience that they sometimes are. I deplore the indiscriminate invention of subspecies based on tiny samples and without prior understanding of variation throughout the range of a species. The practice of guessing at whether a specimen represents an infraspecific population set off by discontinuity in variation has led to an undue proliferation of names that must be stored in synonymy. The creators of nonvalid or weakly differentiated subspecies seem not to realize that the subspecies is *not* an obligate taxonomic category and that science could do just as well, or better, without their creations.

Subspecies could be recognized in several species of *Rhadinaea*, but the infraspecific units would, for the most part, be based on an incomplete knowledge of variation (owing to small sample size or lack of specimens from critical areas); furthermore, most such units would be of a low level of differentiation, and I do not see that nomenclatural recognition would serve any useful purpose. Consequently, I have found it convenient to utilize subspecies only in the case of *Rhadinaea taeniata*. The two subspecies thus recognized, *R. t. taeniata* and *R. t. aemula*, differ strikingly from each other, so much so that *aemula* was originally described as a distinct species "without very close relatives" (Bailey, 1940, pp. 4, 15). Each form occupies a definable and reasonably large range, and so subspecific designation is not for the purpose of a very localized situation, nor does there seem to be any reasonable possibility of a clinal effect that would contradict the use of subspecies. I can readily conceive of only one circumstance that might invalidate the use of infraspecific taxa, and that is if new evidence should indicate that *aemula* ×

taeniata specimens are really interspecific hybrids (I view the known hybrids as secondary intergrades, but there are only four such specimens). The existence of such a possibility illustrates a reasonable but little mentioned use of subspecies, namely the "saving" of a specific epithet that is tentatively considered as belonging to a geographical variant of another named species. Such problems are commonplace in taxonomically difficult groups or in little-known regions, and it sometimes contributes to nomenclatural stability if published data and ideas are stored under a name that might conceivably be returned to specific rank. But such practice requires prudence and is best reserved for geographical units that are sufficiently distinct to be judged either as species or good (easily recognizable) subspecies, depending on the evidence.

ACKNOWLEDGMENTS

I have incurred many debts of gratitude in bringing this study to completion, particularly to Prof. William E. Duellman, who generously shared his unparalleled knowledge of Middle American environments and faunas, who served as the chairman of my doctoral committee, and who introduced me to field work in the tropics. I am especially appreciative to my wife, Joan, who patiently typed and retyped the manuscript, and, even more importantly, who contributed immeasurably through her moral support and her cheerful acceptance of my long absences in the field and at the office.

Most of the excellent pen and ink drawings are the painstaking efforts of Mrs. Ellen E. Bowler and Mr. David M. Dennis, as indicated by the signatures under their respective works, but figs. 1, 2, 16, 24, 44, and 47A were executed by Mrs. Frances W. Gibson and figure 42D by Miss Jeanne Esch. I am pleased to publish photographs taken by Dr. Charles M. Bogert (figs. 13, 25) and Mrs. Isabelle Hunt Conant (figs. 8, 17). All other photographs, and the illustrations of midbody patterns, are my work. I am grateful to Mr. Arthur Singer and other members of the Division of Photography at the American Museum of Natural History, for indispensable help in producing the final illustrations.

Many curators and other persons made available specimens, field notes, and other essential information; some of those listed below will not even remember having given their help, but I am grateful to all: Dr. Kraig K. Adler, Dr. James D. Anderson, Dr. Walter Auffenberg, Dr. Joseph R. Bailey, Dr. William Beecher, Dr. Robert L. Bezy, Dr. Charles M. Bogert, Dr. James E. Böhlke, Mr. W. E. Brode, Dr. Howard W. Campbell, the late Dr. Doris M. Cochran, Dr. Charles J. Cole, Mr. Joseph F. Copp, Dr. William B. Davis, Dr. James R. Dixon, Dr. William E. Duellman, Dr. Harold A. Dundee, Dr. William L. Engels, Mr. George W. Foley, Miss Alice G. C. Grandison, Dr. Jean Guibé, Dr. W. J. Hamilton, Jr., the late Dr. Norman Hartweg, Dr. J. Alan Holman, Dr. Robert F. Inger, Dr. Konrad K. Klemmer, Dr. Arnold G. Kluge, Dr. E. Kramer, Dr. Alan E. Leviton, Dr. Charles H. Lowe, Jr., Dr. John D. Lynch, Mr. Edmond V. Malnate, Mr. Barry Mansell, Mr. Eustorgio Méndez, Dr. John R. Meyer, Dr. Walter G. Moore, Dr. Paul Müller, Mr. Wilfred T. Neill, the Reverend Hermano Nicéforo María, Dr. José Manuel Peláez O., Dr. Günther Peters, the late Dr. James A. Peters, Dr. Harvey Pough, Dr. Joseph Pylka, Dr. Gerald G. Raun, Dr. Neil D. Richmond, Dr. Douglas A. Rossman, Dr. Jánis A. Roze, Dr. Jay M. Savage, Dr. Norman J. Scott, Jr., Dr. Hobart M. Smith, Dr. Philip W. Smith, Mr. A. F. Stimson, Dr. Edward H. Taylor, Dr. Sam R. Telford, Jr., Mr. Robert G. Tuck, Jr., Dr. P. E. Vanzolini, Dr. Greta Vestergren, Mr. Jaime Villa, Dr. Charles F. Walker, Dr. Alexander Wetmore, Dr. Ernest E. Williams, Dr. Larry D. Wilson, Dr. Richard G. Zweifel.

Several persons critically read parts of the manuscript, for which I am grateful to Drs. Charles J. Cole, William E. Duellman, J. Knox Jones, Robert Nunley, Douglas A. Rossman, and Jánis A. Roze. Mr. George W. Foley checked specimens through the identification keys and did much to clarify that section of the manuscript. Miss Janet Lanza handled the computerization of data and rendered other useful assistance.

Dr. Charles M. Bogert made a special effort to obtain *Rhadinaea* in Oaxaca, Mexico, and transported living specimens to New York for my benefit. Drs. William E. Duellman and Norman J. Scott, Jr. obtained living specimens in Costa Rica and carried them alive to my laboratory in Panama City. Such thoughtfulness deserves special thanks.

A part of this work was accomplished while

residing in the Republic of Panama (1964–1967). My association as Visiting Scientist at the Gorgas Memorial Laboratory, in Panama City, has been a rewarding experience owing to the courtesy and helpfulness of the staff. Investigations on the herpetofauna of Panama, in collaboration with Dr. William E. Duellman, were supported by Grant no. GM 12020 from the National Institutes of Health, and, more recently, by Grant no. GB 8139 from the National Science Foundation. A slightly shorter version of the present study, with the same title, was accepted in 1970 as a dissertation in partial satisfaction for requirements of the degree Doctor of Philosophy in Zoology, in the Graduate School of the University of Kansas.

I dedicate this monograph to the memory of James A. Peters (1922–1972), late curator in the National Museum of Natural History. His was a profound influence in Neotropical herpetology.

ABBREVIATIONS

The following abbreviations designate the depositories of specimens to which reference is made:

AMNH, the American Museum of Natural History, New York
ANSP, Academy of Natural Sciences of Philadelphia
BMNH, British Museum (Natural History), London
CAS, California Academy of Sciences, San Francisco
CM, Carnegie Museum, Pittsburgh
CU, Cornell University, Section of Ecology and Systematics, Ithaca
DU, Duke University, Durham, North Carolina
EHT, collection of Edward H. Taylor, Lawrence, Kansas
FMNH, Field Museum of Natural History, Chicago
GML, Gorgas Memorial Laboratory, Panama
IB, Instituto Butantan, São Paulo
JFC, collection of Joseph F. Copp, La Jolla, California
JV, collection of Jaime Villa, Managua
KU, Museum of Natural History, University of Kansas, Lawrence
LACM, Los Angeles County Museum
LSU, Louisiana State University Museum of Zoology, Baton Rouge
MCZ, Museum of Comparative Zoology, Harvard University, Cambridge
MHNS, Museo de Historia Natural La Salle, Caracas
MNHN, Muséum National d'Histoire Naturelle, Paris
NMB, Naturhistorisches Museum, Basel
SMF, Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt am Main
TCWC, Texas Cooperative Wildlife Collection, College Station
TNHC, Texas Natural History Collection, University of Texas, Austin
UAZ, Department of Zoology, University of Arizona, Tucson
UCR, Universidad de Costa Rica, Museo de Zoología, Ciudad Universitaria
UF, Florida State Museum, University of Florida, Gainesville
UIMNH, University of Illinois Museum of Natural History, Urbana
UMMZ, University of Michigan Museum of Zoology, Ann Arbor
USC, University of Southern California, Los Angeles
USNM, National Museum of Natural History, Smithsonian Institution, Washington
ZIUS, Zoologisches Institut der Universität des Saarlandes, Saarbrücken
ZMB, Institut für Spezielle Zoologie und Zoologisches Museum der Humboldt-Universität, Berlin.

SYNOPSIS OF THE GENUS *RHADINAEA*[1] COPE, 1863

THE FOLLOWING SYNONYMY includes strict synonyms, of which there are not many, and also numerous other generic names that have been misapplied to valid and nominal species of *Rhadinaea*. References cited are the first use of a given generic name for a species of *Rhadinaea*, followed by publications that are of major importance because of their generic groupings or geographic coverage. Species having been referred to each of the generic names (except *Rhadinaea*) are listed under their correct epithets, although often it is a synonym that is really applicable. Additional references and information may be found in the synonymies of the indicated species.

The name *Calonotus*, proposed by Jan (1863) for two African snakes, was erroneously placed in the synonymy of *Rhadinaea* by Boulenger (1894b, p. 160) and Romer (1956, p. 581), and is not included below. See Peters and Orejas-Miranda (1970, p. 262) for additional details.

Calamaria, not of Boie: BIBRON, "1855" [1840?], pl. 26. (*R. dumerilii.*)

Urotheca BIBRON, "1843" [184–?], pp. 130, 131 [name a rejected senior synonym of *Rhadinaea*[2] Cope, 1863; also a senior homonym of *Urotheca* Matthew, 1899, p. 40 (Annelida); type species, *Calamaria dumerilii* Bibron (=*Rhadinaea dumerilii*) by monotypy]. BOULENGER, 1894b, pp. 180–184 (part); 1896, p. 636 (part). WERNER, 1929, p. 122 (part). ROZE, 1966, pp. 235–239 (part). (*R. brevirostris, R. decipiens, R. dumerilii, R. flavilata, R. lateristriga, R. multilineata.*)

Coronella, not of Laurenti: GÜNTHER, 1858, pp. 34–42 (part); 1893 (1885–1902), pp. 108–111 (part). (*R. affinis, R. brevirostris, R. decorata, R. fulviceps, R. godmani, R. occipitalis, R. poecilopogon, R. vermiculaticeps.*)

Dromicus, not of Bibron: GÜNTHER, 1858, pp. 126–134 (part); 1893 and 1894 (1885–1902), pp. 111–114 (part). PETERS, 1863, pp. 275–282 (part). GARMAN, 1883, pp. 56–59 (part). BOCOURT, 1890 (1870–1909), pp. 707–715 (part). (*R. affinis, R. brevirostris, R. decorata, R. dumerilii, R. flavilata, R. fulvivittis, R. godmani, R. lachrymans, R. lateristriga, R. laureata, R. multilineata, R. occipitalis, R. omiltemana, R. poecilopogon, R. taeniata* subspp.)

Liophis, not of Wagler: BERTHOLD, 1859, p. 180. BOULENGER, 1894b, pp. 126–143 (part); 1896, p. 634 (part). AMARAL, 1926a (part); 1929a, pp. 87–89 (part); 1929b, pp. 170–175 (part); 1936, pp. 113–116 (part). WERNER, 1929, p. 113 (part). PARKER, 1935, pp. 520–523 (part). PETERS AND OREJAS-MIRANDA, 1970, pp. 179, 180 (part). See also *Cosmiosophis* (subgenus). (*R. affinis, R. brevirostris, R. calligaster, R. decorata, R. flavilata, R. fulviceps, R. fulvivittis, R. gaigeae, R. godmani, R. kinkelini, R. lachrymans, R. lateristriga, R. laureata, R. occipitalis, R. pachyura, R. persimilis, R. poecilopogon, R. pulveriventris, R. serperaster, R. vermiculaticeps.*)

Taeniophis, not of Girard: COPE, 1860a, p. 249. (*R. vermiculaticeps.*)

Diadophis, not of Baird and Girard: COPE, 1860a, p. 250. GARMAN, 1883, pp. 70–73 (part); 1884, p. 29. Bocourt, 1886 (1870–1909), pp. 618–625 (part). (*R. decorata, R. fulvivittis, R. gaigeae.*)

Enicognathus, not of Duméril, Bibron, and Duméril (1854, p. 328 [not of G. R. Gray, 1840, p. 51, Aves]): JAN, 1863, pp. 266–279 (pp. 56–69, in reprint) (part). JAN AND SORDELLI, 1866 (1860–1881), vol. 1, livr. 16, pls. 1–4 (part). See also *Henicognathus* Cope (emendation). (*R. bilineata, R. brevirostris, R. decorata, R. fulvivittis, R. occipitalis, R. persimilis, R. poecilopogon.*)

Cosmiosophis, not of Jan: JAN, 1863, pp. 287, 289 (pp. 77, 79, in reprint) [part: new subgenus of *Liophis*, but type species is *Liophis tricinctus* Jan (=*Pliocercus elapoides*) by subsequent designation *fide* Smith and Taylor, 1945, p. 109]. (*R. lateristriga.*)

Rhadinaea COPE, 1863, pp. 100, 101 (type species, *Taeniophis vermiculaticeps* Cope [=*Rhadinaea vermiculaticeps*] by original designation); 1875a, pp. 138–140; 1886, p. 487; 1895, p. 201; 1900, pp. 754–760. BOULENGER, 1894b, pp. 160–180 (part); 1896, pp. 635, 636 (part). BROWN, 1901, pp. 87, 88. WERNER, 1929, pp. 114–119 (part). DUNN, 1932, pp. 1, 2; 1944, pp. 490–494 (part). STEJNEGER AND BARBOUR, 1933, p. 105; 1939, p. 100; 1943, p. 124.

[1]Gender feminine. Derived from Greek, presumably from the feminine proper name Ῥαδινή (transliterated as *Rhadine*) plus the New Latin, generic-forming suffix -(*a*)*ea* (see p. 19). The name Ῥαδινή is identical with, and evidently derived from, the feminine form of the nominative singular of the adjective ῥαδινός (*rhadinos*). *Rhadinaea* thus carries the connotation of something slender, delicate, or graceful—an appropriate description of most species in this genus.

Cope consistently spelled this name with linked vowels, to show the *ae* diphthong, but ligatures generally are not used in modern nomenclature (International Commission, 1964, appendix E3).

[2]Application will be made to the International Commission on Zoological Nomenclature for conservation of the generic name *Rhadinaea*.

BAILEY, 1940, pp. 1–19. NICÉFORO MARÍA, 1942, pp. 91, 92 (part). SMITH AND TAYLOR, 1945, pp. 115–119. PRADO, 1945a, pp. 74, 75. MERTENS, 1952c, pp. 70–72. TAYLOR, 1951, pp. 111–118; 1954, pp. 736–744. SCHMIDT, 1953, p. 180. PETERS, 1960, pp. 536, 537. STUART, 1963, pp. 112, 113. PETERS AND OREJAS-MIRANDA, 1970, pp. 262–268.

Lygophis, not of Fitzinger: GÜNTHER, 1863, p. 325 (as subgenus of *Dromicus*). COPE, 1868, pp. 132, 133; "1869" [1870?], p. 154. (*R. brevirostris*, *R. lachrymans*, *R. occipitalis*.)

Henicognathus, not of Cope (1868, p. 132, emendation of *Enicognathus* Duméril, Bibron, and Duméril [not of Agassiz, 1846, pp. 138, 178, emendation of *Enicognathus* Gray, 1840, p. 51, Aves]): BOCOURT, 1886 (1870–1909), pp. 625–633 (part). (*R. godmani*, *R. taeniata aemula*.)

Contia, not of Baird and Girard: COPE, 1875a, p. 145. BOULENGER, 1894b, pp. 255–270 (part). AMARAL, 1929b, p. 181. WERNER, 1929, p. 149 (part). (*R. calligaster*, *R. pachyura*.)

Rhadinea GARMAN, 1883, p. 71 (probably an intentional emendation of *Rhadinaea* Cope, 1863, rather than an error; see following text; references are included under *Rhadinaea* throughout.)

Erythrolamprus, not of Wagler: DUGÈS, 1888, p. 181. BOULENGER, 1896, pp. 199–209 (part). (*R. decorata*, *R. guentheri*, *R. lateristriga*, *R. laureata*.)

Ablabes, not of Duméril, Bibron, and Duméril: GÜNTHER, 1893 (1885–1902), pp. 104–106 (part). (*R. decipiens*, *R. serperaster*.)

Tachymenis, not of Wiegmann: GÜNTHER, 1895 (1885–1902), pp. 160–163 (part). (*R. guentheri*, *R. laureata*.)

Taeniophallus COPE, 1895, p. 201, pl. 27, fig. 4 (hemipenis); 1900, p. 734, pl. 25, fig. 4 (hemipenis). [Nominal type species by original designation is *Lygophis nicagus* Cope, but original concept and definition of genus based primarily on material of *Rhadinaea brevirostris* (Peters, 1863), which is here considered to be the type species (pending application to the International Commission on Zoological Nomenclature; see Remarks in account of *R. brevirostris*)].

Leimadophis, not of Fitzinger: BARBOUR, 1914, pp. 338–340 (part). STEJNEGER AND BARBOUR, 1917, p. 86; 1923, p. 96 (*R. flavilata*, *R. lateristriga*.)

Coniophanes, not of Hallowell *in* Cope: AMARAL, 1929b, pp. 216, 217 (part). TAYLOR, 1951, pp. 141–143 (part). (*R. guentheri*, *R. lateristriga*, *R. laureata*.)

Trimetopon, not of Cope: SLEVIN, 1936, p. 79. STUART, 1949, pp. 165–168 (part); 1963, p. 122. PETERS AND OREJAS-MIRANDA, 1970, pp. 308, 309 (part). (*R. hannsteini*, *R. kinkelini*, *R. pilonaorum*, *R. posadasi*.)

Rhadinella SMITH, 1941, p. 7 (type species, *Rhadinella schistosa* Smith [=*Rhadinaea schistosa*] by original designation and monotypy). SMITH AND TAYLOR, 1945, p. 119.

HISTORICAL SUMMARY AND CHOICE OF A GENERIC NAME

The snakes of the genus *Rhadinaea* did not begin to be known to literate man until the middle of the nineteenth century. Their habits and small size, and the montane forest distributions of most, kept them from sight in spite of a remarkable generic distribution of from 35° North latitude to about 35° South. "*Calamaria*" *dumerilii* was named sometime in the 1840s (Bibron, "1855" [1840?]) on the basis of a specimen sent to the Paris Museum from Cuba, where it reputedly had been collected. Actually the specimen must have originated in northwestern South America. Dunn (1944, 1957) seemed to suggest that this specimen might have been part of the collections obtained in Colombia by the famed scientist-explorer Baron Alexander von Humboldt, which still seems a possibility, even though Humboldt did not personally travel in the region from which *dumerilii* is now known. Curiously, the first named species is virtually the last to become known, because, until now, the generic affinities of *dumerilii* have been in doubt and its distribution unmapped.

Next to be named were "*Coronella*" *decorata* and "*Dromicus*" *affinis*, in 1858, and these were followed by "*Liophis*" *lateristriga* in 1859. "*Taeniophis*" *vermiculaticeps*, later to be designated generic type, was the fifth named species, in 1860. Five species were described in 1863, three of them in an important paper by Wilhelm Peters of the Berlin Museum, and, in the same year, Edward Drinker Cope proposed the generic name, *Rhadinaea*. Cope (1861, 1863) confessed to having been much puzzled by his new genus, especially by its relationships to other snakes.

Seventeen additional valid species were named in the period 1865–1900, due mainly to the prodigious activity of Cope, although Albert Günther of the British Museum also added several species and a few were described by other workers of the period. Some of the early named species are beautifully illustrated in Georges Jan and Ferdinand Sordelli's work (1860–1881), although mostly under synonymous epithets in the genus "*Enicognathus*," a name that is correctly applied only to a group of parrots. Perusal of the preceding synonymy will reveal that many other generic assignments were made both before and after the start of the twentieth century. Synopses

of the species, already named and recognized as *Rhadinaea*, were published by Cope in 1875 and 1900, and by George Albert Boulenger (1894b) in the second volume of his monumental catalogue. The use made by Cope of the teeth and absence of vertebral hypapophyses (1868, p. 132; 1875a, p. 138), and, later, his classic studies of hemipenial morphology (1893, 1894b, 1895) allowed him to develop an amazingly modern concept of the genus that he had named, as indicated by the brief synopsis in his posthumously published book (1900, pp. 754, 755). Of 15 species therein listed in *Rhadinaea* by Cope, only two (*melanauchen* and *obtusa*) belong elsewhere, and only one name (*vittata*) seems to be a composite. Boulenger, on the other hand, placed 27 species under *Rhadinaea* in his catalogue (1894b, 1896), more than half of which belong in other genera, mainly in *Liophis*. Under "*Urotheca*," Boulenger included certain long-tailed rhadinaeas with the equally long-tailed, but vividly ringed, snakes that are now called *Pliocercus*. Nonetheless, Boulenger's concise but admirably clear descriptions, and the synonymies, make his work of great value for tracing a name or a concept; the "Catalogue" even remains useful for identifying animals in groups that have not since been revised. Günther fared less well than Boulenger in dealing with the species of *Rhadinaea*, a genus that he refused to recognize as a natural entity. Günther (1885–1902) discussed these snakes under six generic names, and even managed to get each of three members of one species group into a different genus!

Cope died in 1897, Günther in 1914, and, although Boulenger did not retire until 1920, the advance of Neotropical herpetology slowed sharply after the end of the nineteenth century. No valid species of *Rhadinaea* were described from 1898 until 1936, when Joseph R. Slevin named "*Trimetopon*" *posadasi* from Guatemala. Joseph R. Bailey described *Rhadinaea gaigeae* from San Luis Potosí in 1937, and he revised all the Mexican species in 1940, thus causing a renewed interest in the genus; Bailey's key was brought to date in 1945 by Hobart M. Smith and Edward H. Taylor, whose catalogues of Mexican amphibians and reptiles are landmarks in the literature of herpetology. No less than 14 valid species of *Rhadinaea* were named from Middle America in the period 1936–1952, although some of the Guatemalan species were placed in the genus *Trimetopon*, and the monotypic *Rhadinella* was erected for a diminutive Mexican species. For the first time, new species were being named by the collectors themselves—by Smith and Taylor in Mexico, Slevin and, later, Laurence C. Stuart in Guatemala, and Robert Mertens in El Salvador. Specimens were also collected and named from Costa Rica and Panama, by Taylor and Emmett Reid Dunn (working independently), but these specimens represent species in which variation is deceptively complex and I am placing the names in synonymy. An additional valid species was named in 1965, and two others are proposed in the present monograph, in which are recognized 44 species along with one *species inquirenda*. A few species of *Rhadinaea* possibly remain to be discovered and named, and it is conceivable that a few species are still masquerading under other generic names. Any remaining new species are most likely lurking in little-collected highland regions, although this is by no means certain, as one of the new species (*cuneata*) described herein is from low elevations in eastern Mexico. Nonetheless, the descriptive work is mainly done, although much remains to be learned about other aspects of the biology, relationships, and evolution of these snakes. *Rhadinaea flavilata*, of the United States, remains the best known species because of papers published by Edmond V. Malnate in 1939 and by me in 1967.

I have hinted above that the name *Rhadinaea* has not had a smooth course since its proposal a little over a century ago. In part this has been due to lack of a clear understanding of the relationships and variation of the contained species, as exemplified in Günther's work (1885–1902) and, more recently, in that of Afrânio do Amaral (1926a, 1929b), who uncritically transferred many names to *Liophis*, obviously under the influence of Boulenger's catalogue, in which many species of *Liophis* were confused with *Rhadinaea*. Dunn is to be credited for his perception in rescuing part of the genus from synonymy in 1932, and Alcides Prado (1943, 1945b) clearly recognized the relationships of the largely neglected, southeastern Brazilian species. Stuart's (e.g., 1963) use of the generic name *Trimetopon* for some Guatemalan species and Smith's (1941) understandable invention of the name *Rhadinella* for an unusual Mexican species are other modern examples of the confusion that can be blamed on

evolutionary circumstance rather than on any particular author. No one has been complacent or unaware of at least some of the problems; Stuart (1949, p. 165; 1963, p. 8), for example, was at the same time suspicious and practical in his misuse of the name *Trimetopon*, even including species of both "*Trimetopon*" and *Rhadinaea* in a single key in his Guatemalan checklist.

Other problems affecting the stability of Cope's *Rhadinaea* have purely nomenclatural bases. The least of these is the emendation to "*Rhadinea*" by alteration of the diphthong *ae*, of no great concern because this is an "unjustified emendation" and is not to replace the original spelling (International Commission on Zoological Nomenclature, 1964, arts. 32a, 33). Recent writers (e.g., Schmidt, 1953) who used the emendation retained Cope as the author, probably unaware that it is not the original spelling, or under the impression that it is a "justified" correction. According to Jaeger (1944, p. 77), *-ea* is the New Latin ending of generic names taken from personal names ending in *-a*, but some early taxonomists, including Linnaeus, used the suffix for names ending in vowels other than *a*, after first changing the vowel to *a* and then adding the *-ea* (in effect producing a diphthong *ae*+*a*). Since *Rhadinaea* evidently is derived from a proper name (see p. 16n), I presume that the situation discussed by Jaeger is applicable and that early purists, being offended by Cope's derivation, preferred simply to add a final *-a* to any transliterated word ending in another vowel (thus, *Rhadine*+*a* =the emendation *Rhadinea*). To further belabor the subject, I would point out that Cope's derivation was etymologically sound even if not universally acceptable. Although the Greek *'Ραδινή* is transliterated as *Rhadine*, it can legitimately be Latinized as *Rhadina*; the final *η* (e) can be changed to *a* in order to produce closer conformity to normal Latin usage of the nominative singular in the first declension–a procedure now recommended in zoological nomenclature (International Commission, 1964, appendix B, note 6). In any case, I consider the emendation "*Rhadinea*" to be a demonstrably intentional change rather than an incorrect subsequent spelling, which means that it has status in nomenclature as a junior objective synonym, with its own date and author, even though the early emendator doubtless viewed the change only as a needed correction. To the best of my knowledge, the author to be credited with the first change is Samuel Garman (1883, p. 71, and in systematic list; also 1884, p. 29). Arthur Erwin Brown (e.g., 1901, p. 88; 1908, p. 123) was another early writer who adopted the subsequent spelling, and such repeated usage is another indication that the change was intentional.

The only other junior synonyms of *Rhadinaea* are subjective ones, namely *Taeniophallus* Cope, 1895, and *Rhadinella* Smith, 1941. The nominal type species of *Taeniophallus* was placed in the synonymy of "*Rhadinaea*" *undulata* by Boulenger (1894b, p. 174; 1896, p. 635) and under "*Liophis*" *brevirostris* by Parker (1935, p. 522). Actually, however, this is a complex case in that the nominal type species (*Lygophis nicagus* Cope, by original designation) is not congeneric with *Rhadinaea*, and Cope's concept of *Taeniophallus* was based primarily on misidentified *Rhadinaea brevirostris*—which I consider to be the type species pending application to the International Commission on Zoological Nomenclature. Romer (1956, p. 581) placed *Rhadinella* into the synonymy of *Rhadinaea* without comment. I here confirm Romer's action (see discussion under The *godmani* Group), but the name remains available for any worker who might wish to consider the *godmani* group as a separate genus. The relative lack of synonyms (see also below) in such a large genus is related to the fact that these are rather generalized snakes, which authors were able to place in previously named (albeit mostly unrelated) genera.

A significant threat to nomenclatural stability is posed by the generic name *Urotheca* (*ur* from *oura*, the tail, plus connecting vowel plus *theca*, a box, in allusion to a thick tail). This was proposed by Bibron, reputedly in 1843 ("1843" [184–?]), for the species *Calamaria dumerilii* Bibron, "1855" [1840?]. The dating is confused (see discussion under *Rhadinaea dumerilii* in the species accounts), but *Urotheca* is clearly an older name than *Rhadinaea* Cope, 1863. The identity of *Urotheca dumerilii* has remained a mystery until the present monograph, where the specific epithet is combined with the name *Rhadinaea*, and the species is redescribed, and some definite geographic localities are given (the holotype had erroneous locality data). Boulenger (1894b, pp. 180–184) had expanded the concept of *Urotheca* to include, in addition to *dumerilii*, the closely related *lateristriga* and several species of

distantly related coral snake mimics, which are properly grouped in the genus *Pliocercus* Cope, 1860. *Urotheca* was used rather consistently as a senior synonym of *Pliocercus* until 1939, when Dunn and Bailey returned to Cope's original concept of *Pliocercus*; Dunn and Bailey mentioned that the holotype of *dumerilii* had been examined for them by Roger Conant, in Paris, but that they were unable to place it with any recognized species. Dunn later (1944, p. 491) commented on the situation in more detail: "The name *Urotheca* . . . has been used for a mixture of the snakes of the genera *Rhadinaea* and *Pliocercus*. I prefer to use names based on well established type species, and the identity of *U. dumerilii* . . . is not established at all. The snake has never again been reported, and the type seems not to have been examined by anyone well aquainted with Neotropical snakes. Its status is open to three interpretations . . ." Dunn's (*loc. cit.*) second of three possibilities now proves to have been correct, namely: "The species is not Cuban and awaits rediscovery, in which case it may very likely be a species of the later described genus *Rhadinaea*." In a posthumously published paper (1957), Dunn digressed from his main subject (frogs) and noted that, "I now feel pretty sure that *Urotheca dumerilii* Bibron 1843 is the proper name for *Rhadinaea pachyura fulviceps* Cope 1886, and that all *Rhadinaea* should be *Urotheca*." No evidence was presented, and it is not even certain that Dunn had intended his statement for publication (see editorial footnote therein), but Jánis A. Roze (1958) described a new species in the genus *Urotheca* and stated that, "As to the question of *Urotheca* vs. *Rhadinaea*, there can be little doubt, as pointed out by Dunn, 1957, that the earlier name should be used." Roze thereafter (1959, 1964, 1966) used *Urotheca* for *Rhadinaea*, and noted (1964) that he had examined the holotype of *U. dumerilii*. But other authors (Peters, 1960, 1963, p. 64; Peters and Orejas-Miranda, 1970; Stuart, 1963, p. 112; Myers, 1967, pp. 48, 49) refused to abandon *Rhadinaea*, at least not without published documentation as to the identity of *U. dumerilii*. Actually, Roze proves to have been quite correct that *Urotheca* is the proper name under the law of priority, but there was no way that he could have been aware of the extent of the genus and the number of species that would have to be associated with still another generic name. The interests of stability will not, in my opinion, be served by switching names at this late date. Too much confusion has surrounded *Urotheca*, which most frequently has been incorrectly applied to the species of *Pliocercus*. Except for Dunn's suggestive remarks, no author has used *Urotheca* in the same sense as Cope's concept of *Rhadinaea*, not even Roze. The new species (*U. williamsi*) that led Roze to formally resurrect *Urotheca* is not congeneric with *Taeniophis vermiculaticeps*, type species of *Rhadinaea*, as shown by reexamination of the hemipenis (unpubl. data); Roze correctly applied the name *Urotheca* only to the species *multilineata* and *brevirostris*. The International Commission on Zoological Nomenclature will be requested to suppress the name *Urotheca* for the purposes of priority but not of homonymy.

FAMILY STATUS

The genus *Rhadinaea* was placed in the family Colubridae by all authors except Underwood (1967a, p. 127), who put it in the Natricidae after elevating that group from subfamilial status. The family Natricidae, in Underwood's scheme (p. 149), is inserted between the "Homalopsidae" and the greatly reduced Colubridae. Underwood restricted the latter group to those species in which the hemipenes are asymmetrical; while I would not disagree with the usefulness of this character, it is a matter of opinion whether it is sufficient grounds on which to establish a family. The other two "families" mentioned above include species in which the hemipenes are symmetrical. The Natricidae is said to differ primarily because of the simplex retina (lacking rod cells), compared with the duplex retina of the Homalopsidae. It is implied that the Natricidae also differs from the Homalopsidae in a tendency toward loss of a "frontal step" on the parasphenoid bone and the correlated appearance of a "frontal crest," a character that is at least partly associated with the size of the orbit according to Underwood (1967a, p. 14; 1967b, p. 167).

The question of family rank for the natricines aside, I think that Underwood has erred in his association of *Rhadinaea* and assorted genera of other New World snakes with the Natricinae of various authors. Underwood's system, for example, results in the separation of *Rhadinaea* from *Leptodeira*, which he has placed in the subfamily Boiginae of the Homalopsidae, although

the hemipenis of species of *Leptodeira* is remarkably similar to that of some species of *Rhadinaea*. Both of these genera belong to a group of Neotropical snakes informally defined by Dowling (1969, p. 5) as having "a single, capitate, spinose, and calyculate hemipenis with a simple or apically bifurcate sulcus ('dipsadines')." There is somewhat more variation than indicated in this brief definition (see Myers, 1973) but, nonetheless, the hemipenial similarity is so great that I cannot accept an arrangement that places members of the group into three separate families (Dipsadidae, Homalopsidae, and Natricidae). The hemipenial similarities just referred to are not well elaborated in the literature and understandably were not considered by Underwood, who might, however, have profitably taken into account the ideas and embryological data presented by Clark in 1945.

Concerning Underwood's emphasis on retinal condition as a criterion of relationship, the alternate possibility must be considered that a number of stocks have independently lost rod cells upon becoming diurnal, which seems plausible considering the adaptability of the serpent eye. In any case, the retina has not yet been examined in species of *Rhadinaea* or in many other genera.[1] I do not know why Underwood placed *Rhadinaea* with the natricines. Conceivably he did so on the basis of the parasphenoid characters of some other genus supposed to be allied with *Rhadinaea*, but the parasphenoid does not seem to be a reliable character for this purpose. For example, Underwood (1967a) placed *Alsophis* with the natricines, but his illustration (fig. 3Biii) of the parasphenoid of *A. sibonius* shows a small frontal step rather than the crest that is said (p. 14) to be "characteristic" of the Natricidae. Underwood's classification is thought-provoking, but I do not believe his partitioning of the higher snakes to be natural. Consequently, I still regard *Rhadinaea* as belonging to the family Colubridae (*sensu lato*), and not as a member of the subfamily Natricinae (*sensu quivis*!).

Rhadinaea has been placed in various subfamilies. Cope put it into the Coronellinae of the Colubridae in 1886, in the first of a pioneering series of papers on the classification of snakes, and later (1893, 1894b) moved the genus to the Xenodontinae, which he recognized as part of a family Xenodontidae. Cope (1895, 1900) then put the Xenodontinae into the colubrids but subtracted out the majority of the genera, including *Rhadinaea*, as the Dromicinae. Boulenger (1894b) considered *Rhadinaea* as a member of the Colubrinae under the Colubridae, series Aglypha. Dunn (1928) somewhat modified Cope's classification and reassociated *Rhadinaea* and other genera with the Xenodontinae, except that Dunn used the name Ophiinae (in the belief that the generic name *Ophis* should replace *Xenodon*). Dunn (1928, p. 19) recognized the close relationship of the aglyphous *Rhadinaea* and the opisthoglyphous *Coniophanes*; the nature of the posterior maxillary teeth had caused these genera to be separated in previous systems, although near the end of his career Cope (1895, p. 198) had almost concluded that the presence or absence of grooved teeth is of secondary importance. *Rhadinaea* would fall into the tribe Xenodontini of the Colubrinae in Dowling's (1967) tentative, working classification.

None of the preceding classifications has been truly satisfactory, although it has been at least convenient to consider *Rhadinaea* and its allies as "xenodontines." A germ of a more natural arrangement is possibly contained in Dowling's (1969) suggestion that most South American colubrids can be sorted into four undefined groups based on hemipenial characters (see also Myers, 1973).

DEFINITION AND DIAGNOSIS OF THE GENUS

A better concept of *Rhadinaea* will be gained from the generic description following this section than from the abbreviated definition. *Rhadinaea* is difficult to define briefly because of a combination of interspecific and intraspecific variability in its contained species. A differential diagnosis is even more difficult to draw because of the added factor that equivalent knowledge of structure and variation is lacking for many other groups that should be compared. Inclusion of a genus in the diagnosis following the definition does not necessarily indicate close relationship with *Rhadinaea*, only the possibility that contained

[1]Underwood (1967a) helpfully mentioned the species and characters utilized for each in the index of his book. The specimen of *Rhadinaea* studied by him is listed as "*dorsata*," but this is a *lapsus* for *decorata* as is evident from Underwood's unpublished list of specimens (see Underwood, 1967a, p. 6). I thank Ernest E. Williams for providing a copy of the list.

species have been, or might be, confused with rhadinaeas. The diagnosis certainly will prove less than adequate as new information is gathered on the various groups; it is intended only as a temporary guide.

Certain species that have been referred to *Rhadinaea* by other authors actually are not assignable to any genus as presently defined. Three of these species—*genimaculata* Boettger (=*joberti* Sauvage), *obtusus* Cope, and *steinbachi* Boulenger—are under investigation and can conveniently (but improperly) be included in the genus *Liophis*, where they also have been placed by various authors. Also in this category is "*Liophis*" *undulatus* and its several relatives, which comprise an undescribed genus according to Joseph R. Bailey (personal commun.), who has data on the group. None of the above-named species is mentioned in the diagnosis.

DEFINITION: Small to medium-sized, terrestrial colubrids allied to *Taeniophis vermiculaticeps* Cope. Hemipenes symmetrical, distally calyculate, usually capitate, single or slightly bilobate (lobes entirely calyculate and contained in single capitulum), spinose; sulcus spermaticus bifurcate. Posterior vertebral hypapophyses absent. Pupil round. Enlarged rear maxillary teeth present, but rarely grooved. Full complement of colubrid head plates, most bearing minute scale organs (tubercles). Dorsal scales in 15, 17 (usually), 19, or 21 rows, without posterior reduction in most species, rarely with keels or apical pits; anal ridges present or not. Usually brown with darker lines or stripes extending length of body. Head and neck usually with distinctive markings (e.g., pale temporal and canthal lines, ocelli, nuchal spots or collar, dark stripe through eye, or dark-edged pale stripe from eye to corner of mouth).

DIAGNOSIS: *Coniophanes*, *Conophis*, and *Tachymenis* differ in having combination of grooved fangs and posterior scale-row reduction. *Leimadophis*, *Liophis*, *Lygophis* (*sensu stricto*), and *Umbrivaga* differ absolutely in presence of apical discs and absence of calyces on hemipenis, and in general tendencies toward different color patterns (e.g., crossbands, anterior blotches and posterior stripes, dark-checkered venters). *Alsophis* and *Saphenophis* differ in having lobes of hemipenis noncapitate or semicapitate, lobes being not entirely calyculate and not confined within single capitulum, and in tendency toward larger body size and different color patterns. *Trimetopon* (*sensu stricto*, Myers, MS) differs in tendency toward *Tantilla*-like habitus and smaller size (maximum known total length less than 300 mm. in all *Trimetopon* but only four *Rhadinaea*), tendency toward loss of calyces and elimination of capitation of hemipenis, fewer maxillary teeth (less than 14 in all *Trimetopon* but only four *Rhadinaea*), and in general tendency toward fewer dorsal scale rows and fusion of prefrontals or other head plates. *Amastridium* differs in having a projected supraocular region partly concealing top of eye and in presence of hypapophyses on posterior vertebrae. South American *Tantilla*, sometimes confused with *Rhadinaea*, are readily distinguishable by combination of 15 scale rows, no loreal, and grooved fangs. West Indian xenodontines (Maglio, 1970) formerly in *Dromicus* cannot be readily diagnosed from *Rhadinaea* at this time, but they differ in various details, especially of the hemipenis (including more deeply forked sulcus, *Alsophis*-like structure of some [see above], apical projections of others).

DESCRIPTION OF THE GENUS

The genus *Rhadinaea* is comprised of small to medium-sized snakes (maximum total lengths from under 300 mm. to about 900 mm., usually 400–600 mm.), of relatively slender proportions, with head slightly distinct from the neck, and with short to long tails (14–48 percent of total length). They are mostly some shade of brown above, some species being nearly unicolor but most having black or dark brown lines or stripes that extend the length of the body, fading or not on the tail. Several species are black with whitish lines; individuals of two species (*calligaster* and *decipiens*) sometimes have a greenish hue; and one species (*occipitalis*) is highly divergent in being spotted anteriorly. Venters are white, pale greenish, yellow, orange, or red in life, usually unmarked or with irregular dark speckling, but with median black half-moons in *calligaster* and some specimens of *decipiens*. Nuchal spots or a pale collar, or ocelli on neck or head, are present in some species. A pair of close-set, white parietal dots frequently is present. Many species have a conspicuous line or other pale postocular marking in the temporal region, and some have a pale line on the canthus rostralis as well. Many species have a brown or black stripe passing along the side of the head and through the eye, and this is sometimes confluent with a lateral

body stripe. Some species have a short, dark-edged pale stripe that extends obliquely from the eye to the corner of the mouth. The supralabials and infralabials are basically pale, being immaculate or variably marked with dark pigmentation. Specimens frequently lose the stratum corneum after preservation and then may have a grayish ground color.

All species have a more or less "normal" colubrid pattern of head plates. The rostral is inclined slightly forward and is narrowly visible from above, and is about one and a half to two times as wide as high. There is a pair of internasals and a pair of larger prefrontals, each of the latter being in contact with its fellow, an internasal, nasal, loreal, preocular, and the frontal. The canthus rostralis is rounded. The frontal plate is relatively large and pentagonal or slightly hexagonal (with a small anteromedial apex in the latter case). On each side of the frontal is a supraocular that invariably is longer than wide and slightly narrowed in front; the supraocular does not form a projecting shelf over the eye. There is a pair of large parietal plates that are about one and one-third to twice as long as their greatest width. The nasal plate is longer than high and usually has a vertical groove above and/or below the naris; occasionally the grooves are sufficiently deep to term the plate as divided or semidivided. There is a variably shaped loreal that rarely is fused with the preocular or, even more rarely, absent. There is one large preocular or two smaller ones, and many species frequently have a small subpreocular inserted between the corners of two supralabials at the lower front edge of the orbit. There are two postoculars or occasionally one. There is one primary temporal (rarely two) and basically one or two secondaries (i.e., 1+1 or 1+2), although in many species the plates in the second row are subject to frequent fragmentation, or fusion. Usually there are eight supralabials or seven in a few species; other numbers that occur are only intraspecific deviations from the norms. Two supralabials normally border the eye, or three in a few species, usually the third and fourth (if there are seven supralabials) fourth and fifth (if eight), or third to fifth. Infralabials are normally eight to 10, and the members of the first pair almost invariably are separated by the triangular mental. The first four or five infralabials touch the anterior genials except in aberrant specimens, and the fourth and fifth or fifth and sixth are in contact with the posterior genials. The relative sizes of the anterior and posterior pairs of genials are interspecifically and intraspecifically variable, but the suture between the posterior plates is probably always shorter than the anterior intergenial suture. There are minute tubercles (not readily apparent on all specimens), on most or all of the head plates, but usually these are most concentrated on the anterior plates; one species (*brevirostris*) has unpigmented "pits" on the preoculars and postoculars and the intervening supralabials. The eye usually is of moderate size but varies from small to large in relation to the size of the head and length of the muzzle, into which the diameter of the eye goes from one to three times. The pupil is round.

Most species have 17 dorsal scale rows, several have 19 rows, and one each has 15 rows and 21 rows. Almost all species have the same number of rows throughout the body, although *brevirostris* has 17–17–15 and some specimens of *occipitalis* have 15–15–13, and reduction occasionally occurs in species with 19 and 21 scale rows. Reduction, when occurring, involves lateral rows in the *brevirostris* group, and either lateral or paravertebral rows in the *godmani* group. Anal (supracloacal) ridges are present in some species, absent in others. The body scales are smooth (sometimes weakly striated, especially posteriorly) in all species except *decorata*, many specimens of which have weak keels, especially posteriorly. Unpigmented apical "pits" are absent in most species, but some individuals of *brevirostris* and *decorata* have paired or single pits on some of the neck scales. Ventrolateral edges of the body are rounded, not angular. There are 110–197 ventral plates, a divided anal plate (rarely and aberrantly single), and 31–137 pairs of subcaudal plates. The tail is slender and gradually tapering in most species, but in the *lateristriga* group it is conspicuously thick for much of its length. The tail terminates in a conical, slender spine, except that in some species part of the tail has been lost in a high percentage of specimens.

There are teeth on the maxillary, palatine, pterygoid, and dentary bones. There are two distinctive kinds of maxillary dentition: The *godmani* group is characterized by an evidently primitive type in which the ultimate tooth is in line with those anterior, not offset laterad. Approximately the last two to five teeth are

noticeably enlarged and heavier than the anterior teeth, and there is never a conspicuous diastema isolating the last two. A very short gap may be present, but it is just as likely to occur before the antepenultimate tooth as in front of the penultimate, or there may be a tiny gap in both places. All the other species groups have a more advanced dentitional pattern, in which the ultimate tooth is offset laterad from a plane connecting the more anterior teeth. The last two teeth ("fangs") usually are noticeably and abruptly larger than the others, which are subequal or gradually increasing in size from front to rear. The last two teeth often are isolated from the others by a conspicuous diastema, the presence or absence of which is correlated in some species with the total number of teeth present. There are 11–23 maxillary teeth in the *godmani* group, and 10+2–24+2 in all the other groups combined. The teeth are not grooved except in some individuals of one species (*guentheri*), in which shallow grooves are present on the anterior faces of the last two teeth; these grooves, when present, do not extend to the tips of the fangs, the distal parts of which are laterally compressed. At least some species have a weak venom that flows to the rear teeth from the Duvernoy's (parotid) glands (see p. 28).

The posterior precaudal vertebrae lack hypapophyses.

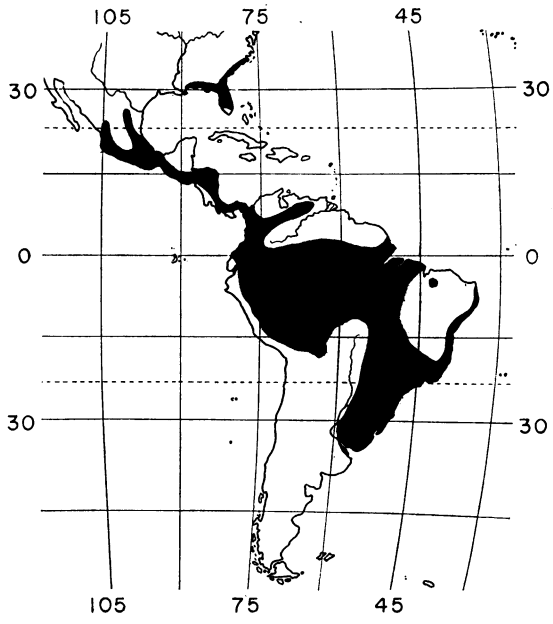
The distal part of the hemipenis is calyculate and, in most species, capitate. The organ is single or, in some species, slightly and primitively bilobate, in which case both lobes are completely calyculate and combined within a single capitulum. The calyces are adorned with soft papillae which, in most species, are replaced by spinules on the asulcate side and periphery of the capitulum. There is never any indication of an apical disc or awn. The midsection of the hemipenis is variably, but in all cases, spinose. The spines are curved except in *R. schistosa* and in the *vermiculaticeps* group, in which the spines are nearly straight. The base is nude except for minute spinules, which may be uniformly scattered or distinctly clustered. The sulcus spermaticus is bifurcate, forking well above the base, in or slightly below the calyculate area and the branches extending or not to the tip of the organ. The greatest length of the sulcus lies on the lateral walls of the retracted hemipenes which, when everted, are seen to be mirror images (i.e., symmetrical, but this is not documented for many species).

The species of *Rhadinaea* are terrestrial snakes and are principally diurnal. Some are quite secretive and perhaps even semifossorial, but most are probably active foragers of the forest floor, where they are predators on small amphibians (including eggs) and lizards. All are oviparous insofar as known.

DISTRIBUTION OF THE GENUS

Rhadinaea is essentially a continental, Neotropical genus, with a large majority of its species occurring between the tropics of Cancer and Capricorn. Extralimital species included, the genus extends approximately to latitude 35° North (Cape Hatteras, North Carolina) and 35° South (east-central Argentina). The elevational range is from sea level to about 3200 meters (10,500 feet). A few species have reached offshore islands along the Atlantic coast, but this is of rare occurrence.

Rhadinaea mainly inhabits humid forested regions, except possibly in the extreme southern part of the range. Thus, the genus is unrepresented in the area between the Mississippi River and the terminus of the Sierra Madre Oriental in northeastern Mexico, or on most of the Mexican Plateau, Yucatan Peninsula, parts of



MAP 1. Distribution of the genus *Rhadinaea* Cope.

the Pacific side of Central America, open regions on both sides of the Amazon Basin, or in the coastal desert of western South America.

The following list shows the species actually known from each country. The countries are given in geographic order from north to south, and then west to east.

Unites States (one sp.): *flavilata*.

Mexico (20 spp.): *bogertorum, cuneata, decorata, forbesi, fulvivittis, gaigeae, godmani, hannsteini, hesperia, hempsteadae, lachrymans, laureata, macdougalli, marcellae, montana, myersi, omiltemana, quinquelineata, schistosa, taeniata*.

British Honduras: None known.

Guatemala (eight spp.): *decorata, godmani, hannsteini, hempsteadae, kinkelini, lachrymans, pilonaorum, posadasi*.

El Salvador (five spp.): *godmani, kinkelini, montecristi, pilonaorum, pinicola*.

Honduras (two spp.): *godmani, kinkelini*.

Nicaragua (three spp.): *decorata, guentheri, kinkelini*.

Costa Rica (eight or nine spp.): *calligaster, decipiens, decorata, godmani, guentheri, pachyura, pulveriventris, serperaster*, species inquirenda (*lateristriga* group).

Panama (10 spp.): *calligaster, decipiens, decorata, fulviceps, godmani, guentheri, pachyura, pulveriventris, sargenti, vermiculaticeps*.

Colombia (five spp.): *brevirostris, decipiens, dumerilii, fulviceps, lateristriga*.

Venezuela (one sp.): *multilineata*.

The Guianas (one sp.): *brevirostris* (French Guiana).

Ecuador (four or five spp.): *brevirostris, decorata, fulviceps, lateristriga, ?decipiens*.

Peru (three spp.): *brevirostris, lateristriga, occipitalis*.

Brazil (six spp.): *affinis, bilineata, brevirostris, occipitalis, persimilis, poecilopogon*.

Bolivia (two spp.): *brevirostris, occipitalis*.

Paraguay (two spp.): *occipitalis, poecilopogon*.

Argentina (two spp.): *occipitalis, poecilopogon*.

Uruguay (two spp.): *occipitalis, poecilopogon*.

TAXONOMIC CHARACTERS AND METHODOLOGY

IT IS HERE RECOGNIZED, although not belabored in the following discussion, that caution must be exercised when comparing taxonomic data from juvenile and adult snakes, inasmuch as natural selection frequently seems to result in significant differences in the extent of variation (particularly in scutellation) in different age groups (Dunn, 1942a; Inger, 1943). This has not been a serious problem in the present study because juveniles are infrequent in collections of *Rhadinaea* and comprise a significant part of the samples of only a few uncommon species. If an important specimen happens to be a juvenile it is indicated in the species accounts. Particular care has been taken in a few cases involving specimens hatched in captivity when it seemed probable that unusual variations were the result of unnatural environmental influences on the developing embryos (e.g., see Remarks under *R. godmani*). I have previously mentioned the difficulty in distinguishing between heritable and nonheritable variation in *Rhadinaea* (Myers, 1967, pp. 68, 90, 91).

COLOR AND PATTERN

Color and, especially, color pattern are extremely important in the taxonomy of *Rhadinaea*, both in distinguishing species and in establishing relationships. Indeed, once some idea has been gained of intraspecific variation, color pattern offers the most generally reliable method of identifying species because no two forms have identical patterns and many are strikingly different. There are exceptions, of course. *Rhadinaea serperaster* and specimens from the southern population of *R. godmani*, for example, are more easily identified by counting scale rows than by consideration of minor pattern differences. All species have relatively limited variation in at least some key aspects of pattern, and in many the entire pattern is rather stable. Geographic variation is considerable in a few species with large ranges, as for example *R. hesperia* and especially *R. taeniata*, but is relatively slight in some other wide-ranging species, as for example in the *flavilata* group. *Rhadinaea calligaster*, of uncertain relationships, has a remarkably variable body pattern, and the variation is largely uncorrelated with geography. I have not detected any sexual dichromatism in the genus. Ontogenetic variation in pattern is generally minor, although it seems that the young of *R. fulviceps* and *R. pachyura* have a pale collar that disappears with age (more information is needed on these species); not many young rhadinaeas are in collections, but they frequently seem to be somewhat brighter than adults and to have more sharply contrasted patterns. Most species have a striped pattern, although a few have virtually unicolored bodies and one (*occipitalis*) has blotches anteriorly; a few small species in the *godmani* group have pale dashes in the center of dark scales. The usual stripes tend to be distinct for the length of the body, fading or not on the tail, and to have straight edges, although in *R. brevirostris* the edges tend to be wavy or serrated, or both. Many species have the dark dorsal coloring extending onto the tips of the ventrals where it may form either a serrated or straight edge; the nature of the ventrolateral demarcation usually is more of an intraspecific rather than interspecific variation.

Head patterns tend to be distinctive. Most species of the *godmani* group have a dark-edged, pale postocular bar extending obliquely from the eye to the corner of the mouth. The conspicuous feature of head pattern in the *calligaster* group is the boldly black-margined supralabials. A few species in groups other than the *godmani* and *calligaster* assemblages also tend to have distinctive patterns below the level of the eyes, but mostly the emphasis is on a lateral dark stripe through the eye and a well-defined temporal (and sometimes canthal) line, ocellus, or other dorsolaterally placed marking. A few have conspicuous, pale vermiculations atop the head, and a pair of close-set, pale parietal dots is widespread in the genus. Other characteristic markings include pale ocelli, nuchal spots, or collar on the neck. Sometimes a collar is broken by an anterior extension of a vertebral dark line, which in the *godmani* group also tends to extend forward through a pale tan or yellowish blotch on the frontal plate.

Hue itself is less important than pattern, mainly because most species are basically brown or black, but also because few collectors bother

recording the sometimes bright colors of labials, venter, iris, and tongue, and comparative data are thus available only for a minority of the species. Venters are white, pale greenish, yellow, orange, or red in life, but they invariably turn white or yellowish after a fairly short time in preservative. Also, no particular reliance should be placed on isolated descriptions of hue, because there is geographic variation in at least a few cases. Ventral coloration may also be subject to ontogenetic changes, as in *R. calligaster*.

Color and pattern similarities need not always indicate relationship within the genus *Rhadinaea*. Even the unusual occurrence of an identical green hue on the dorsums of some specimens of two species is not sufficient to override major structural differences, not even when the unique green coloring is correlated with the presence of equally unique midventral dark markings (see discussion under The *calligaster* Group). If uncritical reliance were placed on color and pattern, then *Rhadinaea schistosa* and *R. taeniata aemula* might be placed in the genera *Tantilla* and *Coniophanes*, respectively. But the generalization that color and pattern is of utmost importance in the taxonomy of *Rhadinaea* is not invalidated by these interesting exceptions to the rule.

Most species have a linear pattern of stripes and lines. As intended herein, a line is no wider than the equivalent width of a dorsal scale row, usually less; a stripe is at least the equivalent of a dorsal scale row in width. But I have been unable to maintain complete consistency in following these arbitrary definitions. The adjectives "primary" and "secondary" are sometimes applied to bold and fainter stripes, respectively, in the same species, but these are descriptive terms and I imply nothing phylogenetic by their use. The illustrations of midbody patterns are my own pencil shadings on generalized, printed scale outlines. Although based on the individual specimens cited, these illustrations are somewhat diagrammatic. They are intended to be rather closer to the pattern as it appears to the naked eye than as it looks under magnification, although all were drawn with the aid of a dissecting microscope. There is not often such a thing in *Rhadinaea* as a uniformly pigmented dorsal scale, but rather one sees under magnification a variegation and clumping of chromatophores on a paler ground, or irregular pale areas on a solid ground. Although these minute patterns are themselves a reflection of the genotype, I have tried to remember that, "You can look at a thing so close that it ceases to be itself" (attributed to Walter Murch).

MAXILLARY DENTITION

The nature of the maxillary teeth is of great importance in snake taxonomy. Interspecific and even generic differences are also to be found in the palatine, pterygoid, and dentary dentition, but generally these teeth are less likely to be modified and were not utilized in the present study, mainly because of the time it would have taken to obtain significant amounts of data for so many species. I once thought that the maxilla had to be excised to be properly studied, but actually it can easily be examined *in situ* by the following method: The maxilla is first completely loosened from the upper lip with the fine point of forceps or stiff teasing needle (scalpel for large specimens), and the lip is propped up against the head with two pins anchored behind the maxilla. With the lip out of the way, the soft tissue concealing teeth and bone can be removed by alternate use of watchmaker forceps and a fine teasing needle (I use an entomological minuten pin in a wooden handle). It is helpful, but not absolutely necessary, to dry the exposed bone with a jet of compressed air. The teeth and frequently intervening sockets (the teeth are usually shed alternately) can now be counted, using the fine teasing needle to mark place, to probe possible sockets, and to feel for grooves on the posterior teeth. Care must be taken not to overlook the anteriormost tooth or socket, the detection of which often requires use of the fine probe and readjustment of the specimen under the microscope. The first tooth tends to spring from the very tip of the maxilla, and its empty socket may be hard to see because of the anterior curvature of the bone. I have thought it advisable to explain this simple technique because, judging from museum specimens, many workers seem unable to examine maxillary teeth without first slitting the angle of the jaws, a completely unnecessary mutilation that may make it difficult or impossible to determine the number of labial plates.

Almost all species of *Rhadinaea* have the last two or several teeth noticeably and rather abruptly enlarged in comparison with the more anterior ones, which are nearly uniform ("subequal") in size or which increase in length only

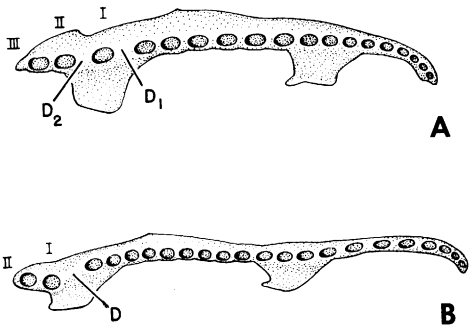


FIG. 1. Maxillae of *Rhadinaea* spp., ventral aspect, showing positioning of tooth sockets. A. *R. lachrymans*, USNM 110369. B. *R. decorata*, KU 80239.

Abbreviations: D, diastema; I–III, enlarged, posterior teeth.

Note that in A the last two sockets are approximately on the same plane with anterior sockets, whereas in B the last two sockets are not both in linear sequence with more anterior ones. In the case of maxillae of the second type, the last socket is said to be offset laterad (although sometimes it would be equally proper, as in this case, to say that the penultimate socket is offset mediad).

gradually in an anterior to posterior direction. The enlarged teeth presumably are a specialization that facilitates entry of a weak venom into the prey animal from an overlying Duvernoy's (parotid) gland. Actual presence of venom, however, has been demonstrated only for *R. flavilata* (*q.v.*), and it is interesting that this species seems to make full use of its venom and enlarged teeth only on its larger and more difficult to manage prey (Myers, 1967, p. 66). Because of the existence of venom in *R. flavilata*, the presence of weak grooves on the rear teeth of some specimens of *R. guentheri* (and all species of the related *Coniophanes*), and the enlarged teeth generally, it seems a fair assumption that many, if not all, species of *Rhadinaea* have venom.

The rear teeth are modified in two fundamentally different ways in *Rhadinaea*. The *godmani* group has what I consider the primitive arrangement. Approximately the last three to five teeth are noticeably enlarged and heavier than the others (fig. 2A); less commonly there are only two visibly enlarged teeth. The enlarged

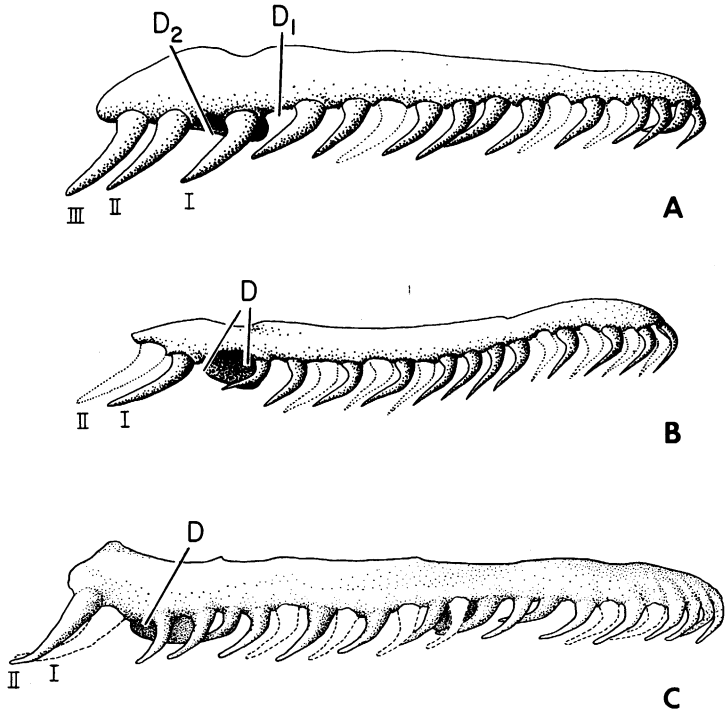


FIG. 2. Maxillae of *Rhadinaea* spp., lateral aspect. × 12.8. A. *R. hempsteadae*, JFC 66-60. B. *R. vermiculaticeps*, FMNH 109721. C. *R. taeniata*, UMMZ 125731.

Abbreviations: D, diastema; I–III, enlarged, posterior teeth.

teeth lie on the same plane, none being set off to one side of the others (fig. 1A). There is never a broad gap, or diastema, between any of the teeth and frequently there is no diastema at all. A very short diastema may be present, but it is just as likely to occur anterior to the antepenultimate tooth as in front of the penultimate, or there is often a gap in both places (fig. 2A).

All the other species groups are characterized by a dental arrangement in which there are only two enlarged teeth (fig. 2B–C), the posteriormost of which is offset to the side (laterad) as shown in figure 1B. A broad (fig. 2B) to short (fig. 2C) diastema is usually present, but not always. Addition or loss of prediastemal teeth in a species seems most often to be the cause of variability in the size of the diastema. The presence of a diastema presumably allows the posterior fangs to be more efficiently embedded in the prey, and there are probably counterbalancing selective forces for the diastema and the number of prediastemal teeth, as the latter serve the important function of holding the prey until the fangs can be used. I use the word "fang" in its common connotation of a large piercing tooth. The usually ungrooved fangs of *Rhadinaea* seem to serve the same function as the grooved or tubular teeth for which some herpetologists reserve the word.

The maxillary formula for most species is given as the number of "prediastemal" teeth plus two fangs (e.g., 17+2); even if a diastema is absent there are obviously only two specialized teeth, except in the *godmani* group. The formula for species in this group is given as a single number, the total, because of the intraspecific variation in the position of the diastema and in the number of "fangs."

A table showing the intraspecific and interspecific variation in number of teeth is given for each species group. Geographic variation in number of teeth is separately demonstrated in some cases. Comparison of the tabular data is sometimes useful in indicating relationships or identifying species. Some of the data from the species group tables are summarized in table 1 as a guide in assessing taxonomic significance in tooth count differences. As might be expected, the groups with the largest number of species tend to show the greatest range of variation, because of adaptive radiation within the groups; but the *lateristriga* group, the third largest, shows limited variation contrasted to other, smaller groups. The difference between extreme counts for the single most variable species in each group is two to eight, but only two species show a difference as high as seven or eight. One is a geographically variable species (*R. decorata*) whose regional differences are in the magnitude of three and four, and the other (*R. affinis*) shows yet unexplained variation in the length and thickness of the teeth. Some of the less variable species are also influenced by geographic variation. Judged from the data, it seems a justified

TABLE 1

DEGREE OF VARIATION IN NUMBER OF MAXILLARY TEETH IN THE SPECIES GROUPS OF *Rhadinaea*

Species Group	No. of Species	No. of Maxillae[a]	Difference Between Extreme Counts	
			Most Variable Species	Entire Group
brevirostris	6	66	8[b]	10
calligaster	1	19	4	4
decorata	11	180	7[c]	10
flavilata	2	29	2	5
godmani	11	99	4	12
lateristriga	8	64	3	6
taeniata	3	54	5	5
vermiculaticeps	3	9	2	2

[a]A single maxilla from each specimen.

[b]*Rhadinaea affinis*, which also shows unusual variation in whether the teeth are short and thick or relatively longer and more slender. In other species of the group, the maximum difference between counts is only 4.

[c]*Rhadinaea decorata*, a geographically variable species whose regional differences are only in the magnitude of 3 and 4.

assumption that variation in number of maxillary teeth is relatively slight, especially in geographically limited areas, and that differences of just a few teeth may be ascribed taxonomic importance, even when data are few. For example, *Rhadinaea bogertorum* and *R. macdougalli* are rather similar appearing snakes restricted to seemingly allopatric ranges in the highlands of Oaxaca. They are known only from a total of five specimens and there is a difference of four between a single count for *bogertorum* and the maximum known number of prediastemal teeth in *macdougalli*. It is conceivable that the counts will eventually be found to overlap, but, if one wanted to argue that *macdougalli* and *bogertorum* were really the same species, it would be necessary to admit that this species had a total range of from at least 14 to 20 prediastemal teeth. This is not suggested to be an impossibility, but it certainly would not fit the generic pattern in which such a range in counts is seen only in the peculiar *R. affinis* and in a few species of large geographic distribution.

HEMIPENIS

The paired, eversible copulatory organs are among the most important characters in snake taxonomy, although their potential has been incompletely exploited. Within the "xenodontines," at least, the hemipenis frequently seems to provide proof of relationship when divergence and convergence have obscured the usefulness of scutellation, color pattern, and dentition, all of which appear generally more susceptible to adaptive radiation than the hemipenis. This is not to claim that taxonomic use of the hemipenis is not liable to the same pitfalls that beset other characters. Evolution does not permit universally reliable taxonomic criteria, and even the snake hemipenis is not so conservative as formerly thought. Inger and Marx (1962) provided an instance of intraspecific variability in the hemipenis, and additional examples are given in the present monograph (an extreme case is shown in fig. 16).

The hemipenis is admittedly esoteric, whether as a functional organ or as a systematic tool. The uninitiated are referred to the excellent account by Dowling and Savage (1960). A paper by Hugh Clark (1945) is also recommended. Although containing material of basic interest, Clark's paper has rarely been cited.

The hemipenis may be studied either in its retracted or everted condition. Preferably it should be examined in both states, because different kinds of data are thus obtainable (see below). Relatively few museum specimens have completely everted hemipenes, because even when specimens are preserved by professionals, there is sometimes difficulty in making complete eversions. Before injecting the tail base, it may help to slit the tail and sever the retractor muscle as recommended by Dowling and Savage (1960). Another frequently helpful technique, after killing the specimen (injection of diluted sodium pentobarbital, or "Nembutal," is a good way), is to wait for the better part of an hour before trying to evert the organ so that all muscles are completely relaxed. This method is scarcely necessary for many species, but I have had success with it on hemipenes that offer special problems, as for example the slender terminal structures in some *Micrurus*, and I now use the waiting technique with any rare specimen. Museum specimens often have only partially protruded organs, which are virtually useless in that condition. If only the base is everted, the tail can be opened and the organ pulled back and studied in the retracted position. I found that more fully but incompletely everted hemipenes can often be rescued if they are not already punctured or desiccated. The organ is carefully dissected out by cutting around (not through) the base. The retractor muscle is severed where it disappears into the hemipenis, which is then gently pressed to remove excess air and liquid. The severed end of the muscle is pushed into the hemipenis, followed by the tip of a hypodermic needle, after which the organ is firmly tied onto the needle. The needle is attached to a syringe filled with hot, melted paraffin and, with luck, the hemipenis can be expanded to its full dimensions. This operation can also be carried out with the organ still attached to the snake, but it is much easier if the hemipenis is removed and everted in hot water to prevent the needle being plugged by cooling paraffin. Substitute use of such other substances as formalin, alcohol, or liquid latex, usually causes the partially everted organ to burst when pressure is applied, and so the secret seems to be in the intense heat of the paraffin. (However, an improved and completely different technique for everting hemipenes of preserved specimens has been recently developed by Mrs. Frances W. Gibson [unpublished]).

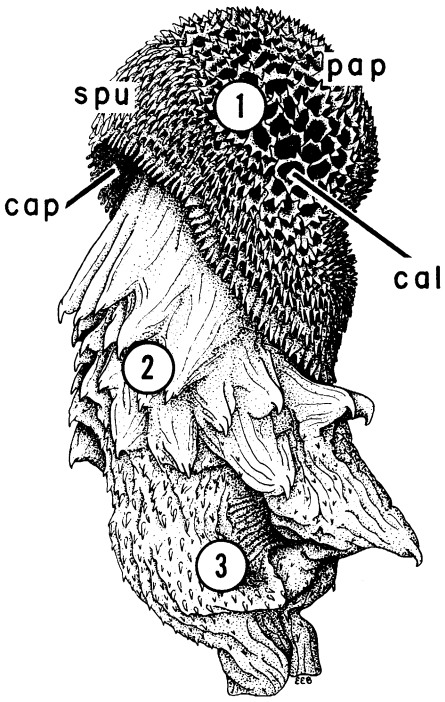


FIG. 3. Side view of everted hemipenis (of *Rhadinaea taeniata*), showing some characteristic structures. Asulcate surface is left and sulcate side is right (sulcus spermaticus is not visible from this aspect). ×6.

Abbreviations: 1, capitulum; 2, spinose midsection; 3, spinulose basal section; cal, calyx (plural [in herpetology] calyces); cap, overhanging edge of capitulum; pap, soft papillae on distal calyces; spu, ossified spinules on basal calyces.

If the retracted hemipenis is to be studied, the base of the tail should be carefully slit along its ventral midline, not to one side as done by some workers. This allows both organs to be exposed without further mutilation; the two halves of the ventral wall of the tail can be pinned apart, and either organ is more easily accessible than if the tail is incised along some other plane. For detailed study the hemipenis, especially of small snakes, is best removed and pinned out after its length has been noted *in situ*. It should be slit, at least partly, before removal to insure that different organs are all opened along the same plane. I find it advisable to slit the organ along its midventral surface, as recommended by Cope (1895, p. 190), but others prefer to make an incision along the medial surface.

Specialized terms used in this monograph are italicized at first mention in the following discussion of penial morphology; the terminology is largely consistent with that recommended by Dowling and Savage (1960), with one major exception.

The hemipenis in *Rhadinaea* is divisible into three regions (fig. 3)—a *capitulum* (head), followed by a *spinose* section (the spines are unossified in juvenile snakes), and a variably sized basal section that is ornamented only with tiny *spinules*. The greatest length of the *sulcus spermaticus* is on the lateral wall of the retracted hemipenis, and, whether the organ is retracted or everted (fig. 4), the position of the sulcus determines the *sulcate side* as opposed to the *asulcate side*.[1] Most *Rhadinaea* have a *capitate* hemipenis, which is to say that the capitulum has a free overhanging edge except where crossed by the sulcus spermaticus. The capitulum is *calyculate*, or surfaced with a reticulum of *calyces*. Each calyx bears soft *papillae* or ossified spinules on the top edges of its walls, and these structures largely conceal the calyculate pattern. The spinules, when present, occur in a narrow to broad band around the periphery of the capitulum, with the papillae being confined to the more distal calyces; either spinules or calyces may become relatively large and specialized on the asulcate side of the capitulum, sometimes forming a conspicuous cluster. One or more calyces may also become unusually large on this region of the head, sometimes forming a conspicuous *distal naked pocket* when the organ is everted; a pocket may also be formed between fusions of the edge of the capitulum to the underlying stalk (fig. 4). Capitation has been lost completely in a few species, in which the calyces grade directly to the stalk, but even in these it may be convenient to refer to the calyculate region as a "capitulum." A characteristic that may differ even between closely related species is whether the asulcate side of the capitulum is drawn into either a *single fold* or a *double fold* when the hemipenis is in its retracted position. The hemipenis is either *single* or slightly *bilobate*. In the latter case there is a dorsal and a ventral *lobe* as viewed in the retracted position. Slight bilobation is not always detectable when the hemipenis is everted. It is important to note that, in *Rhadinaea*, any bilobation is confined within a single, completely calyculate capitulum. The insertion of the major *retractor muscle* is of course divided into two slips

[1]A departure from the terminology suggested by Dowling and Savage (1960, pp. 19, 21), as explained elsewhere (Myers and Trueb, 1967).

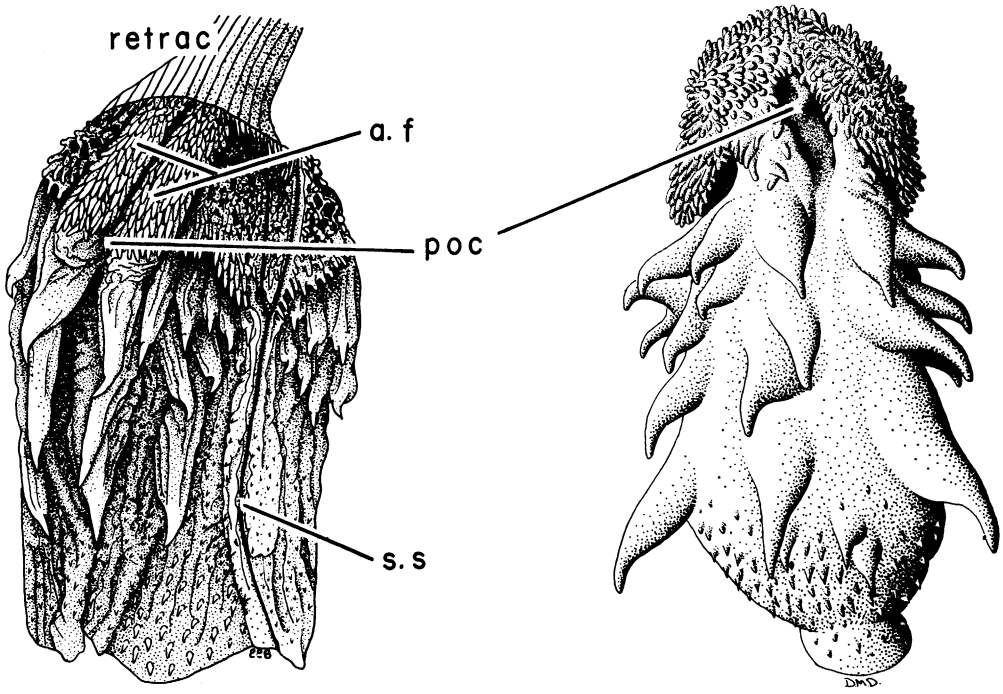


FIG. 4. Retracted and everted hemipenes (of *Rhadinaea lateristriga*). Retracted organ, left, was cut open along midventral surface and spread flat. Everted organ is viewed from asulcate side. *Abbreviations*: a.f, asulcate fold (doubled) of capitulum; poc, distal naked pocket in asulcate edge of capitulum (compare with fig. 3); retrac, major retractor muscle; s.s, sulcus spermaticus.

if the hemipenis is bilobed, but in some species it is also slightly divided even when the retracted hemipenis is indisputably single—presumably evidence of ancestry from a bilobed condition. "Retractor muscle," as used herein, refers to the *m. retractor penis magnus*.

Spines are invariably present below the capitulum in *Rhadinaea*. They are usually more numerous or at least larger toward the asulcate side, whereas the spines tend to be small close to the sulcus spermaticus, the lips of which may bear spinules. Most species have a nude gap between the spines on the midline of the asulcate side, and in some this nude region takes a characteristic shape and size when the hemipenis is everted. The spines are hooked or gently recurved in the great majority of species but are virtually straight in a few. Related species often differ in the number of spines present, but unless the difference is great I have not emphasized this as a taxonomic feature. Usually not enough organs were seen to enable me to judge the extent of intraspecific variation in spine number, and it was difficult to obtain repeatable counts in species where the spines grade in size to the adjacent spinules.

The basal region varies from short to long, even occasionally within the same species, and is ornamented only with minute spinules, which are scattered or clustered, depending on the species. The spinules disappear at the extreme base, which is completely nude. The basal region is alternately ridged and furrowed when the hemipenis is in its retracted position. In some species one of the furrows is a conspicuously smooth *basal naked pocket* devoid of spinules. The basal naked pocket often is conspicuous even when the hemipenis is fully everted.

Species of *Rhadinaea* have a bifurcate sulcus spermaticus, which forks well up the hemipenis, close to or on the calyculate area. The branches of the sulcus usually are equivalent in length, but in a few species one of the branches is noticeably shorter than the other, giving a hint as to how a simple sulcus might evolve from a bifurcate condition. Another way this could happen is indicated by the hemipenis of *Rhadinaea myersi*, in which the capitulum has

evidently shortened, thus leading to reduction in the length of the branches. So far as I have noticed, the right and left organs of a pair are *symmetrical* to each other when both are everted, which is to say that they are mirror images in geography of structure. The retracted hemipenes also are symmetrical, but Underwood (1967a, p. 132) pointed out that this is not necessarily an indication of the everted condition. The greatest length of the sulcus is on the lateral wall when the hemipenis is retracted. The only exception noted to this rule was the case of a specimen of *Rhadinaea godmani* (UMMZ 95156), in which the sulcus of the left hemipenis was on the medial wall and the asulcate cluster of spinulate calyces was on the lateral wall; this hemipenis also was aberrant in lacking spines, although their normal locations were indicated by enlarged tissue bases. The right hemipenis of this specimen was normal in its geography. If both organs had been everted, they presumably would have been *asymmetrical*, but aberrantly so and probably not equivalent to the colubrine condition.

There are interspecific and some intraspecific variations in length of the entire hemipenis and its retractor muscle; organ and muscle lengths are indicated by noting the number of subcaudal plates spanned. There also is variation in lengths of the different sections of the hemipenis, and this is indicated by noting the relative length of one section to another. I used dividers to step off relative proportions within the organ, but this method is crude and is intended only to show gross differences. The greatest length of the capitulum is on the sulcate side, from the tip of the organ to the base of the calyculate area, although in a few species the capitulum is very nearly equivalent on all sides. Proportionate length of the capitulum was determined on the sulcate side, and was found in most cases to be approximately the same in both everted and retracted organs, although the apex of the former is often not equivalent to the apex of the latter. This is proved by the branches of the sulcus, which usually terminate at or near the tip of the retracted hemipenis but often extend no more than halfway up the capitulum of the everted organ. There are a few exceptional species in which the branches terminate at the apex in both states. Proportionate length of the capitulum changes most drastically due to real changes in the length of the aspinose base of the hemipenis. It also can change noticeably in the same individual if the capitulum is tipped strongly back when the hemipenis everts, thus increasing the relative length of the capitulum on the sulcate side; this is exemplified by *Rhadinaea flavilata*.

The various hemipenial characteristics discussed above are all useful in defining and differentiating between individual species, but the following also are useful in defining whole groups of related species. These are listed in approximately decreasing order of importance: 1) presence or absence of bilobation of hemipenis and/or retractor muscle; 2) presence or absence of a basal naked pocket; 3) specialization near periphery of asulcate side of capitulum (pockets, large papillae or spiny knobs); 4) presence or absence, and distribution, of spinules on proximal calyces; 5) straight versus curved spines; 6) condition of asulcate fold of capitulum (whether single or doubled) on retracted hemipenis; 7) tendency toward loss of capitation. These features are summarized for each species in table 2.

SIZE AND PROPORTIONS

Total length is the best single measurement of the size of a snake in that it is most readily visualized and probably tends to partly cancel out the usual sexual dimorphism of longer snout-vent length in females and longer tail length in males. Nonetheless, females tend to attain a larger size than males, and, because of the problems inherent with small and heterogeneous samples, the only use I have made of the total length measurement is to indicate the maximum known sizes of males and females. All measurements are to the nearest millimeter and were taken from preserved specimens that had been straightened and slightly stretched against a metric rule. Tail length was measured from the end of the anal plate to the tip of the tail; snout to vent (body) length, when needed, was obtained by subtracting tail from total length.

The relative length of the tail is of particular use in characterizing species of *Rhadinaea* and is expressed as a percentage of total length; it also is indirectly expressed by the number of subcaudals. Tail length is a sexually dimorphic feature and data for the sexes are given separately. It also varies ontogenetically, as juveniles average proportionally shorter tails than do adults. For example, compare the following data from *Rhadinaea flavilata* (mean and standard

TABLE 2

DISTRIBUTION OF SELECTED CHARACTERS OF THE HEMIPENIS IN SPECIES OF *Rhadinaea*[a]

Species	Bilobation of Hemipenis	Division of Retractor Insertion	Basal Pocket	Distal Asulcate Pocket	Spinules on Calyces	Spiny Asulcate Knobs	Enlarged Asulcate Papillae	Asulcate Fold	Straight Spines	Capitation	Remarks
The *flavilata* Group											
R. flavilata	−	−	+	−	+	−	−	2	−	+	Branches of sulcus unequal
R. laureata	−	−	+	−	+	−	−	1	−	+	Branches of sulcus unequal
The *decorata* Group											
R. bogertorum	−		−	−	+	−	−		−	+	
R. cuneata	−	−	−	−	+	−	−		−	+	
R. decorata	−	−	−	−	+	−	−	1	−	+	Geographic variation
R. forbesi	−	−	−	−	+	−	−	1	−	+	
R. gaigeae	−	−	−	−	+	−	−	1	−	+	
R. hesperia	−	−	−	−	+	−	−	2	−	+	
R. macdougalli	−	−	−	−	+	−	−	1	−	+	
R. marcellae	−	−	−	−	+	−	−	1	−	+	Many spines
R. montana	−	−	−	−	+	−	−	1	−	+	
R. myersi	−	−	−	−	+	−	−	2	−	+	Disproportionately short capitulum
The *taeniata* Group											
R. fulvivittis	−	−	−	−	+	−	−	2	−	+	
R. omiltemana	−	−	−	−	+	−	−	2	−	+	
R. taeniata	−	−	−	−	+	−	−	2	−	+	
The *godmani* Group											
R. godmani	+	+	+	−	+	−	−	2	−	+	Enlarged calyx. Geographic variation
R. hannsteini	+	+	+	−	+	−	−	1	−	+	
R. hempsteadae	+	+	+		+	−	−	1	−	+	Enlarged calyx
R. kinkelini	+	+	+	−	+	−	−	2	−	+	Resembles *hannsteini*
R. lachrymans	+	+	+	−	+	−	−	2	−	+	
R. montecristi	+	+	+	−	+	−	−	2	−	+	
R. pilonaorum	+	+	+	−	+	−	−	1	−	+	Capitation weak
R. posadasi	+	+	+	−	+	−	−	1	−	+	
R. schistosa	−	+	+	−	+	−	−	1	+	+	Resembles *vermiculaticeps*
R. serperaster	+	+	+	−	+	−	−	1	−	+	

TABLE 2—(*Continued*)

Species	Bilobation of Hemipenis	Division of Retractor Insertion	Basal Pocket	Distal Asulcate Pocket	Spinules on Calyces	Spiny Asulcate Knobs	Enlarged Asulcate Papillae	Asulcate Fold	Straight Spines	Capitation	Remarks
The *calligaster* Group											
R. calligaster	+	+	−	−	−	−	−	−	−	−	
The *vermiculaticeps* Group											
R. sargenti	−	−	+	−	−	−	−	1	+	+	
R. vermiculaticeps	−	−	+	−	−	−	−	1	+	+	
The *lateristriga* Group											
R. decipiens	−	−	−	+	+	−	−	2	−	+	
R. dumerilii	−	−	−		−	−	−	2	−	−	
R. fulviceps	−	−	−	+	+	−	−	1	−	+	
R. guntheri	−	−	−	+	+	−	−	1	−	+	
R. lateristriga	−	−	−	+	+	−	−	2	−	+	
R. multilineata	−	−	−	+	+	−	−	2	−	+	
R. pachyura	−	−	−	+	+	−	−	2	−	+	
R., species inquirenda	−	−	−			−	−	2	−	+	One juvenile
The *brevirostris* Group											
R. affinis	−	+	−	−	−	−	+	−	−	+[b]	
R. brevirostris	+ or −	+	−	+	+	+ or −	+	1	−	+	Branches of sulcus unequal Enlarged calyx
R. occipitalis	+ or −	+	−	−	+	+	+	1 or 2	−	+	
R. persimilis	−	+	−	−	−	−	+	−	−	−	
R. poecilopogon	−	+	−	−	−	−	+	−	−	+[b]	

[a]Hemipenes were not examined of the following species: *R. quinquelineata* (*decorata* group); *R. pinicola* (*godmani* group); *R. pulveriventris* (*vermiculaticeps* group). Also, *R. bilineata* (*brevirostris* group) is not included because too few data were obtained from a hemipenis of a juvenile.

[b]Semicapitate (capitation much reduced, limited to a slight overhang near apex of asulcate side).

Symbols: Absence of a structure is denoted by a minus sign, presence by a plus sign. Blank spaces in the table mean that a character was not recorded, usually because only everted or only retracted organs were available for a given species; hemipenes in both conditions must be examined to obtain all characters.

error of mean of tail length expressed as a percentage, followed by range and number of specimens):

MALES
Juveniles: 30.0±0.26, 28.7–30.7 (9)
Adults: 32.6±0.15, 30.2–35.9 (47)
FEMALES
Juveniles: 28.6±0.42, 27.0–30.6 (9)
Adults: 29.8±0.15, 27.5–32.0 (42)

These differences are seen to be relatively slight, although significant, and, because very few juveniles (if any) are represented in most other samples, the data for juveniles are not usually distinguished in the text or tables, particularly if the data fall within the ranges for adults. But see table 13 for a notable exception in the case of *Rhadinaea calligaster*, in which the tail-length proportion differs greatly between adults and hatchlings.

The tails of many *Rhadinaea* are long (and consequently have high subcaudal counts), often more than 30 percent of total length, but exceptionally long tails are attained in some species of the *lateristriga* and *decorata* groups. In *R. decorata* the tail of one male was 47.6 percent of the total, the maximum recorded for the genus. Normally the tails, whether long or short, are slender and tapering, but in the *lateristriga* group the long tail is disproportionately thick and the tapering more gradual (fig. 5). Even when most of the tail is broken off, which usually is the case, a specimen is easily assignable to the *lateristriga* group because of the conspicuously thickened tail.

Proportions of the various head shields are of very limited taxonomic usefulness. The relative length of the interparietal suture in relation to the frontal plate is mentioned as a difference between *Rhadinaea fulviceps* and the closely related *R. pachyura*, but even in this case the character is too variable to be relied upon for identification. A few species (*R. brevirostris*, *R. dumerilii*) have noticeably short muzzles in relation to a relatively large eye, and the smaller members of the *godmani* group (e.g., *R. pilonaorum*) tend to have relatively small eyes (possibly correlated with semifossorial habits), but I have not emphasized eye or snout characters for a diagnostic purpose, although they are potentially useful.

DORSAL SCALE ROWS

The dorsal scales were counted at three places—a head's length behind the head, at midbody, and a ventral or so in front of the anal plate. A fourth count was made on many specimens, starting with the dorsal scale bordering the posterior corner of the first ventral and proceeding diagonally to the starting place for the

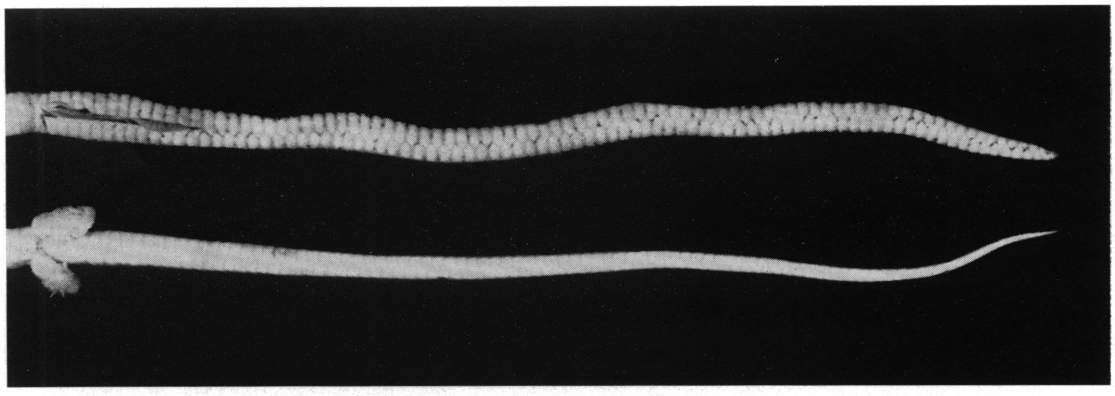


FIG. 5. Intrageneric differences in relative thickness and tapering of tail. *Top*: *Rhadinaea lateristriga*, AMNH 23028 (male; total length 405 mm., tail 131 mm.). *Bottom*: *R. fulvivittis*, AMNH 100895 (male; total length 377 mm., tail 130 mm.).

In the *lateristriga* species group (top), the tail is disproportionately thick for most of its length—a feature that usually allows a specimen to be allocated to the *lateristriga* group even when most of the tail is missing (as is usually the case in this group). Slenderly tapering tail of *Rhadinaea fulvivittis* (bottom) is more or less representative of situation in other species groups.

first standard count. The extra count was devised (Myers, 1967, p. 50) to serve as a standard, repeatable measurement of the highly variable area immediately behind the head, but it proved to be of little taxonomic usefulness. A pattern did emerge, however; *Rhadinaea* and some other small colubrids that I have examined normally seem to have one more scale in this count than at a head's length behind the head; occasionally the same count is obtained, rarely more or less. For example, a snake with a standard formula of 17–17–17 rows would typically have a formula of 18–17–17–17 if the scales immediately behind the head are added. Those wishing to use this count might want to make it from both sides of the body to account for the variation sometimes obtained, for example, 18/19–17–17–17. Hardy and Cole (1968) used a slight modification of the count in their study of a species of *Tantilla*, and found no deviation from the 15 rows obtained by counting farther back on the neck; presumably this is a reflection of the modified habitus of *Tantilla*, in which the head region is scarcely distinct from the neck. The anteriormost count was not intended to be used as a replacement for the first standard count, as unfortunately was done by Gyi (1970, p. 52) in a monograph of the homalopsine snakes.

Most species of *Rhadinaea* have the same number of scale rows from the neck to the end of the body, and in the great majority this number is 17. Any deviation from the generalized pattern is of considerable taxonomic usefulness. Thus, one species (*occipitalis*) is easily defined by its 15 rows, whereas some members of the *godmani* group are easily distinguished from most of their congeners in having 19 or 21 rows. Posterior reduction from 17 to 15 rows occurs regularly in *R. brevirostris*, and reduction from 15 to 13 rows occurs in some specimens of *R. occipitalis*. Elsewhere in the genus, reduction occurs with some frequency only in certain species of the *godmani* group. The method and place of reduction often can be simply stated, but reduction in specimens of *R. godmani* (normally 21 rows) and *R. hempsteadae* (19) is sometimes complex and of considerable interest in relation to the possibility of hybridization. So it has been desirable to give a reduction formula for a few specimens. This is done after the method suggested by Dowling (1951a), except for two changes.[1] A formula is read from left (head) to right (tail). Figures on the midline represent the number of scale rows at various points. Changes on the right and left sides of the body are respectively indicated by numbers above and below horizontal lines. The level of the ventral plate at which a change occurs is shown in parentheses, and the total number of ventrals is shown at the extreme right of the formula. Loss of a row is indicated by a minus sign before the number of the row, addition by a plus sign before the number of the row, fusion of rows by insertion of a plus sign between two numbers, and the formation of two rows from one is shown by a division sign. When a row is "lost" the scales become smaller and the row disappears. Fusion of two rows is indicated by an enlarged scale at the place of reduction. Addition or division of rows are simply the reverse of loss or fusion of rows, all such changes being defined according to their occurrence in a caudad direction.

VENTRAL PLATES

The large plates of the venter were counted after the method of Dowling (1951b), who defined the first ventral as "the first plate bordered on both sides by the first row of dorsals." This may leave uncounted a few wider than long plates which I occasionally find cause to refer to as "preventrals," as when comparing counts obtained by other workers, especially in connection with type specimens. Sagitally divided ventrals, and half-ventrals, are occasional in some species of *Rhadinaea*, but they are definitely aberrations and some, if not all, are reflections of vertebral duplication (see King, 1959). I arbitrarily ignored half-ventrals (except in *R. flavilata*, see Myers, 1967, p. 76), but counted the two halves of a divided ventral as one. The most frequent aberration is the appearance of a half-ventral immediately behind the last full ventral; this occurred in 11 percent of all specimens of *R. flavilata* (*fide* Myers, *loc. cit.*) and I have the impression that the anomaly is as common in various other species of the genus.

Male snakes typically have fewer ventrals than females, this being correlated with the

[1] 1) The letter "P" is used, in place of a number, to designate a paravertebral scale row. 2) As here defined, the notation " ÷3" shows splitting of the third scale row, which carries ipso facto the information that a new fourth row has been created caudad to the split. Dowling (*op. cit.*, p. 133) and others would use the longer notation "3 = 3 + 4" to express the same thing.

usual sexual dimorphism in body size. There may be considerable, even complete overlap in the observed ranges, although the overlap tends to be much less in samples from the same population. Usually there is a significant difference of at least several ventrals between means for males and females, but in a few cases there seems to be relatively little dimorphism. In *R. brevirostris* and *R. fulviceps*, the means are actually higher for males; although the differences are not statistically significant, it is interesting that this pattern holds for geographically restricted samples of *brevirostris* as well as for the total sample combined. The ventrals sometimes seem to be sensitive indicators of geographic gradients, but *R. decorata* is noteworthy for its virtual lack of geographical variation in spite of the fact that it ranges from Mexico to Ecuador.

Approximate ranges of variation in ventral counts are incompletely known in many species of *Rhadinaea*, and the taxonomic value of the character varies from group to group. For example, the number of ventrals seems to be of no use in identifying a specimen in the *vermiculaticeps* group but may be of considerable help in the *decorata* group. Wherever possible I have avoided the use of ventrals in the keys and diagnoses because it is a nuisance to the user and because less variable characters are frequently available. Nonetheless, the ventrals (and subcaudals) should be counted if there is any doubt about identification of a specimen. The comparative data are conveniently arranged in tabular form for each species group, and a geographic breakdown of the data may be given in the individual accounts in the case of species with large geographic ranges.

ANAL PLATE

A divided anal shield is characteristic of the genus *Rhadinaea*. A single, undivided shield occurs only as a rare aberration and was noted only in three specimens, namely one *R. fulvivittis* from Oaxaca and two *R. godmani* from different populations in Costa Rica.

SUBCAUDAL PLATES

The plates under the tail are paired, except as rare aberrations when some (never all) are fused. The subcaudals are counted along one side of the tail, starting with the first plate behind the anal scute that makes full contact with its opposite member. The subcaudal counts given in text and tables refer to the number of pairs. The unpaired, terminal scale or "spine" is not counted. The terminal scale, when complete, is a slender taper, but often it has been blunted. In many cases the tail is incomplete, and if only the terminal spine is missing it is virtually impossible to know if all the subcaudals are present, and many counts were discarded for that reason. The number of subcaudals is roughly proportional to tail length, as would be expected. Thus the species with the shortest tails also have the lowest number of subcaudals and vice versa. If the data are plotted, however, there is considerable spread owing to the facts that actual tail lengths cannot be directly compared because of growth factors and interspecific size differences and that proportionate tail length is affected by relative differences in body length. Because male snakes average longer tails than females, it follows that there is sexual dimorphism in the number of subcaudals. There may be extensive, but rarely complete, overlap in ranges of subcaudal counts for males and females, but the overlap tends to diminish when only geographically homogeneous samples are considered, and the means are always separated. The number of subcaudals frequently varies along geographic gradients.

Allowing for the above variables, the number of subcaudal plates is a taxonomically important feature for characterizing species, and can be quite helpful in identification. Because specimens frequently have incomplete tails, I have tried to emphasize other, more dependable and easily used characters in the keys and diagnoses, but comparative subcaudal data are made readily available in the tables that accompany each species group. Unusually high numbers of subcaudals occur in species of more than one group, but this correlated with a conspicuously thickened tail is diagnostic of the *lateristriga* group.

HEAD PLATES

The dorsal head shields do not vary in number or kind in *Rhadinaea* and so are of no diagnostic value within the genus (see also Size and Proportions). Virtually the same remark can be made concerning the genials, nasal, and loreal, although the last is rarely fused with the preocular or, even more rarely and aberrantly, it may be absent. Much was formerly made in

snake taxonomy of an entire versus divided nasal. In *Rhadinaea* this plate usually bears a vertical groove above and/or below the naris. In some cases one of the grooves is sufficiently deep so that the nasal may be called semidivided, but this is subjective and of no diagnostic worth. Thus, we are left to consider the preoculars and postoculars, temporals, and supralabials and infralabials as characters of potential importance.

Most species of *Rhadinaea* have one preocular and two postoculars, but some species normally have two of each and others one of each. These are average conditions that help to characterize a species, but generally there is too much intraspecific variation to permit reliable use of the number of oculars in identification. The number of preoculars varies geographically in *R. decorata*.

Some species frequently have a small subpreocular scale inserted between the corners of two supralabials (usually the third and fourth) at the lower front edge of the eye. I (Myers, 1967, p. 84) have called this scale a "pseudopreocular" because it seems possibly to have originated by splitting off from a labial. "Pseudopreocular" is probably the oldest available name (e.g., Jan, 1863, p. 302; Cope, 1900, p. 754), but "subpreocular" has also been used in *Rhadinaea* (e.g., Bailey, 1940) and certainly is more descriptive. The presence or absence of this scale tends to be fairly consistent as noted by Cope (*loc. cit.*), but still there is too much intraspecific variation to rely on it as a diagnostic feature. Nonetheless, a subpreocular is useful in defining species groups as well as species and its presence or absence is mentioned throughout the accounts.

I define the temporals as those plates lying singly or in vertical rows between the parietals and supralabials. In *Rhadinaea* there is a single anterior, primary temporal (two only as a rare aberration), behind which is a secondary temporal or, more commonly, a vertical row of two secondaries. The basic temporal formulae in *Rhadinaea* are thus $1+2$ or $1+1$. Some authors have considered as temporals an adjacent row of scales that touch on the posterior margins of the parietal and ultimate supralabial, but, by my definition, only rarely are there three rows of temporals, as by the aberrant division of the primary temporal to give a formula of $1+1+2$ or $1+1+1$. The temporal region is quite unstable in the genus as a whole. One common variation is the vertical division of one or rarely both of the secondary temporals in row 2, which causes a basic formula of $1+2$ to be altered to $1+\frac{1}{2}$, $1+\frac{2}{1}$, or rarely $1+\frac{2}{2}$. Another, perhaps even more common variation is for one of the secondary temporals to be fused with an adjacent posttemporal or, less commonly, with the primary temporal, resulting in a greatly elongated plate. Other variations occur less commonly, as for example the rare contact of a supralabial and parietal in front of the primary temporal. Such deviations usually are easily recognized as being the result of intraspecific variation and do not in themselves destroy the diagnostic value of the temporals. But in many species having a basic formula of $1+2$ are found individuals with a formula of $1+1$, on one or both sides of the head, and the reverse situation occurs also. Consequently, the temporals are of limited reliability for the identification of single specimens.

The number of supralabials is relatively constant in some species of *Rhadinaea* and variable in others, but seven and eight are the only numbers normal to the genus. Higher or lesser counts are due to anomalous splitting or fusion of plates and occur only as deviations within species. More than 80 percent of the species normally have eight supralabials, with the second and third touching the loreal (second only in *brevirostris* group) and the fourth and fifth in contact with the eye (third to fifth in *brevirostris* group). At least seven species normally have seven supralabials, with either the second or second and third touching the loreal (depending on the species) and the third and fourth in contact with the eye. The supralabials are useful in characterizing species and species groups, but intraspecific variability makes them much less useful in identifying specimens.

The normal numbers of infralabials are eight, nine, or 10; higher or lower numbers are intraspecific deviations. The first pair of labials is usually in contact behind the mental, but rare specimens have these plates separated. When there are eight infralabials, the first four are in contact with the anterior genials. The first four or five are in contact with the anterior genials in specimens having nine infralabials, and the first five are in contact with the anterior genials when there are ten infralabials. The last infralabial that touches an anterior genial, and the labial after that one, are also in contact with a posterior genial, regardless of the total number of infralabials. The infralabials are of even less

diagnostic value than the supralabials, temporals, or oculars.

SCALE ORGANS

Several kinds of scale organs occur in *Rhadinaea*, namely minute tubercles on the head, anal ridges on the scales above the cloacal region, "pits" on circumocular plates and neck scales, and keels on the dorsal scales. The pits and keels occur in only a few species of *Rhadinaea*, whereas the other characters are widespread. Some or all of these structures are innervated and probably provide the snake with information about its environment. Underwood (1967a, p. 42) suggested that the tubercles are probably tactile and the pits possibly radiation receptors. Noble (1937) demonstrated the tactile nature of tubercles on the chins of natricine snakes. Additionally, Noble's work suggests that anal tubercles and ridges may aid in cloacal placement preliminary to copulation.

The head tubercles are minute and not always easily seen, their visibility being at least partly dependent on how well a specimen is preserved, and they are more easily seen on a dark surface than on the white chin. The tubercles occur dorsally, laterally, and ventrally on the head, but they seem most concentrated anteriorly. Some interspecific differences seem to exist in the distribution, abundance, and prominence of the tubercles, but I have not attempted to use these structures as a taxonomic character except to note their occurrence as a generic characteristic.

Anal (supracloacal) ridges could better be called tubercles in some cases, but it seems likely that the ridges (keels) and tubercles are homologous inasmuch as they are in the same position (on horizontal midline of a scale) and, in some cases, one or two tubercles extend from a ridge-like base. Therefore, I follow Bailey (1939, p. 17) in adopting a single term, which is the one originally coined by Blanchard (1931) for the elevated, supracloacal scale organs of otherwise smooth-scaled snakes ("knobbed anal keels" was used for keeled-scale species). It has been generally assumed, following Blanchard, that the ontogenetic development of anal ridges more or less coincides with the onset of sexual maturity, and this has been objectively documented in the case of *Diadophis punctatus* (see Myers, 1965, p. 83). It has been known that anal ridges appear in occasional females and precocious juveniles, but Myers (1967, p. 73, fig. 9) demonstrated that the structures occur on about 39 percent of adult female *Rhadinaea flavilata*. Subsequent observation confirms that anal ridges occur too frequently in female rhadinaeas to be a reliable indicator of sex, although their presence does seem usually to indicate sexual maturity. Although their presence or absence helps characterize some species and groups of *Rhadinaea*, anal ridges are of limited taxonomic value because of intraspecific and intragroup variation.

Scale "pits," not to be confused with the facial and labial pits of crotalids and boids, are slightly depressed or at least unpigmented areas on some of the head plates or dorsal scales. Relatively large, circumocular pits are conspicuous on most specimens of *Rhadinaea brevirostris* but are absent in other species of *Rhadinaea* in so far as I have noticed. The circumocular pits of *Rhadinaea brevirostris* are similar to those seen in some other genera, as for example *Alsophis* and *Chironius*. Underwood (1967a, p. 42) made the pertinent observation that such pits are on a part of the head that does not rub against surrounding objects during normal movement of the snake, as contrasted with the positioning of head tubercles.

Presence or absence or apical pits, and whether single or paired, have been much used as a taxonomic character of colubrid snakes. Certainly it is a useful character if the pits are conspicuous and always present, or if some pits are greatly modified as has occurred in some *Chironius*, but it is becoming increasingly apparent that considerable interspecific and intraspecific variation occurs in some groups, and that pits may be present but very hard to find. Downs (1967, p. 21) found that apical pits were present in a majority of *Geophis*, but that scales often had to be detached and examined microscopically by transmitted light before the pits could be detected. Unless all species of a genus are so treated, it seems unsafe to claim that pits are present in some species and absent in others, which might simply have small pits not visible to the naked eye or under the dissecting microscope. Some specimens of *Rhadinaea decorata* and, especially, *R. brevirostris*, have conspicuous pits (paired or single) on some of the scales of the neck. I have not observed pits elsewhere in the genus or elsewhere on the body, but I have examined scales of only a few species by transmitted light and I would not even be surprised

to have overlooked pits that should have been visible under the dissecting microscope. Therefore, apical pits are not utilized taxonomically in the present study. To those who would generalize about the phylogenetic significance of apical pits, I would suggest a possibility in need of investigation, namely that the pits may be polyphyletically derivable above nerve endings already present in colubrid snakes generally.

Keeled scales have not been previously reported in *Rhadinaea* but they are present in many specimens of the wide-ranging *R. decorata*, although absent in all other species. The keels, when present, are likely to be confined to the posterior portion of the body, but some individuals have keeled scales from the neck back. An individual keel lies on the midline of its scale but does not extend to the apex of the scale; the keels are faint to moderately strong in comparison with adjacent striations that are characteristic of *decorata* scales, but no specimen can be described as strongly keeled. The keel may be of uniform elevation for its entire length or higher in some places than in others, particularly on the basal part of the scale, where the keels of some specimens are shortened and tubercle-like. This observation indicates that the keels may be homologous with the anal ridges of other species, but there seems to be no sexual dimorphism in frequency of keeling, thus suggesting an altered function of the structures. It seems fairly certain that the keels of *Rhadinaea decorata* are a new structure in the genus.

CHARACTERS NOT USED

It is seldom feasible for a reviser to consider every character that might be of taxonomic value. In the present study, for example, I did not utilize any skeletal characters except maxillae and presence or absence of vertebral hypapophyses. Because of the relatively large number of species involved, the initially obscure relationships of most, and the rarity of many, I did not bother requesting permission to dissect out skulls and vertebrae. Also, I was aware that osteological features (except dentition and vertebral hypapophyses) have not often been effectively utilized in generic revisions of colubrid snakes, and I was hesitant to commit time to what might be an entire study in itself. Furthermore, because of the extensive variation in all other major characters, it would be an a priori absurdity to present data or illustrations of the osteology of one or a few "typical" species of *Rhadinaea*, even if such a thing as a typical skull should be later proved a reality. This scarcely denies the need for an osteological investigation nor covers the fact that the present monograph is incomplete as a consequence. I hope that the presently proposed intrageneric groupings will later be tested by a comparison of the skulls and vertebrae of selected species; such a study would also be useful in comparisons with other genera.

It also seems possible that a study of the microsurfaces of scales might be taxonomically rewarding. Some species of *Rhadinaea*, notably *R. decorata*, have distinctly striated scales, especially on the posterior part of the body, whereas others seem to have perfectly smooth scales when viewed under a dissecting microscope. A survey of the scale surfaces of all species under the scanning electron microscope would be of special interest. Numerous other anatomical structures might also be studied, and some might eventually be found that will elucidate intrageneric relationships. Knowledge of the many characters discussed by Underwood (1967a) might elucidate intergeneric and especially suprageneric relationships.

It might be noted that I have thus far not mentioned any of many potentially interesting biochemical, physiological, and behavioral features that might be studied. Such kinds of data will be welcomed for any species, but, as living specimens are required, it will probably be a long time indeed before non-morphological information could become really important in the taxonomy of *Rhadinaea*. The problem will be in obtaining *comparative* data on enough of the 40-odd species occurring between latitudes 35° North and 35° South.

TABLE 3

DISTINGUISHING CHARACTERISTICS OF EIGHT SPECIES GROUPS OF *Rhadinaea*

Character	*flavilata* Group	*decorata* Group	*taeniata* Group	*godmani* Group	*calligaster* Group	*vermiculaticeps* Group	*lateristriga* Group	*brevirostris* Group
Ultimate fang	Offset	Offset	Offset	Not offset	Offset	Offset	Offset	Offset
Hemipenis[a]	Single; branches of sulcus unequal; basal naked pocket present; no special asulcate features on capitulum; asulcate fold 1 or 2	Single; no specialized features on asulcate side of capitulum; asulcate fold 1 (usually) or 2	Single; spinules occur in relatively and uniformly wide band around capitulum; no special features on asulcate side; asulcate fold 2	Mostly bilobated, but various stages in loss of bilobation detectable; basal naked pocket present; often enlarged spinules, papillae, or calyces on asulcate side; asulcate fold 1 or 2	Bilobated; not capitate; no spinules on calyces	Single; no spinules on calyces; spines virtually straight; basal naked pocket present; asulcate fold 1	Single; distal naked pocket present on asulcate edge of capitulum; asulcate fold usually 2	Usually single (intraspecific variation in 2 species), but retractor insertion is divided; enlarged asulcate papillae present; spinules absent from calyces (except for stubby knobs in 2 species); capitation present to absent
Color pattern[a]	Tendency toward golden brown body with reduced and diffused striping; head darker than body with pale lines or not; lips with unusual salt and pepper pattern in	Variably striped, but always an indication of lateral dark line on row 4 or 5; pale postocular marking invariably present on temporal or outer parietal region	Head and body tend to be continuously and vividly marked with broad brown or black stripes on pale ground; dorsal color does not encroach onto and darken	Tendencies for: oblique pale bar from eye to corner of mouth, ∩-shaped dark mark on rostral, dark-edged supralabials, pale frontal blotches, collar. Head darker than	Body gray, brown, or green with variable stripe pattern; supralabials boldly margined in black; some individuals with a pale bar from eye to corner of mouth;	Tendency for a broad dorsal stripe that diverges on nape, breaking into pale reticulum atop head in 2 of 3 spp.; often a median, pale break in dorsal stripe	Body brown to black with 1 or 2 white lateral lines; usually no dark stripes; tendency either for head to be paler than body, or for pale ocelli on head and/or neck	Body striped or anteriorly spotted; a tendency either for pale canthal-temporal line or for pale postocular marking, except in *R. brevirostris*

TABLE 3—(*Continued*)

Character	*flavilata* Group	*decorata* Group	*taeniata* Group	*godmani* Group	*calligaster* Group	*vermiculaticeps* Group	*lateristriga* Group	*brevirostris* Group
	specimens of both species		ventral tips	body, which is striped or with pale dashes on dark scales	regular midventral black markings			
Dorsal scales[a]	17–17–17	17–17–17	17–17–17	17–17–17 19–19–19 21–21–21	17–17–17	17–17–17	17–17–17	17–17–17 17–17–15 15–15–15(13)
Anal ridges[b]	Present	Present	Present	Present in most species	Usually(?) absent	Present	Absent (occasional in *R. guentheri*)	Invariably absent
Tail length as a percentage of total	27–36	25–48	27–37	14–27	19–29	26–35	27–47 (usually > 35; tail is disproportionately thick for much of its length)	17–31
Subpreocular[b]	Absent	Present	Present	Invariably absent	Invariably absent	Usually absent	Present	Invariably absent
Temporals[b]	1+2	1+2	1+2 (except 1+1 in *R. fulvivittis*)	1+2 (except 1+1 in *R. schistosa*)	1+1	1+2	Usually 1+1 (1+2 in 2 species)	1+2
Supralabials[b]	7	8	8	8 (except 7 in *R. posadasi*)	8	8	8	7 or 8 (2nd touches loreal; 3rd–5th in orbit when there are 8 plates)
Infralabials[b]	9	10	10	8 or 9	8	10	8, 9, or 10	8 or 9

[a]Variation is mostly interspecific unless noted otherwise.
[b]Normal condition, subject to intraspecific variation.

SPECIES GROUPS AND IDENTIFICATION OF SPECIES

I DIVIDE the 45 species of *Rhadinaea* into eight, seemingly natural groups, as follow:

The *flavilata* group, two species
The *decorata* group, 11 species
The *taeniata* group, three species
The *godmani* group, 11 species
The *calligaster* group, one species
The *vermiculaticeps* group, three species
The *lateristriga* group, eight species
The *brevirostris* group, six species

The above list is arranged in geographic order from north to south. The names of the groups are based on relatively common, well-known, or wide-ranging species, without regard to priority of publication. The species group, after all, is a convenience and has no status in formal nomenclature; it is often equivalent to the subgenus of some animal groups, but herpetologists seldom feel the need for a formal category between the levels of genus and species, primarily because of the relatively small number of species to be classified, compared with the insects for example.

It would be possible to make a case for according separate generic status to some of these assemblages, but, considering the present state of colubrid systematics, I think it would only confuse rather than clarify relationships. The *godmani* group, for example, is quite distinctive, but its transfer out of *Rhadinaea* would remove a geographic, and seemingly phylogenetic, nucleus to which the other groups can be related (fig. 51). Without the *godmani* group, in fact, the whole scheme seems to fall apart, with little or no evidence of monophyly to hold the remaining groups together. Removal of any of the other groups would not cause so much of a problem, and it is conceivable that new interpretations or evidence might necessitate reducing (or increasing) the size of the genus. The affinities of the South American *brevirostris* group are especially in need of further study. A summary of the distinguishing features of each species group is given in table 3.

It is often easier to identify species of *Rhadinaea* by immediate use of their diagnostic characters rather than to determine first the species group, which is defined partly by internal structure and various attributes that may not be possessed by every single specimen. The following key to the species is divided into a North American (including Panama) and a South American part to facilitate usage. A few species come out in two places in the key in order to account for intraspecific variation or misinterpretation of a given character. It will be noted that the key can be worked in reverse order should the need arise. Naturally, the key will not always work, but I have tried to make it as easy to use as possible, relying chiefly on characteristic features of color pattern and easily determined aspects of scutellation. After a specimen has been identified, it should be checked against statements of diagnosis and distribution and compared with the head and midbody illustrations; if doubt remains, the user should consider carefully the text descriptions and tables of data.

KEY TO THE SPECIES OF *Rhadinaea*

PART 1. NORTH AMERICA

1. Dorsal scales in 17 rows 5
   Dorsal scales in 19 or 21 rows 2
2(1). Dorsal scales in 19 rows[1] 3
   Dorsal scales in 21 rows[1] . . . . *godmani*
3(2). Bold lateral dark stripe on scale row 3 and part of each adjacent row, and bold ventrolateral dark stripe on edges of ventrals and lower part of first scale row (fig. 28C) . . . . . *montecristi*
   No such combination of stripes 4
4(3). Body pattern complex, including dark line or stripe on adjacent edges of scale rows 1 and 2 (fig. 28D) . . . . . *serperaster*
   Body pattern variable (e.g., fig. 28K–M), but not including a conspicuous line or stripe on adjacent edges of rows 1 and 2 . . . . . *hempsteadae*
5(1). Definite white line, solid or broken, on scale row 1 (may also involve row 2); dark lines or stripes absent or very vague . . . 19
   No definite while line on first scale row; body striped, unicolor, or speckled 6
6(5). Well-defined pale line, stripe, ocellus, or wedge-shaped marking lying close behind

[1]This character is known to break down in the highlands of Chiapas. Specimens with 19 or 21 scale rows, from Chiapas and adjacent Guatemala, should be compared with the descriptions and illustrations of both *R. godmani* and *R. hempsteadae*.

upper rear edge of eye and extending either horizontally toward neck or obliquely across temporal region toward rear of mouth or side of neck 23

No conspicuous pale marking in *upper* postocular or temporal region (exception: some *flavilata* of SE United States) . . . 7

7(6). At least one obvious dark line or stripe on side of body 8

Body without dark lines or stripes, or with only vertebral dark line (lateral dark stripes completely absent or vague due to diffusion of pigment) 13

8(7). Series of dark spots, transverse markings, or even solid stripe down middle of belly (fig. 34) . . . . . *calligaster* (part)

Belly immaculate or speckled, but no series of midventral dark markings 9

9(8). Black stripe along side of head, and a middorsal black stripe that is usually short and confined to neck (figs. 36C, 38) . . . . . *pulveriventris* (part)

No such markings 10

10(9). Large pale blotch(es) on frontal plate (e.g., fig. 27B), *or*, if absent (some specimens of *lachrymans*), usually more than 154 ventrals 11

Frontal plate essentially dark, without large pale area (e.g., fig. 27A); usually less than 154 ventrals 12

11(10). Pattern includes pair of bold ventrolateral and lateral blackish brown stripes on each side of body (fig. 28A, B). . . *lachrymans*

Body with more complex pattern of brown lines and stripes (fig. 29E), not dominated by pair of bold ventrolateral and lateral dark stripes . . . . . *kinkelini*

12(10). Dorsolateral dark lines present; lateral dark stripe occupying adjacent halves of scale rows 3 and 4 (fig. 29D); usually only one postocular scale . . . . . *hannsteini*

No dorsolateral dark lines; lateral stripe covering all of row 4 and part of each adjacent row; two postoculars . *pinicola*

13(7). Series of dark spots, transverse markings, or even solid stripe down middle of belly (fig. 34) . . . . . *calligaster* (part)

No series of midventral dark markings . 14

14(13). Body scales (at least in lateral rows) with pale dashes or speckling (fig. 29A–C); often only a single postocular scale and never a subpreocular; diminutive snakes from Mexico and upper Central America . 15

Body scales (even in lateral rows) lacking pale dashes or conspicuously pale speckling; usually two postoculars; subpreocular present or absent; normal-sized species from southeastern United States and lower Central America 17

15(14). Tail short, less than 20 percent of total length and with fewer than 50 pairs of subcaudals . . . . . *schistosa*

Tail much longer, usually more than 30 percent of total length and with more than 80 pairs of subcaudals 16

16(15). Head and neck very pale (white in preservative) except for some dark brown mottling atop head (fig. 27D) . . . . *pilonaorum*

Head dark, sharply contrasted from pale collar on neck (fig. 27C) . . . . *posadasi*

17(14). Head lighter than body; ventral plates tipped with dark pigment 18

Head usually darker than body, never lighter; edges of ventrals not tipped with dark pigment . . . . . *flavilata*

18(17). Conspicuously lighter color of head (or pale collar in juveniles?) extending three or four scales behind ends of parietal plates; supralabials intensely spotted and speckled with dark pigment, including encroachment of pigment along common labial sutures (fig. 40C) . . . . *fulviceps* (part)

Slightly lighter color of head extending less than three scales behind parietals; supralabials pigmented mostly along tops and bottoms; no encroachment of dark pigment along common sutures of supralabials (fig. 40H) . . . . . *species inquirenda* (*lateristriga* group)

19(5). Pair of white ocelli on rear of head (on outer side of each parietal plate) and sometimes additional ocelli on neck (fig. 40E); two white lines on each side of body (fig. 41A) . . . . . *guentheri*

No pale ocelli on head or neck; one or two white lines on each side of body . . . 20

20(19). Two narrow white lines on each side of body, on scale rows 1 (or 1–2) and 5 (fig. 41D) . . . . . *decipiens* (part)

One narrow white line or series of white dashes on each side of body, on row 1 or rows 1 and 2 (any pale area in the vicinity of row 5 is broad and diffuse, as in fig. 41H, I) 21

21(20). Pale collar across rear of head, *or* head about as dark as body (fig. 40A); a white stripe across dark supralabials (fig. 40A, lower two heads). . . . . *decipiens* (part)

No pale collar (except in juveniles?), but entire upper surface of head conspicuously lighter than body; supralabials variously pigmented but lacking white stripe . 22

22(21). Light head color (pale collar in juveniles?) extending one or two scales behind tips of parietal plates; supralabials lightly marked with brown; usually 1+1 temporals

(fig. 40B) . . . . . *pachyura*

Light head color (pale collar in juveniles?) extending three or four scales behind parietals; supralabials heavily pigmented; usually 1+2 temporals . *fulviceps* (part)

23(6). Body golden brown with middorsal gray stripe three to five scales broad, and little or no indication of lateral striping; dark head set off by white line across neck and with a vivid horizontal white line extending from canthus rostralis to temporal region (figs. 6C, 7C) . . . . . *laureata*

Not so marked 24

24(23). Middorsal black or gray stripe, usually confined to neck (rarely extending length of body) and tending to bifurcate on nape; body otherwise nearly uniform brown for most of length, except for lateral dark line (figs. 36C, 37C, 38) . . *pulveriventris* (part)

Not so marked 25

25(24). Broad middorsal black stripe broken by pale line down the middle (also might be interpreted as paired paravertebral dark stripes); conspicuous pale reticulum on head (figs. 36B, 37B) . . . *vermiculaticeps*

No such combination of markings; pale reticulum absent or present; middorsal dark stripe, if present, not broken by pale line in middle 26

26(25). Lower several scale rows uniformly blackish; *and* a pale reticulum on head; no discrete dark lines on body (figs. 36A, 37A) . *sargenti*

No such combination of markings . . . 27

27(26). Lateral dark *stripe* at least two half-scale rows in width and involving at least the lower edge of row 5; ends of ventral plates not conspicuously darkened by pigment from lower sides (which are never very dark), although discrete spots sometimes present; ventrals 148–197; *taeniata* group . . . 28

Lateral marking usually a dark *line* or narrow stripe[1] on scale row 4 or 5 (*or*, if wider, not touching row 5, *or* ventral plates conspicuously tipped with dark pigment); lower sides and ventral tips light or dark; ventrals 110–186; *decorata* group 31

28(27). Middorsal brown stripe occupying median five scale rows plus an edge or larger part of each adjacent (sixth) row; a darker vertebral line present (fig. 20F) . . . . . *omiltemana*

Middorsal stripe brown or black and not so broad, occupying median three scale rows plus part of each adjacent (seventh) row; a darker vertebral line present or absent . 29

29(28). Lateral and dorsal stripes brown, with conspicuously darker edges; lateral stripe centered on row 4 and overlapping onto each adjacent row (fig. 20E) . . *fulvivittis*

At least lateral stripe is black, without darker edges; lateral stripe not centered on row 4 (except in some intraspecific hybrids) . 30

30(29). Lateral black stripe completely covering scale rows 4 and 5 as well as adjacent parts of rows 3 and 6; dorsal stripe also black; dorsolateral white stripe continuous above eye to snout (figs. 19D, 20D) . . . . . *taeniata aemula*

Lateral black stripe narrower, occupying parts of rows 4 and 5; dorsal stripe usually brown and containing a darker vertebral line; dorsolateral pale brown stripe interrupted at eye (figs. 19A, 20A) . . . . . *taeniata taeniata*

31(27). Lateral dark line usually confined to middle or lower edge of scale row 5, or, sometimes equally shared between rows 4 and 5. 32

Lateral dark line mainly on row 4, sometimes including lower edge of row 5 33

32(31). A distinct dark line down middle of vertebral row of scales (fig. 11K–M); ventrals 139–177 . . . . . *hesperia*

No distinct line in middle of vertebral row, although wider dark streak often present (covering one or more scale rows); ventrals 110–134 . . . . . *decorata*

33(31). Postocular pale marking usually wedge-shaped, not a line or stripe (fig. 10F) . . . . . *cuneata*

Postocular pale marking a line or narrow stripe, in some cases broken 34

34(33). Postocular pale line sharply inclined, extending from upper edge of eye to behind corner of mouth; usually less than 150 ventrals 35

Postocular pale line horizontal or oblique, but, in latter case, not extending to behind corner of mouth; usually more than 150 ventrals (except in *R. myersi*) 37

35(34). White line across nape and pale vermiculations atop head (fig. 10H); about 50 spines on hemipenis. . . . . *marcellae*

No white line across nape; pale vermiculations absent or inconspicuous; fewer than 30 spines on hemipenis. 36

36(35). Ventrals usually conspicuously tipped with dark brown or black; vertebral dark line usually unbroken; lateral dark line thick; ground color darker (fig. 11D); ventrals (nine specimens) 136–149 . . . . *forbesi*

Ends of ventrals spotted or inconspicuously

[1]This line is sometimes obscured if the lower sides of the body are dark (for example, see fig. 11D, J, K), or if there is an intensification of pigment between it and a *lighter* dark line on row 4 (fig. 11L).

tipped with brown; dark vertebral line essentially absent; lateral dark line narrow; ground color lighter (fig. 11F); ventrals (three specimens) 119–131 . . *macdougalli*

37(34). Sharply defined vertebral dark line usually set on a median ground color of gray or pale brown, *or*, if not, lateral light stripe occupying scale row 5 and adjacent parts of rows 4 and 6; vertebral dark line often preceded on neck by short pale line . 38

Vertebral line usually broken and vague (not solid black), on a brown ground color; no lateral light stripe, only a vague pale area nearly confined to row 5; no short pale line on midline of neck 40

38(37). Paravertebral light areas sharply defined by *dark-edged* dorsolateral brown stripes; lateral light stripe occupying row 5 and adjacent halves of rows 4 and 6 (fig. 11A) . . . . . *montana*

No discrete dorsolateral brown stripes, or at least not with darker edges; lateral light stripe often higher, usually including most or all of row 6 39

39(38). Lateral light stripe conspicuously paler than lower sides, and not extending onto row 7 (fig. 11B); 81–112 pairs of subcaudals . . . . . *gaigeae*

Lateral light stripe not much paler than lower sides, and extending onto lower part of row 7; 76 subcaudals in only known specimen (female) . . . . *quinquelineata*

40(37). Ventrals more than 145 (158 in only known male, 163 in only known female); postocular pale line touching on ultimate supralabial (fig. 10J); small pale spots (interrupting lateral dark line) situated on posterodorsal section of each scale in row 4 (fig. 11G); capitulum of hemipenis comprising about half of length of organ . . . . . *bogertorum*

Ventrals less than 145 (132, 135 in two males, 139 in only female); postocular pale line edging but not encroaching onto ultimate supralabial (fig. 10K); small pale spots in row 4 absent or situated dorsomedially on each scale (fig. 11H); capitulum of hemipenis only about two-fifths of total length of organ (fig. 12B) . . . . . *myersi*

Part 2. South America

1. Pale line along canthus rostralis, dark blotches on anterior part of body (figs. 45A, 46E, 48); dorsal scales in 15 rows, at least on anterior half of body . . . *occipitalis*

Canthal line present or absent, body striped or unicolor; scales in 17 rows, at least on anterior half of body 2

2(1). Dorsal scales 17–17–15; body stripes usually with slightly undulating and/or serrated edges (fig. 46C, D) . . . . . *brevirostris*

Dorsal scales in 17–17–17 rows; body stripes straight-edged or indistinct or absent. . 3

3(2). Pale line along canthus rostralis to temporal region (fig. 45B, C) 4

No distinct canthal line, although pattern of pale lines may be present on top of snout 5

4(3). Dark wedge of color extending behind jaws and forward for short distance along lower edge of mouth (fig. 45B); sides of body dark (fig. 46F) . . . . . *poecilopogon*

No dark wedge on lower jaw (fig. 45C); sides of body not conspicuously darkened (fig. 46G) . . . . . *bilineata*

5(3). Top of head conspicuously lighter brown than body; no pale line or ocellus behind upper edge of eye or in temporal region . 6

Top of head about same color or darker than dorsum of neck; pale line or ocellus present or not 8

6(5). Small pale spot or ocellus situated above and slightly behind corner of mouth (fig. 40D); no white line along lower sides of body (fig. 41F) . . . . . *dumerilii*

No discrete pale spot behind mouth; often a white line on scale rows 1 or 1 and 2 . . 7

7(6). Dark supralabials broken by horizontal white area (fig. 40A, lower two); sharply defined white line on row 1 or rows 1 and 2 (fig. 41D, E) . . . . . *decipiens*

Supralabials spotted or speckled with dark pigment but without horizontal white stripe (fig. 40C); white line on lower scale row absent or not sharply defined (fig. 41I) . . . . . *fulviceps*

8(5). White line or series of dashes on first scale row 9

No such marking 10

9(8). Pale temporal line continuous from eye to body, there fusing with usually well-defined tan stripe occupying row 5 and part of each adjacent row (figs. 40F, 41C); never a pale collar behind head or pale line on row 5 . . . . . *multilineata*

Pale temporal marking, if any, not continuous to body; tan dorsolateral stripe usually absent or at least poorly defined; often a pale collar behind head and/or pale line on row 5 (figs. 40G, 41B) . . . . *lateristriga*

10(8). Lateral dark line on lower part of row 5 or between rows 4 and 5 (fig. 11J); tail long, greater than 35 percent of total length (often broken) . . . . . *decorata*

Lateral dark line on row 4 or rows 3 and 4

(fig. 46A, B); tail shorter, less than 35 percent of total length 11

11(10). Pale marking, usually wedge-shaped, behind upper rear edge of eye; no enamel white line on supralabials (fig. 45F) . . . *affinis*

No pale marking immediately behind eye (small ocelli may be present farther back on parietals); enamel white line on supralabials (fig. 45D) . . . . . *persimilis*

ACCOUNTS OF SPECIES, BY GROUP

THE *flavilata* GROUP

ONLY TWO SPECIES are included in the *flavilata* group, *Rhadinaea flavilata* from coastal regions in the southeastern United States and *R. laureata* from elevations of about 1500–3100 meters in the mountains west and south of the Mexican Plateau. The apparent relationship of these species was recognized by Malnate (1939), Bailey (1940), and Myers (1967) on the basis of features of the color pattern and number of supralabials. The relationship is here reaffirmed by use of hemipenial characters, and the two species are given group status.

The group is defined especially by the following combination of characters (see also table 3): The branches of the sulcus spermaticus are of unequal length and a basal naked pocket is present on the unbilobated hemipenis. There are normally seven supralabials and a subpreocular is usually absent. Body coloration tends toward golden brown, and there has been great reduction in the intensity of dark stripes, which are diffused or even absent. Specimens from some populations of *Rhadinaea flavilata* resemble *R. laureata* in having the lips intensely peppered with dark pigment, which gives an appearance seen elsewhere only in *R. fulviceps* of the *lateristriga* group.

The *flavilata* group is unique in the genus in having no semblance of geographic unity. Its members probably are peripheral relicts of a group that was broadly distributed, but which has since been largely replaced by species of the *decorata* and *taeniata* groups.

Rhadinaea flavilata (Cope)

Figures 6A, B, 7A, B, 8, 9A; maps 2, 3

Dromicus flavilatus COPE, 1871, pp. 222, 223; 1875b, p. 38. YARROW, 1882, pp. 15, 191; 1883, p. 15. GARMAN, 1883, p. 58; 1884, p. 27.

Liophis flavilatus (Cope): BOULENGER, 1894b, p. 143.

Rhadinaea flavilata (Cope): COPE, 1894a, p. 428; 1895, p. 202, pl. 27, fig. 6 (retracted hemipenis); 1900, pp. 759, 760, fig. 164 (details of scutellation), pl. 25, fig. 6 (retracted hemipenis). BROWN, 1901, p. 88. DITMARS, 1907, p. 330, figs. 2, 6 (poor photographs of heads of preserved specimens); 1939, pp. 100, 102, pl. 2 (poor photographs of preserved specimen); 1951, pp. 269, 270, pl. 81, fig. 2 (poor photograph of head of preserved specimen). WERNER, 1929, p. 118. DUNN, 1932, p. 1. STEJNEGER AND BARBOUR, 1933, p. 105; 1939, p. 100; 1943, p. 124. MALNATE, 1939, pp. 359–366, pl. 1 (photograph of living specimen). SCHMIDT and DAVIS, 1941, pp. 113–115, fig. 24 (details of cephalic scutellation), pl. 9 (photograph of living specimen). SCHMIDT, 1953, p. 180. CARR AND GOIN, 1955, p. 269, pl. 55 (photograph of living specimen). WRIGHT AND WRIGHT, 1957, pp. 627–631, fig. 182 (several poor photographs). CONANT, 1958, p. 140, pl. 24 (small illustration of whole specimen in color). AUFFENBERG, 1963, pp. 171, 172, fig. 19 (drawings of a fossil vertebra). MYERS, 1967, pp. 47–97, fig. 1 (photograph of living specimen), fig. 10 (photographs of heads showing geographic variation in color pattern). LANGEBARTEL, 1968, p. 30, fig. 4J (drawing of hyoid).

Leimadophis flavilatus (Cope): STEJNEGER AND BARBOUR, 1917, pp. 86, 87; 1923, p. 96.

Urotheca flavilata (Cope): NEILL, 1963, p. 205.

HOLOTYPE: Formerly ANSP 5583 (now lost), from approximately 8 miles westward of Fort Macon, on Bogue Banks, Carteret County, North Carolina; H. C. Yarrow, collector. See Myers (1967, p. 51) for additional information.

DIAGNOSIS: *Rhadinaea flavilata* differs from most of its congeners in having a nearly unicolor (golden brown) body, without pale lines or solid dark markings, although some individuals have a weak, diffused line of dark pigment on the vertebral row and/or on rows 2–3. *Rhadinaea pulveriventris* also has a nearly unicolored, golden brown body, but differs in having a characteristic Y-shaped marking on the nape. *Rhadinaea dumerilii* has a darker brown body, and a long tail and a small, pale ocellus behind the mouth (*flavilata* sometimes has a vague yellowish spot on each side of the neck, but these markings lack dark edges). Specimens with nearly unicolored bodies occur in some species of the *godmani* group but these either have 19 or 21 rows of scales (17 in *flavilata*), or a tendency for pale streaks on the centers of some or all scales. No other species of *Rhadinaea* occurs near the geographic range of *flavilata*.

DISTRIBUTION: *Rhadinaea flavilata* occupies a narrow coastal range, from the vicinity of Cape Hatteras, North Carolina (Carteret County), south through the northern four-fifths of the

TABLE 4

ASPECTS OF INTERSPECIFIC VARIATION[a] IN THE *flavilata* GROUP

Species	N	Ventrals		Subcaudals		Tail Length as a Percentage	
		Males	Females	Males	Females	Males	Females
flavilata[b]	184	112–134 (91) 124.2±0.28	118–139 (93) 129.7±0.30	68–83 (60) 72.9±0.31	59–75 (60) 67.6±0.40	28.7–35.9 (60) 32.0±0.18	27.0–32.0 (57) 29.5±0.14
laureata	37	150–167 (21) 157.9±0.90	160–176 (16) 167.4±1.21	86–97 (20) 91.0±0.68	73–92 (14) 82.4±1.24	28.4–32.8 (20) 31.1±0.27	27.1–30.4 (13) 28.4±0.31
Combined ranges	221	112–167	118–176	68–97	59–92	28.4–35.9	27.0–32.0

[a]The following statistics are given: Above, range followed by number of specimens in parentheses; below, mean and standard error of the mean.
[b]See Myers (1967) for a geographic breakdown of these data on ventrals and subcaudals.

TABLE 5
NUMBER OF MAXILLARY TEETH IN THE *flavilata* GROUP

Species	N[a]	No. of Teeth 10+2	11+2	12+2	13+2	14+2	15+2	Range
flavilata	10[b]					9	1	14+2–15+2
laureata	19	3	10	6				10+2–12+2

[a]A single maxilla from each specimen.
[b]Specimens from Florida only. Based on data given by Myers (1967, p. 77) but showing only one maxilla (the right when both of a pair were examined) from each specimen.

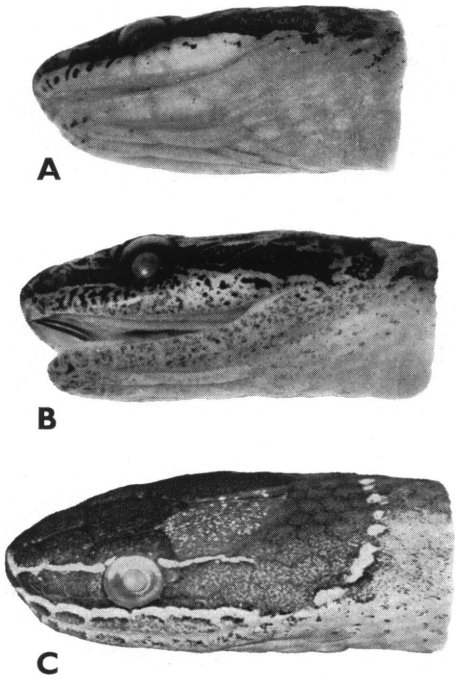


FIG. 6. Head patterns in the *flavilata* group. A, B. *Rhadinaea flavilata*, from Florida and North Carolina, respectively (after Myers, 1967). C. *R. laureata*, KU 62509, from Michoacán, Mexico.

Florida peninsula (to Palm Beach County), and west into Louisiana east of the Mississippi River. Known localities are less than 55 meters above sea level and no more than about 112 kilometers (70 miles) from the coast. The primary habitat is the pine flatwoods of the lower coastal plain, but specimens have also been taken on offshore islands, in broadleaf "hammocks," and in a few other situations (Myers, 1967, pp. 57–61).

DESCRIPTION (192 SPECIMENS): The largest female is 387 mm. total length, 114 mm. tail length; the largest male is 363 mm. total, 125 mm. tail length. The tail is 28.7–35.9 percent of total length in males, and 27.0–32.0 percent in females (see Taxonomic Characters, Size and Proportions, for a comparison of adults and juveniles). The dorsal scales are in 17–17–17 rows; anal ridges are usually present on adult males, commonly on females, and rarely on juveniles. There are 112–139 ventrals (112–134, males; 118–139, females), and 59–83 subcaudals (68–83, males; 59–75, females). There are seven supralabials (rarely eight) and nine infralabials (rarely seven, eight, or 10). There is one preocular (2/2 in one), usually no subpreocular, two postoculars, and a basic pattern of 1+2 temporals. There is frequently a vertical division of one of the temporals in the second row, but other alterations (e.g., 1+1) of the temporal formula are rare (Myers, 1967, pp. 84–86). A subpreocular, between labials 2 and 3, has been observed in only two specimens.

The body is golden brown above, paler and more yellowish on the first two rows of scales. The lower four scale rows in many cases have a diffusion of melanophores, which sometimes form a faint dark streak on rows 2–3 anteriorly and row 4 posteriorly. Some individuals also have a dark streak on the vertebral scale row, where the melanophores are most concentrated on the apexes of the scales. Some specimens have a sparse scattering of melanophores over the entire dorsum; the dark pigment specks, even when concentrated on the second and third and vertebral rows, are sometimes not evident until the stratum corneum falls away in preservative.

The top and upper sides of the head are brown, usually darker than the body, immaculate or with some dark speckling or inconspicuous, pale reticulations. A brown stripe extends from the end of the snout through the eye and to the angle of the jaws. This stripe is bordered above

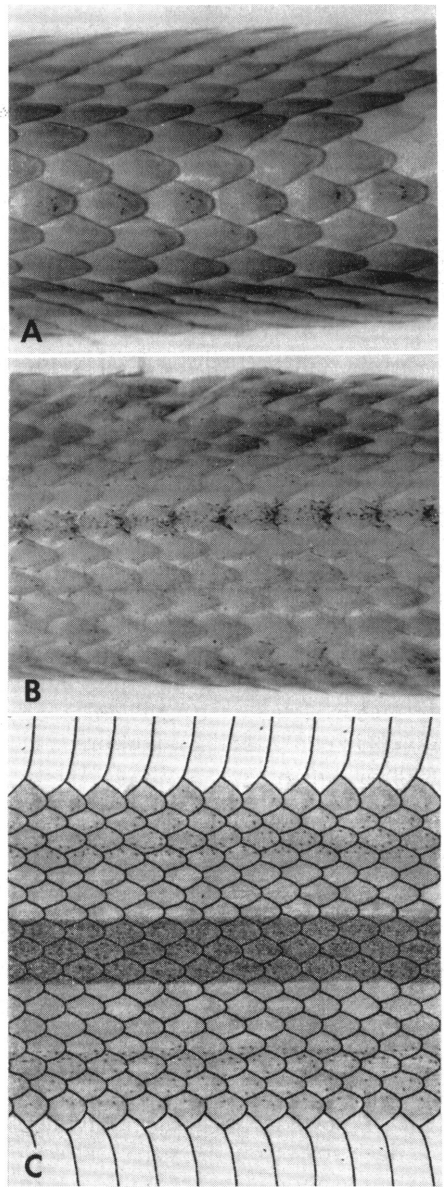


FIG. 7. Midbody color patterns in the *flavilata* group. A, B. *Rhadinaea flavilata*, UF 3271 from Florida, and DU specimen from North Carolina (24 miles southwest of Morehead City), respectively. C. *R. laureata*, USNM 110370, Michoacán, Mexico.

by a vague, sometimes scarcely discernible, pale line, and the bottom edge is a blackish line, which often is diffused and broken and which sometimes meets with its fellow on the rostral plate. The supralabials and infralabials are white, variably dotted or speckled with black and in some cases with faint splotches of brown. The dorsal coloration does not encroach onto the sides of the immaculate white venter.

In life the body is rich golden brown, with a more yellowish cast on the lower sides. The labials and underside of head and neck are white, and the rest of the venter ranges from white in some individuals to chartreuse (yellow-green) in others. This description applies to living specimens from northern Florida; it is possible that the labials are pale yellowish in some parts of the geographic range (see Myers, 1967, pp. 75, 76).

There are 14+2 or 15+2 maxillary teeth. The fangs are enlarged and the last is offset laterad. There are 11–13 palatine teeth, 19–23 pterygoid teeth, and 19–22 dentary teeth. [Maglio's (1970, p. 53) count of 24+2 maxillary teeth for this species is probably a typographical error.]

The retracted hemipenis of two specimens extended *in situ* to the level of subcaudals 7 or 8, and various everted organs extended to subcaudals 6–9. The retractor muscle usually originates at the level of subcaudal 21, but it originated at subcaudal 24 in one specimen. The capitulum comprises approximately a third the length of the retracted hemipenis on its sulcate side; but, when the organ is everted the capitulum is tipped back so that it comprises about half the length of the sulcate side of the hemipenis. The calyces are spinulate toward the periphery of the capitulum and over most of the asulcate fold, and papillate over most of the sulcate side. The sulcus spermaticus forks at, or slightly above, the edge of the capitulum. One branch of the sulcus extends to the end of the retracted organ but only about halfway up the capitulum when the organ is everted; the other branch is shorter, being more than half, but less than three-fourths, the length of the first branch. The wall of the capitulum forms a thick fold on the asulcate side of the retracted hemipenis; there is a shallow, longitudinal crease that gives the fold a slightly doubled appearance. The fold is deeply notched at the basal end, where the capitulum overhangs a deep, nude area that is also obvious (but more shallow) on the everted organ. There are 34–37 small to medium-large, slightly recurved spines below the capitulum. The spines are largest on the asulcate side, where there is a nude space flanked by two rows of three spines each and bordered by another spine

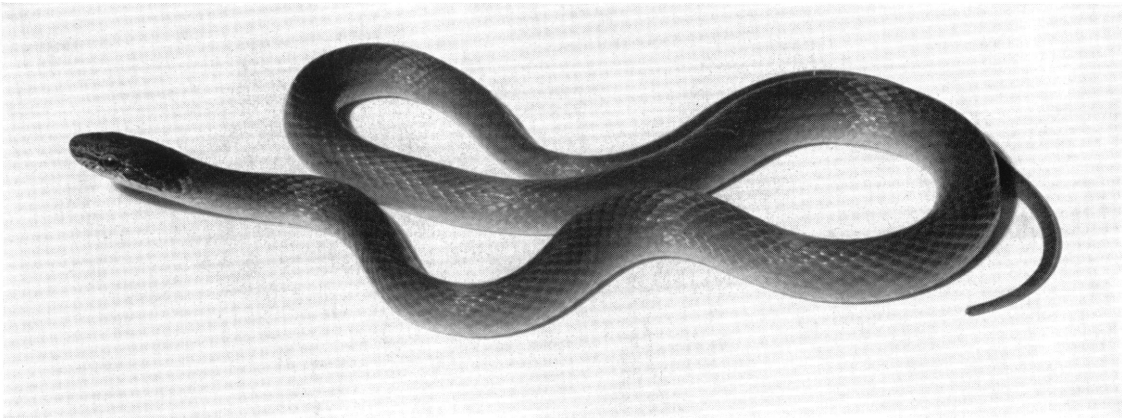
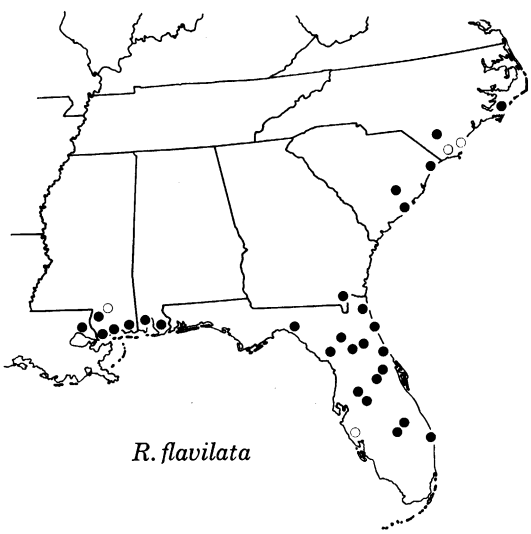


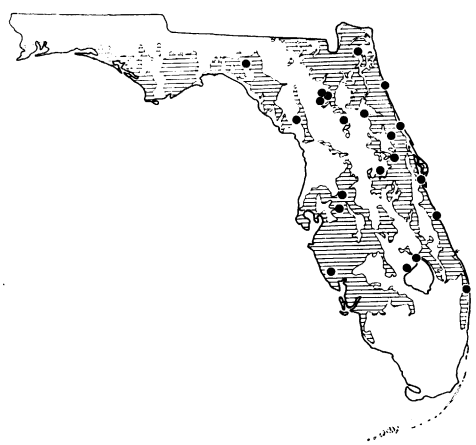
FIG. 8. A pine woods snake, *Rhadinaea flavilata*, from Burbank, Marion County, Florida. (Photograph by Isabelle Hunt Conant.)

below. The basal fourth or third of the hemipenis is unadorned save for minute spinules. There is a basal naked pocket on the dorsal wall, between the base and the spinose zone; this broad groove is most conspicuous on the retracted hemipenis but is also discernible on the everted organ. The preceding description is based on the retracted hemipenes of AMNH 63363 and 63434, on everted hemipenes of AMNH 103817 and 103819 (illustrated), and on data in Myers (1967). Cope's illustration of the retracted hemipenis (1895, pl. 27, fig. 6; 1900, pl. 25, fig. 6) is too diagrammatic to be of any use.

GEOGRAPHIC VARIATION: Snakes from the northernmost part of the range, i.e., North Carolina, usually have the labials intensely speckled with dark pigment. There is a southward decrease in labial pigmentation until, in Florida, there are relatively few dark markings on the labials, some of which may be immaculate. Specimens from the Carolinas usually have a dark vertebral streak, which is absent in about 10 percent of specimens from Alabama, Mississippi, and Louisiana, and absent in about 45 percent of specimens from Florida. This marking, when present, is usually weak in the



MAP 2. Locality records for *Rhadinaea flavilata* in southeastern United States. (From Myers, 1967.) Open symbols indicate literature records.



MAP 3. Locality records for *Rhadinaea flavilata* in Florida, showing close association with pine flatwoods (linear pattern). (From Myers, 1967.)

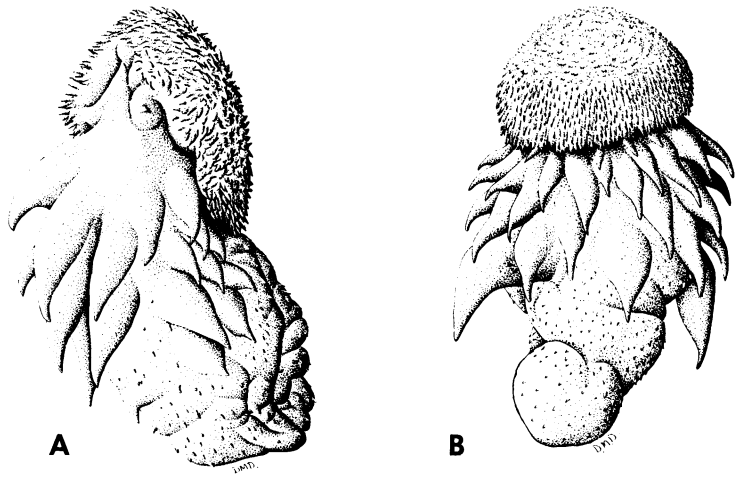


FIG. 9. Hemipenes of the *flavilata* group. A. *Rhadinaea flavilata*, AMNH 103819, left organ. ×7.5. B. *R. laureata*, UMMZ 119280, left organ. ×6.

southern specimens and relatively strong in the northern ones. The number of ventrals increases slightly from north to south (Myers, 1967, fig. 11).

The preceding variation in color pattern and number of ventrals is clinal in nature. Other interpopulational variation is regional and/or microgeographic in nature: Certain minor scale aberrations occur in highest frequency in Florida. Another aberration, an extra plate lying between the fifth supralabial and anterior temporal, occurs most frequently in the western part of the range (Alabama to Louisiana). Frequency of occurrence of anomalous temporal plates seems to vary from population to population on a distinctly microgeographic basis.

REMARKS: The distribution of the pine woods snake closely approximates that of the low pine flatwoods, which constitute its principal habitat (Myers, 1967, figs. 3–5). Also, it is known to have colonized islands along both the Atlantic and Gulf coasts (Myers, 1967; Jackson and Jackson, 1971). The species is most commonly found in pine logs and stumps during March and April; it becomes more difficult to find with the approach of warmer weather and drier conditions in May and June.

Except for the description of the hemipenis, the present account is taken almost entirely from my earlier study (Myers, 1967), to which the reader is referred for a more detailed analysis of variation and a discussion of the distribution, natural history, and probable evolution of the species. Fossil and recent vertebrae are described by Auffenberg (1963, pp. 171, 172, fig. 19) and the hyoid by Langebartel (1968, p. 30, fig. 4J). The toxic effect of the saliva on prey animals was noted by Neill (1954) and Myers (1967, p. 66), and experimentally demonstrated by Willard (1967).

I previously (Myers, 1967, p. 52) discussed possible alternatives regarding the formation of the specific epithet, which I think is compounded from the adjectives *flavus* (gold colored or, more commonly, yellow) plus *latus* (broad or extensive, full or rich), in allusion to the rich, golden brown coloring of the body. The book name "yellow lipped snake" often has been applied—inappropriately in my opinion—but I have suggested (*loc. cit.*) that "pine woods snake" is more suitable for those who feel the need for an English name.

Rhadinaea laureata (Günther)

Figures 6C, 7C, 9B; map 4

Dromicus laureatus GÜNTHER, 1868, p. 419, pl. 19, fig. E (dorsal and lateral views of head of holotype); 1893 (1885–1902), p. 112, pl. 40, fig. A (color pattern of whole specimen, and details of head). BOCOURT, 1888 (1870–1909), pl. 45, figs. 1, 1a–e (dorsal and ventral views of head and neck, and details of nasal, rostral, and anal plates); 1890 (1870–1909), pp. 710, 711.

Rhadinaea laureata (Günther): COPE, 1875a, p. 140; 1887, p. 80 (name misspelled "*loreata*"); 1900, pp. 755, 756. BOULENGER, 1894b, p. 179. WERNER,

1929, p. 117. DUNN, 1932, p. 2. BAILEY, 1940, pp. 5, 6, pl. 1, fig. 5 (midbody pattern of BMNH 92.10.31.48). SMITH, 1943, p. 465, pl. 32, fig. 4 (photograph of E. H. Taylor–H. M. Smith no. 5527 [probably now FMNH 103229]). SMITH AND NECKER, 1943, pp. 189, 190, pl. 4, fig. 2 (redescription and photographs of head of holotype of *Erythrolamprus grammophrys* Dugès). SMITH AND TAYLOR, 1945, p. 118.

Erythrolamprus grammophrys DUGÈS, 1888, pp. 181, 182, fig. 1 (details of head scutellation of holotype, which is in Museo Alfredo Dugès, Colegio del Estado de Guanajuato, from Tengohecho, Michoacán, Mexico); 1890, pp. 402, 403, pl. 27, fig. 13 (the name is misspelled "*grammophris*" in this Spanish translation of the original description; details of head appear redrawn but are properly cited in the text as "Fig. 13," contrary to Smith and Smith, 1969, p. 18).

Tachymenis grammophrys (Dugès): GÜNTHER, 1895 (1885–1902), p. 162.

Liophis laureatus (Günther): AMARAL, 1929b, p. 172.

Coniophanes grammophrys (Dugès): AMARAL, 1929b, p. 217.

HOLOTYPE: BMNH 1946.1.9.2 (originally BMNH 68.4.7.9, not seen), obtained by Doorman "in the neighbourhood of the city of Mexico."

DIAGNOSIS: *Rhadinaea laureata* is recognizable at a glance, because of its unique color pattern. There is a broad (three to five scale rows), gray dorsal stripe on a golden brown body, and little or no indication of lateral striping. There is a pale line through the top of the eye and another pale line that crosses the neck immediately behind the head; the last line may be confluent at its lower end with a line on the supralabials.

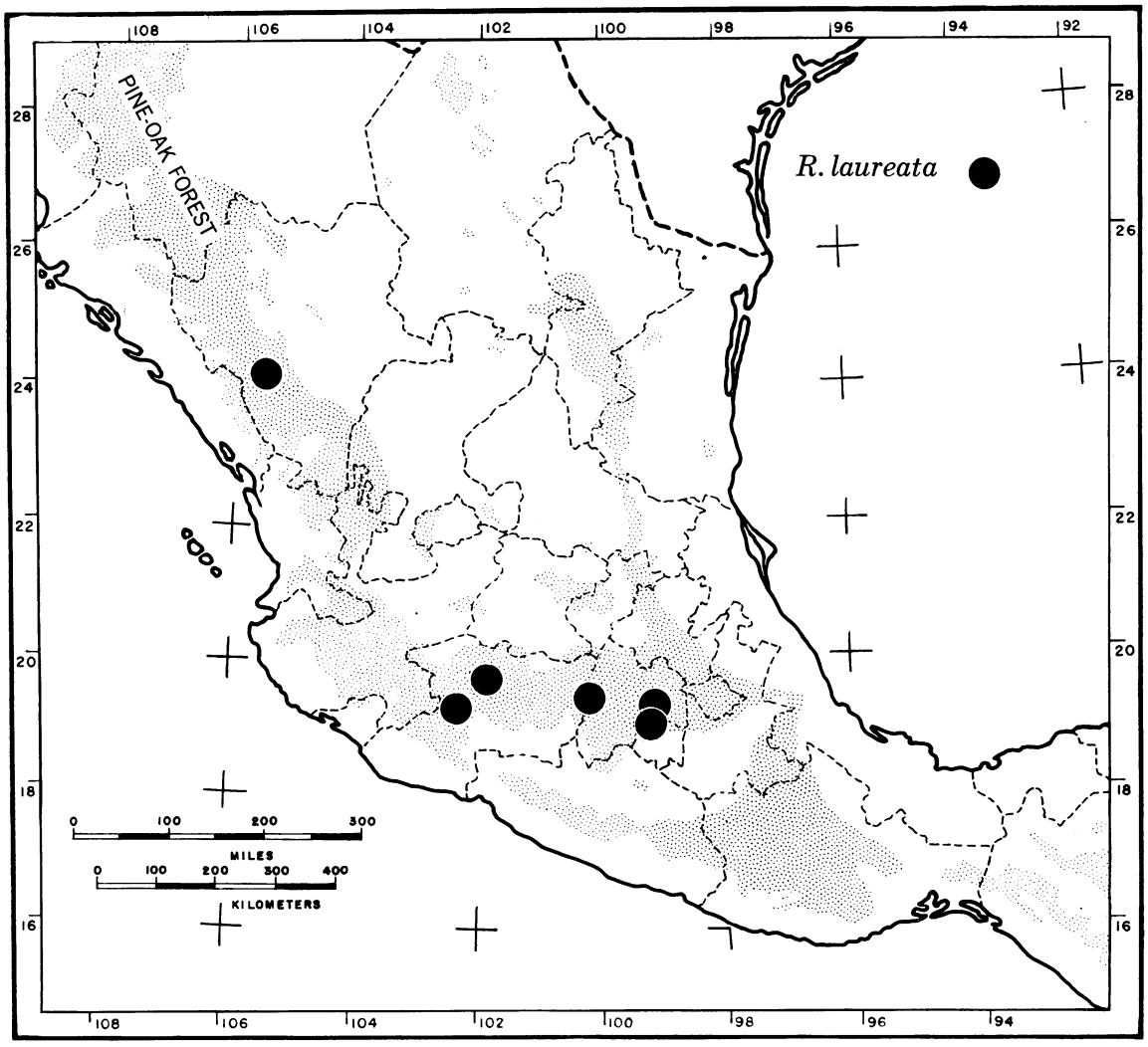
DISTRIBUTION: The pine-oak zone of the Sierra Madre Occidental and the Cordillera Volcánica, from central Durango south to central Michoacán and then east to México and Morelos. The known elevational range is 1524–3079 meters.

DESCRIPTION (37 SPECIMENS): The largest female is 650 mm. total length, 177 mm. tail length; the largest male is 580 mm. total length, 190 mm. tail length. The tail is 28.4–32.8 percent of the total length in males and 27.1–30.4 percent in females. The dorsal scales are in 17–17–17 rows; anal ridges are usually present on adult males. Ventrals number 150–176 (150–167, males; 160–176, females) and subcaudals 73–97 (86–97, males; 73–92, females). There are seven supralabials (8/8 in one specimen) and nine infralabials (9/10 in one). There is one or occasionally two preoculars, two postoculars (3/2 in one), and 1+2 temporals. There normally is no subpreocular, but one specimen has such a scale inserted between the upper edges of the second and third labials on one side of the head.

The body is golden brown above, with a conspicuous medium or dark gray dorsal stripe on the middle three or five rows of scales; the broad gray stripe starts on the nape and extends onto the tail, fading or not before the tip is reached. Some individuals have the sides of their bodies perceptibly darkened by black speckling on the lower four scale rows and sometimes including the bottom edge of the fifth row; this speckling is very sparse in other individuals and probably not noticeable until they lose the stratum corneum after being preserved. The lateral dark speckling may be uniformly distributed, or intensified along or near row 4, thus producing a weak stripe of diffused pigment.

The head is dark brown above and very finely speckled with whitish; a pair of pale parietal dots may be present. There are two white lines on the side of the head and each is continuous across the top or bottom of the rostral with the correspondent line from the other side of the head. The upper white line is thin and extends along the canthus rostralis through the top of the eye and terminates a short distance behind the eye, on the edge of the parietal or on a temporal scale. The lower white line is broader, but often less conspicuous, and extends the length of the upper lip immediately below the dark upper edges of the supralabials. The supralabials below this line are whitish with dense, dark specks, which may be so clustered as to form dark brown or black spots. The dark head is set off from the body by a thin whitish line that crosses the nape and which is often continuous with the horizontal white line from the upper lip.

The infralabials, and often the genials, are whitish with a dense peppering of black. There is little or no encroachment of the brown body pigmentation onto the tips of the ventral plates. The venter usually is nearly immaculate white, but in some specimens it is lightly to heavily speckled with black. The color in life has not been described, but the dorsal coloration is essentially as described above for preserved specimens, judged from a color transparency



MAP 4. Locality records for *Rhadinaea laureata* in Mexico. Stipple pattern indicates approximate distribution of pine-oak forest. There also is a record for the State of Jalisco ("La Cumbre de los Arrastrados," Boulenger, 1894b).

taken by William E. Duellman of a specimen from Michoacán.

There are 10+2 to 12+2 relatively heavy maxillary teeth. All the prediastemal teeth are anterior to the front edge of the ectopterygoid process. The last fang is offset laterad.

The hemipenis is variable in length, extending to the levels of subcaudals 7, 9, and 12 in three retracted organs and to subcaudal 8 in one everted organ. The retractor muscle originates at subcaudal 35 in one case. The capitulum is very nearly as long on the asulcate as on the sulcate side, and comprises roughly a third of the total length of the hemipenis; the head has a peculiar caplike appearance on the everted organ (see figure). The calyces are papillate on the distal part of the capitulum and spinulate in a broad peripheral band. The sulcus spermaticus forks just above the edge of the capitulum and one branch extends virtually to the tip of both the retracted and everted hemipenis, whereas the other branch is only half as long and terminates about midway on the capitulum. The wall of the capitulum forms a single thin fold toward

the asulcate side of the retracted organ. There are between 30 and 40 small to relatively large, slightly recurved spines below the capitulum. The spines are most numerous on the asulcate side and the largest ones are basalmost. There are no spines, only minute spinules, on the basal two-fifths. There is a basal naked pocket that remains well defined on the everted organ. This description is based on the right everted (illustrated) and left inverted hemipenis of UMMZ 114656, and the retracted right organs of AMNH 68360 and USNM 110370. The left organ of the last specimen is amorphous internally, and probably was not capable of being everted by the snake.

REMARKS: I failed to detect any geographic variation, but the available specimens were not all examined at one time. The full range of variation in the amount of dark speckling on the venter can be seen in samples from single localities, as for example from the vicinity of Tancítaro, Michoacán.

The hyoid is described by Langebartel (1968, p. 30).

Bocourt [1890 (1870–1909), p. 710] placed *Trachimenis* (*sic*) *melanocephala* Peters as a synonym of *laureata*, but *Tachymenis melanocephala* is considered by recent authors to be a synonym of *Coniophanes lateritius* Cope.

As a point of technical interest, the names *Rhadinaea* "*loreata*" (see Cope, 1875a, p. 140) and *Erythrolamprus* "*grammophris*" (see Dugès, 1890, p. 402) are to be considered misspellings for *laureata* and *grammophrys* (=*laureata*), respectively. Not only are they not "demonstrably" intentional changes, but Cope (1900, p. 755) and Dugès (1896, p. 481) used the correct, original spellings in later publications. Therefore, the former names are not emendations and have no possible status in nomenclature.

Specimens of *Rhadinaea laureata* have been found under rocks and logs (Davis and Smith, 1953; Smith, 1943). Duellman (1961, p. 107) reported that the species is abundant in Michoacán, where "Most specimens were found beneath volcanic rocks imbedded in the ashy soil in pine forest between 1800 and 2300 meters." The specific epithet evidently is formed of the noun *laureus* (the laurel tree or, by extension, a crown of laurel or a crown in general) plus the suffix *-ata* (provided with), in allusion to the pale lines that set off the dark top of the head.

THE *decorata* GROUP

The following 11 species comprise the *decorata* group as here defined: *Rhadinaea bogertorum*, *R. cuneata*, *R. decorata*, *R. forbesi*, *R. gaigeae*, *R. hesperia*, *R. macdougalli*, *R. marcellae*, *R. montana*, *R. myersi*, and *R. quinquelineata*. One species, *R. decorata*, ranges from San Luis Potosí to Ecuador, but the others are exclusively Mexican, occurring mainly in the area of the Sierra Madre Oriental to the Sierra Madre del Sur.

The *decorata* group is defined especially by the following combination of characters (see also table 3); The hemipenis is single and without special features (table 2). There is normally a subpreocular, and anal ridges are usually present on adult males. The body is variably striped or lined, but there is invariably at least a hint of a narrow, linear dark marking involving row 4 or 5, and this in some cases is bordered above by a pale streak or series of small pale spots. There is invariably a conspicuous, pale postocular marking extending from, or lying a short distance behind, the upper rear edge of the eye; this marking may be in the form of an ocellus or wedge, but in most species it is a broken or single line, which is in some cases confluent with a pale stripe on the side of the neck. The line may extend horizontally toward the neck or obliquely toward the corner of the mouth.

These are prettily striped little snakes, but they are rather generalized and lack special features of the kind that set off other species groups of *Rhadinaea*. There seem to be two major core assemblages: The series *montana-gaigeae-quinquelineata-forbesi* forms one subgroup, and is characterized by a tendency for a pale grayish stripe or streak (absent in *forbesi*) on each side of a well-defined vertebral dark line. Often there is a short white line on the midline of the nape, in front of the vertebral dark line. Except for *forbesi*, there is a tendency for a relatively high number of ventrals and lack of encroachment of the dorsal ground color onto the ventral tips, which, however, may be dotted or spotted with dark pigment. The remaining seven species possibly form another natural subgroup, but it is less well defined: They exhibit a tendency toward interruption and loss of the vertebral dark line (except in *hesperia*). There are lower numbers of ventrals than in the other subgroup, and often the lower sides (below the lateral dark

TABLE 6

ASPECTS OF INTERSPECIFIC VARIATION[a] IN THE *decorata* GROUP

Species	N	Ventrals		Subcaudals		Tail Length as a Percentage	
		Males	Females	Males	Females	Males	Females
bogertorum	2	158 —	163 —	80 —	65 —	29.7 —	26.1 —
cuneata	2	153 —	153 —	115 —	95 —	34.3 —	34.7 —
decorata[b]	191	110–127 (96) 117.5±0.38	114–134 (95) 124.1±0.43	85–123 (50) 106.5±1.15	88–120 (49) 102.7±0.98	37.9–47.6 (49) 42.9±0.36	35.3–44.7 (47) 40.4±0.32
forbesi	9	138–144 (7) 141.1	136, 149 142.5	56–67 (7) 63.1	— —	24.8–29.0 (7) 26.9	— —
gaigeae	85	156–175 (39) 166.6±0.72	161–184 (46) 175.2±0.77	87–112 (33) 101.0±0.98	81–104 (29) 94.1±0.93	28.6–34.2 (33) 32.1±0.30	27.5–33.0 (27) 29.9±0.23
hesperia[b]	50	139–164 (30) 153.9±1.18	147–177 (18) 164.2±1.88	110–137 (21) 121.9±1.53	104–118 (14) 110.5±1.11	35.4–41.6 (20) 38.8±0.45	32.3–39.0 (14) 35.5±0.58
macdougalli	3	119 —	124, 131 127.5	74 —	60, 64 62.0	35.6 —	29.3, 31.3 30.3
marcellae	1	128 —	— —	77 —	— —	32.6 —	— —
montana	4	171 —	173–186 (3) 178.7	100 —	97–101 (3) 98.7	33.0 —	29.6–32.4 (3) 30.0
myersi	3	132, 135 133.5	139 —	79, 79 79.0	72 —	32.8, 34.7 33.8	29.9 —
quinquelineata	1	— —	179 —	— —	76 —	— —	26.2 —
Combined ranges	351	110–175	114–186	56–137	60–120	24.8–47.6	26.1–44.7

[a]The following statistics are given if the sample is sufficiently large: Above, range followed by number of specimens in parentheses (if more than two); below, mean and standard error of the mean.

[b]A geographic breakdown of ventral and subcaudal counts is given in the species account. For purposes of identification, the species of the *decorata* group should be compared with the Mexican populations of *R. decorata*.

TABLE 7
NUMBER OF MAXILLARY TEETH IN THE *decorata* GROUP

Species	N[a]	No. of Teeth 14+2	15+2	16+2	17+2	18+2	19+2	20+2	21+2	22+2	23+2	24+2	Range
bogertorum	1	—	—	—	—	—	—	1	—	—	—	—	20+2
cuneata	2	—	—	—	—	—	—	—	2	—	—	—	21+2
decorata[b]	119	—	—	—	1	2	18	21	33	21	17	6	17+2–24+2
forbesi	7	—	1	3	3	—	—	—	—	—	—	—	15+2–17+2
gaigeae	25	—	—	4	8	8	5	—	—	—	—	—	16+2–19+2
hesperia[b]	14	—	—	—	—	1	1	4	1	2	5	—	18+2–23+2
macdougalli	3	1	—	2	—	—	—	—	—	—	—	—	14+2–16+2
marcellae	1	—	—	—	1	—	—	—	—	—	—	—	17+2
montana	4	—	—	—	3	—	1	—	—	—	—	—	17+2–19+2
myersi	3	—	—	—	—	—	1	1	1	—	—	—	19+2–21+2
quinquelineata	1	—	—	—	—	—	1	—	—	—	—	—	19+2
Combined	180	1	1	9	16	11	27	27	37	23	22	6	14+2–24+2

[a]A single maxilla from each specimen.
[b]A geographical breakdown is given in the species account.

line on row 4 or 5) are somewhat of a darker hue than the rest of the body.

Rhadinaea bogertorum, new species

Figures 10J, 11G, 13; map 5

Rhadinaea species (*decorata* group), BOGERT, 1968, p. 15.

HOLOTYPE: AMNH 100907, an adult male from 10.5 miles (16.8 kilometers) by road north of Cerro Pelón, near km. 123 on Tuxtepec Road, 6650 feet (2027 meters), Sierra de Juárez, Oaxaca, Mexico. The specimen was caught by Martha R. Bogert on August 27, 1967.

PARATYPE: AMNH 100906, a female from 10 miles (16 kilometers) by road northeast of Cerro Pelón, near km. 120 on Tuxtepec Road, 6800 feet (2073 meters), caught by Charles M. Bogert on August 10, 1967.

DIAGNOSIS: *Rhadinaea bogertorum* seems to be most closely related to, and likely to be confused with, one or two other species of the *decorata* group that also occur in the state of Oaxaca. It most nearly resembles the geographically isolated *R. myersi*, as both species have only a weak indication of a narrow, dark vertebral line, and a gray or black lateral line that may be interrupted by a pale spot on the upper part of each scale in row 4. But *R. bogertorum* has a greater number of ventral plates, and the male organ has a larger capitulum, which comprises at least half the length of the hemipenis (sulcate side) rather than about two-fifths as in *myersi*.

Rhadinaea bogertorum is distinguished from the neighboring *R. macdougalli* in having more ventrals, a slightly different pattern (see Remarks), and probably in larger size and more maxillary teeth.

DISTRIBUTION: Known only from the type locality and vicinity, in the Sierra de Juárez (part of the Sierra Madre del Sur) of north-central Oaxaca, in cloud forest at 2025–2075 meters elevation.

DESCRIPTION OF HOLOTYPE AND PARATYPE: The following is a combined description, but points of difference between the male holotype and female paratype are noted in the appropriate places.

The holotype is 448 mm. total length, of which the tail is 133 mm. (29.7 percent) of the total, and is presumed to be an adult because of the presence of anal ridges on the body and fully ossified spines on the well-developed hemipenes. The paratype is 341 mm. total length, of which the tail is 89 mm. (26.1 percent) of the total; if not an adult, this individual was at least approaching sexual maturity, judged from its size and the condition of the ovaries, which contain maturating ova as large as 2 mm. in greatest length. Dorsal scales lack apical pits and are smooth, in 17–17–17 rows. Anal ridges are present on the male and absent on the female.

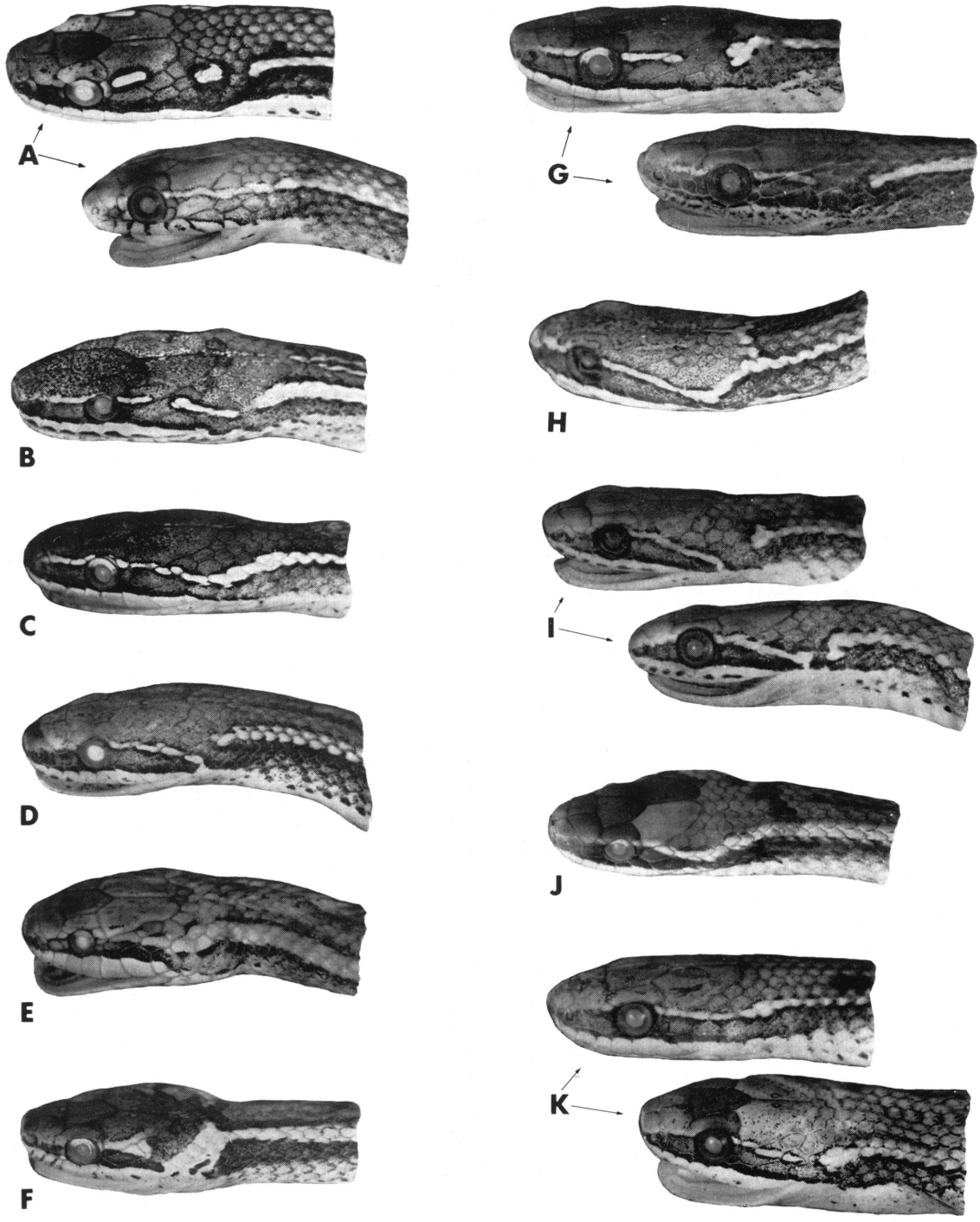


FIG. 10. Head patterns in the *decorata* group. A. *Rhadinaea decorata* (see also fig. 15)—upper, UIMNH 35471, Veracruz; lower, USNM 166933, Ecuador. B. *R. montana*, FMNH 30826 (holotype), Nuevo León. C. *R. gaigeae*, UAZ 26582, Tamaulipas. D. *R. forbesi*, USNM 110365 (holotype), Veracruz. E. *R. quinquelineata*, USNM 31350 (lectotype), Puebla. F. *R. cuneata*, UAZ 26580 (holotype), Veracruz. G. *R. hesperia*—upper, TCWC 7489, Guerrero; lower, TCWC 7378, Morelos. H. *R. marcellae*, LSU 270 (holotype), San Luis Potosí. I. *R. macdougalli*—upper, UIMNH 37163, no data; lower, AMNH 89618, Oaxaca. J. *R. bogertorum*, AMNH 100907 (holotype), Oaxaca. K. *R. myersi*—upper, UIMNH 6317; lower, LSU 7566 (holotype), both from Oaxaca.

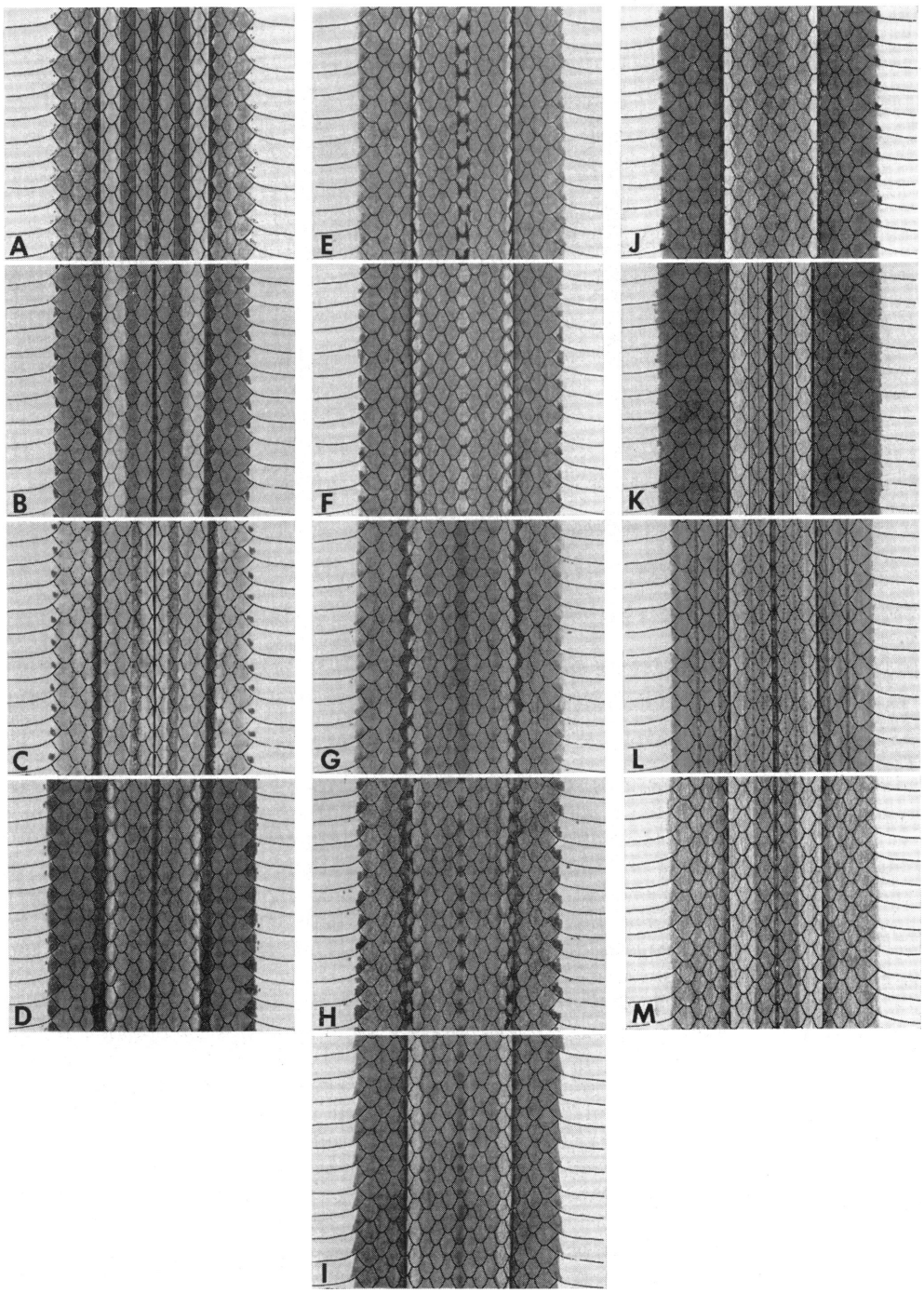


FIG. 11. Midbody color patterns in the *decorata* group. A. *Rhadinaea montana*, FMNH 30826 (holotype), Nuevo León. B. *R. gaigeae*, KU 24016, San Luis Potosí. C. *R. quinquelineata*, USNM 31350 (lectotype), Puebla. D. *R. forbesi*, USNM 110364 (paratype), Veracruz. E. *R. marcellae*, LSU 270 (holotype), San Luis Potosí. F. *R. macdougalli*, UIMNH 3775 (holotype), Oaxaca. G. *R. bogertorum*, AMNH 100907 (holotype), Oaxaca. H. *R. myersi*, UIMNH 6317, Oaxaca. I. *R. cuneata*, UAZ 26580 (holotype), Veracruz. J. *R. decorata*, KU 112443, Panama. K–M. All *R. hesperia*, as follows: K. TCWC 7000, Morelos. L. KU 80871, Sinaloa. M. TCWC 7490, Guerrero.

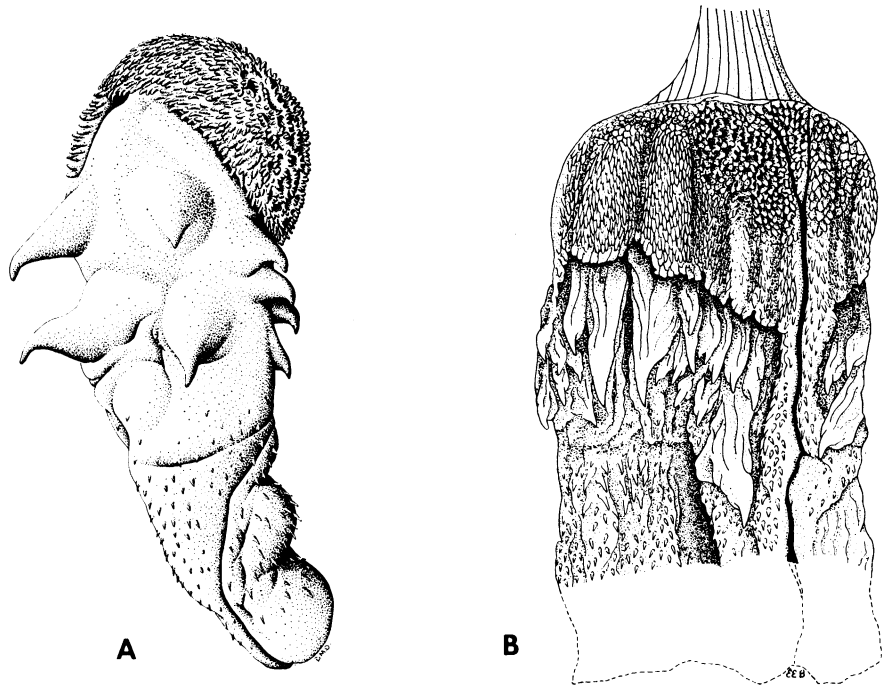


FIG. 12. Hemipenes of the *decorata* group. A. *Rhadinaea decorata*, KU 112446, left organ. ×8. B. *R. myersi*, LSU 7566 (holotype), right organ. ×8.

The male holotype has 158 ventrals, two preventrals, and 80 subcaudals; the female paratype has 163 ventrals, two preventrals, and 65 subcaudals. The anal plate is divided. The rostral plate is about one and one-half (in the holotype) or two times wider than high and is visible from above. The internasals are wider than long and somewhat more than half the length of the prefrontals, which also are wider than long. The frontal plate is barely pentagonal, as there is only a hint of posterolateral corners, and is less than one and one-third times longer than wide. The frontal is equal in length to the interparietal suture, and is either equal in length to the distance from its anterior edge to the tip of the snout (in the holotype) or distinctly longer than this distance. The parietals are about one and two-thirds longer than wide. The supraocular is longer than wide, narrowed in front, and its greatest width is either slightly less than (holotype), or slightly more than, the greatest width of the frontal. The nasal plate has a deep groove below the naris and a more shallow groove above. The loreal is nearly square in the holotype and irregularly shaped in the paratype. The paratype has one large preocular, but in the holotype there are two, of which the bottom one is about as tall as, but narrower than, the upper one. The holotype lacks a subpreocular, but the paratype has one situated between the upper edges of labials 3 and 4. There are two postoculars, the lower being narrower than the upper and only about half as high, and 1+2 temporals. There are eight supralabials, with 2 and 3 touching the loreal, and 3–5 (holotype) or 4 and 5 touching the eye. The holotype has 10 infralabials on each side, with the first five touching the anterior genials and the fifth and sixth touching the posterior genials. The paratype has nine infralabials on each side, with the first four touching the anterior genials and the fourth and fifth the posterior genials. The first pair of infralabials are in contact behind the mental. The posterior genials have a short suture and are longer than the anterior genials, which are in contact for most of their length. The diameter of the eye is equal to the distance from its anterior edge to the rear edge (in holotype) or center of the naris, going about one and two-thirds (in holotype) or

one and one-half times into the length of the snout. Tiny scale organs (tubercles) are present dorsally and ventrally on the head, being most numerous anteriorly.

The holotype is mostly dark grayish brown, but the paratype is a light brown and has a noticeable grayish tinge only on its sides. The vertebral row and adjacent edges of the paravertebral rows are occupied by a gray streak that starts on the neck and extends onto the tail, where it becomes a thin, weak line that goes nearly to the end of the tail. This median streak is paler on the paratype, which, however, has tiny spots of the dark pigment on the bases of the vertebral scales, especially on the neck. The vertebral gray line is least conspicuous on the holotype because this specimen has the median seven scale rows dark grayish brown, which fades to a light brown in row 5 and a part of row 4. A dark lateral line occupies row 4, except for a light brown, posterodorsal section of each scale, and overlaps onto the extreme lower edges of scales in row 5. This lateral line is black in the holotype but in the paratype it is light gray, except for tiny black dashes along the lower edge of the fifth row. The lateral line disappears toward the end of the tail. The sides below the lateral dark line are grayish brown, and in the paratype the sides are slightly darker than the dorsal surface. The grayish ground color low on the side of the tail (row 1) appears as a relatively pale line because it is bordered by the dark lateral line above and dark subcaudal tips below.

The top of the head is dark (holotype) or light brown and lacks a pair of parietal dots. An indefinite whitish line extends along the canthus rostralis and through the top of the eye, becoming a conspicuous white line that slants slightly posteroventrally to a point above the corner of the mouth, then rising posteriorly to the neck and becoming continuous with the pale brown streak above the lateral dark line. The pale streak is widest and most conspicuous on the neck, where it occupies part of row 6 as well as row 5 and the adjacent spots in row 4. There are fragments of a black edge above the white postocular line, and there is faint, dark edging above the pale stripe on the neck. A black line crosses the rostral of the paratype and is continuous with a dark stripe alongside of the head, whereas the holotype has only a few dark dots on the rostral and the dark stripe starts on the anterior edge of the nasal plate. The dark stripe extends through the eye and below the postocular white line, crossing the corner of the mouth to the neck, where it is continuous with the lateral dark line. The lateral head stripe is mainly black except on the loreal and prefrontal where it is mostly brown; the stripe is narrow where it crosses the corner of the mouth and, although it broadens to the width of about two and one-half scales immediately behind the mouth, it shortly reduces in width to the confines of the fourth scale row. The supralabials are white below the lower edge of the lateral dark stripe, with a few tiny black dots on the first two labials of the holotype and a larger black dot on the first labial of the paratype. The holotype has a few dark dots on the mental and first several infralabials; the paratype has a few inconspicuous specks on the mental and first pair of infralabials. The underside of the head and the venter are yellowish white. The ventrals under the neck have a small, distinct blackish spot on each side, but posteriorly the tips of the ventrals are grayish brown and the dark spots are diffuse and have less contrast. The outer ends of the subcaudals are blackish. The paratype has a black line of pigment across the anterior lip of the partly extruded cloaca, and also a thin, zigzag dark line on the ventral midline of the base of the tail.

A color transparency shows that the paratype in life was overall a rich, almost reddish, brown; the "white" line on the head was pale brown, turning light brown along row 5 on the body; the supralabials were pale yellowish and the top of the iris was pale, reddish brown. The ventral coloration is unfortunately not shown.

The right maxilla of the holotype was examined *in situ*. It bears 20 subequal teeth, followed by a short diastema and two ungrooved fangs, which are about one and one-half times larger than the prediastemal teeth. The last fang is offset laterad. The ultimate prediastemal tooth lies posterior to the front edge of the ectopterygoid process. The maxillae of the paratype are in poor condition but seem to possess about the same number of prediastemal teeth as the holotype, plus or minus one.

The everted hemipenis extends to the base of subcaudal 6 and the retractor muscle originates at the level of subcaudal 23. The capitulum comprises more than half the length of the organ on its sulcate side. The calyces are papillate

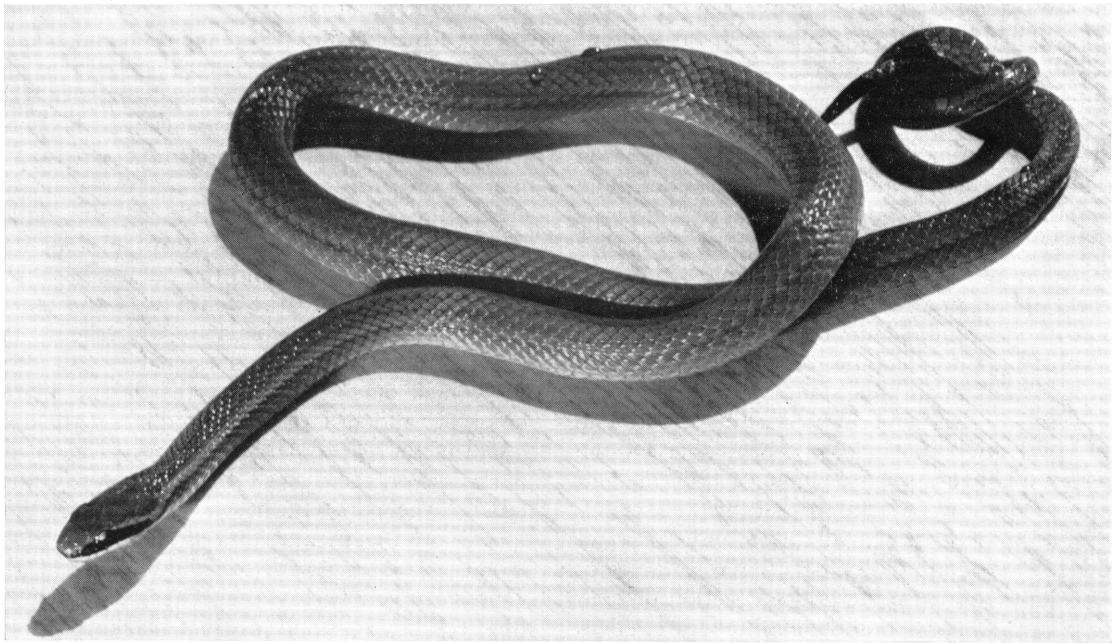


FIG. 13. *Rhadinaea bogertorum.* Paratype (AMNH 100906) in life, from Oaxaca, Mexico. (Photograph by Charles M. Bogert.)

except around the base of the capitulum, where the papillae are replaced by tiny spines in a peripheral band that is narrow on the sulcate side and broad on the asulcate side (probably including most of the asulcate side of the capitulum when the organ is retracted). The sulcus spermaticus forks a third of its length up the capitulum, with the branches extending halfway onto the capitulum. It is not known whether the asulcate wall of the capitulum would form a single or a double fold in the retracted hemipenis. There are 18 or 19 small to medium-sized, slightly recurved spines below the capitulum. Most of the spines, including all the largest ones, are on the asulcate side. The basal fourth of the organ bears spinules only. This description is based on both everted hemipenes of the holotype, the right organ of which was removed and injected with latex.

REMARKS: I at first considered these specimens as representatives of a disjunct population of *Rhadinaea myersi*, a snake of similar habitus and color pattern and one which probably occupies a similar habitat (in or near cloud forest). External differences seem relatively minor, except for the considerably higher numbers of ventrals in *R. bogertorum*. The postocular white line has a slightly greater dip on the two specimens of *bogertorum* than on the three known specimens of *myersi*. The postocular line in *bogertorum* touches on the ultimate supralabial before slanting up and becoming confluent with a light marking on the neck. The postocular line stops short of the supralabial on the specimens of *myersi* and extends to the neck only on one side of one specimen. The small pale spots that interrupt the lateral dark line of *bogertorum* are situated on the posterodorsal section of each scale in the fourth row; the pale spots are situated dorsomedially on the scales of two specimens of *myersi*, and are absent in a third individual. It is possible that additional material will demonstrate an overlap in all features of the color pattern. The hemipenes are the most convincing evidence that two species are involved. The capitulum comprises somewhat over half the length of the organ (sulcate side) in *bogertorum*, as opposed to only two-fifths of the length in *myersi*. Also, there are notable differences in the relative lengths of the parts of the sulcus spermaticus on the capitulum. Thus, each of the branches is twice as long as the undivided part of the sulcus

in *bogertorum*, but the sulcus forks higher in *myersi* and the short branches are only one-third to somewhat less than one-half as long as the undivided part. Unfortunately, the hemipenes of available specimens of *myersi* are in the retracted position and those of *bogertorum* are everted, but the relative lengths of various parts (especially the sulcus) of the hemipenis are usually not much changed from one position to the other.

Comparisons must also be made with *Rhadinaea macdougalli*, which heretofore has been reported only from the Sierra Madre de Chiapas, east of the Plains of Tehuántepec. However, I have identified as *macdougalli* a specimen (AMNH 89618) from Yelagago in the Sierra Madre del Sur; this locality is on the northern part of the Cerro Zempoaltepec ridge—only about 60–70 kilometers southeast of the *bogertorum* localities, but at a lower elevation and separated by the valley of the Río Cajónos. The three known specimens of *macdougalli* have a light brown dorsum (with a scarcely noticeable vertebral line of dark dots) and contrasting darker brown sides. There are pale dashes above a lateral dark line, which is not broken by small, pale spots. This pattern is sufficiently close to that of *bogertorum* and *myersi* that some overlap might be expected when the ranges of variation are better known. The supralabials are most conspicuously spotted in *macdougalli*, but the main difference in head pattern is that the postocular white line of *macdougalli* is somewhat more sharply inclined, and is confluent with the white throat color or very nearly so. Nonetheless, the postocular pattern approaches the condition of *bogertorum* in the specimen of *macdougalli* from the Sierra Madre del Sur. Although the postocular line reaches the throat of this individual (AMNH 89618), there is a short posterodorsad extension that nearly causes a fusion with the pale line on the neck. *Rhadinaea macdougalli* seems to be a smaller, more slender snake than either *bogertorum* or *myersi*, but there is no assurance that *macdougalli* might not attain a larger size than suggested by the three known specimens, which are only 291–297 mm. in total length. Although supposed differences in size are inconclusive because of the small samples, and although color patterns are somewhat similar, I think it unlikely that *bogertorum* and *macdougalli* are conspecific. The specimens of *macdougalli* have 32–39 fewer ventrals and four to six fewer maxillary teeth than the types of *bogertorum* (see discussion on p. 30). All differences combined indicate that these are distinct species.

It is a pleasure to name the species in honor of Charles and Martha Bogert, who collected the only known specimens in the course of their herpetological explorations of the Oaxacan highlands. Bogert (1968, pp. 13–15; 1969, pp. 3, 4) gave some brief notes on the region of cloud forest in which the type locality is situated. Additional notes on the habitats at Cerro Pelón, and a map showing the relationship of the Sierra de Juárez to neighboring ranges, are given by Musser (1964, pp. 3, 4; 1969, pp. 10–12, fig. 2).

Rhadinaea cuneata, new species

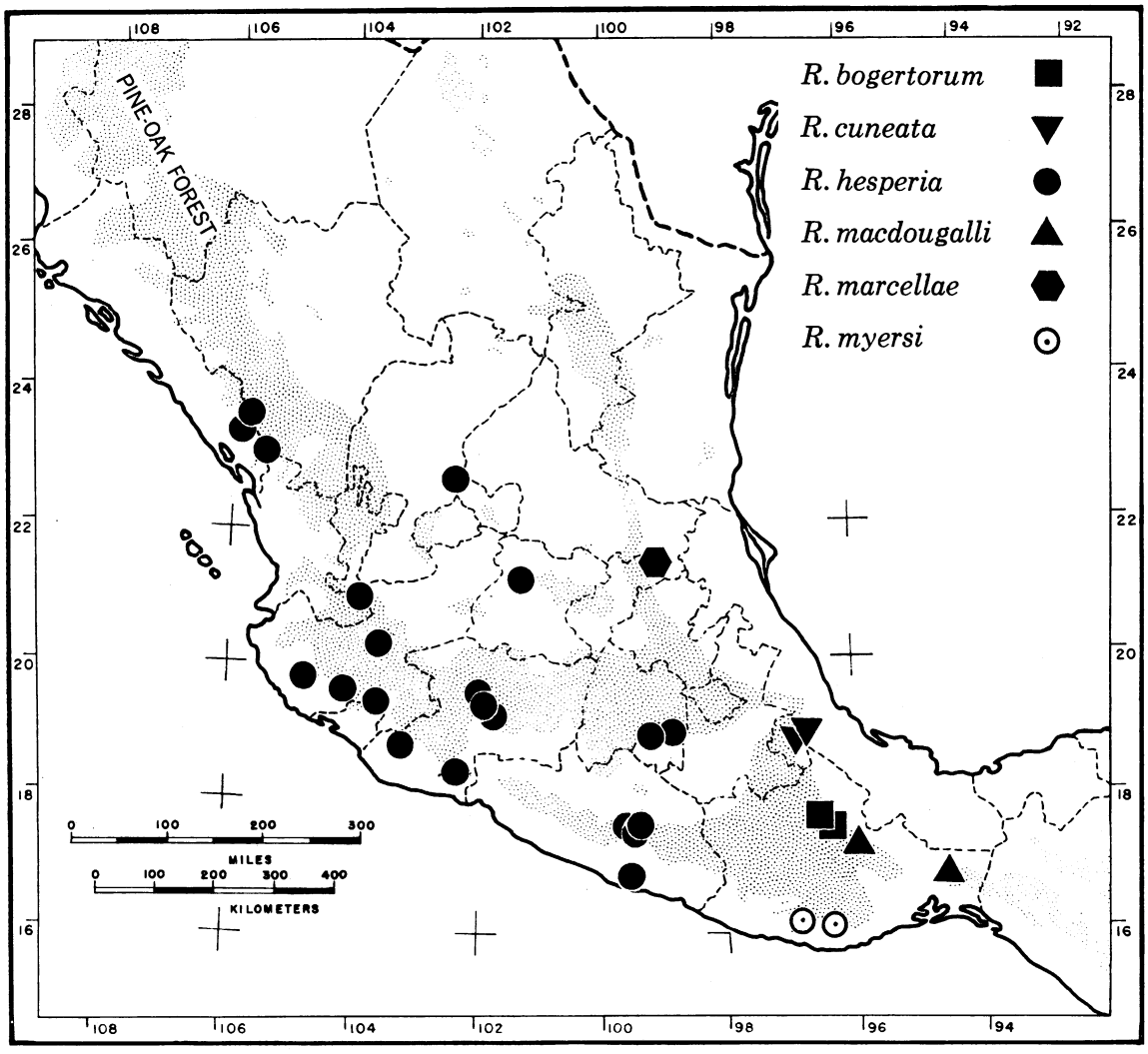
Figures 10F, 11I; map 5

HOLOTYPE: UAZ 26580 (Field No. 3521, R. L. Bezy), a female in good condition, from Ojo del Agua, Nacimiento del Río Atoyac, about 10 kilometers (air line) north-northeast of Córdoba, Veracruz, Mexico. The specimen was purchased from an Indian by Robert L. Bezy and Charles J. Cole, on September 28, 1966.

PARATYPE: UMMZ 128998 (originally UMMZ 95074), a juvenile male from about 9 kilometers southwest of Fortín, Veracruz, Mexico. Purchased from a local resident by Norman Hartweg, in 1940 or 1941.

DIAGNOSIS: *Rhadinaea cuneata* is the only North American species of *Rhadinaea* that has a pale postocular marking in the shape of a wedge. The point of the wedge is at the upper rear edge of the eye, and the wide posterior part occupies about equal portions of the parietal plate and temporal region. There is a pair of large pale blotches immediately behind the head, forming an incomplete collar that is broken on the dorsal midline. Additional specimens conceivably might show the wedge-marking to be variable in shape, but probably this marking is invariably more than a thin line and probably there is always the pair of large pale blotches behind the head.

Sympatric populations of *Rhadinaea decorata* also are characterized by two conspicuous markings on each side of the head and nape, but in *decorata* the markings are paler and heavily rimmed in black, and the one behind the eye is unexpanded and nearly confined to the edge of the parietal plate, with little or no overlap onto



MAP 5. Locality records for six species of the *decorata* group in Mexico. Stipple pattern indicates approximate distribution of pine-oak forest.

the temporal scales. Also, there are significant differences in numbers of ventrals.

DISTRIBUTION: Known only from the Córdoba region of central Veracruz, on the east side of the Sierra Madre de Oaxaca. The elevation is not recorded for either of the two specimens.

DESCRIPTION OF HOLOTYPE AND PARATYPE: The following is a combined description, but points of difference between the female holotype and the juvenile male paratype are noted at the appropriate places.

The holotype is 514 mm. total length, of which the tail is 175 mm. (34.7 percent) of the total; the specimen is presumed to be sexually mature because of its size. The juvenile paratype is 204 mm. total length, of which the tail is 70 mm. (34.3 percent) of the total. Dorsal scales lack apical pits and are smooth, in 17–17–17 rows. Anal ridges are absent on the juvenile, but the female holotype has a few tiny supracloacal tubercles that are indicative of anal ridges. Both specimens have 153 ventrals and a divided anal plate. The holotype has two preventrals and 95 subcaudals; the paratype has one preventral and 115 subcaudals. The rostral plate is more than twice as wide as high and is visible from above. The internasals are a little longer than wide (holotype) or distinctly wider than long,

and are about two-thirds (holotype) or a half as long as the prefrontals. The prefrontals are as wide as long. The frontal plate is barely pentagonal as the posterolateral corners are rounded, especially in the holotype, and the plate is roughly one and one-half (holotype) to one and three-fourths longer than wide. The frontal is a little shorter (holotype) or a little longer than the interparietal suture and is longer than the distance from its anterior edge to the tip of the snout. The parietals are about one and two-thirds (holotype) to nearly twice as long as wide. The supraocular is longer than wide, narrowed in front, and its greatest width is a little more than half of the greatest width of the frontal. The nasal plate has a deep groove below the naris but none above. The loreal is rectangular and longer than high (holotype) or rhomboidal. There is a single large preocular and two postoculars, of which the lower is less than half the size of the upper. The temporals are 1+2. The holotype lacks a subpreocular on the right, but has one on the left side, behind the posterior corner of labial 3 and above the suture between labials 4 and 5; the paratype has a subpreocular between the upper edges of the third and fourth labials. The holotype has nine supralabials, with 2 and 3 touching the loreal and 5–6/4–6 touching the eye; the paratype has eight supralabials, with 2–3 in the loreal and 4–5 in the eye. There are 10 infralabials, except on the left side of the paratype where there are nine. The first pair of infralabials touch behind the mental, the first five touch the anterior genials, and the fifth and sixth touch the posterior genials. The posterior genials are longer than (holotype) or equal to the anterior ones; the posterior genials have a short suture in the holotype but in the paratype they are separated by an azygous scale. The diameter of the eye is equal to the distance from its anterior edge to the center of the naris, going about one and one-half times into the length of the snout. Tiny scale organs (tubercles) are present dorsally and ventrally on the head and are most numerous anteriorly.

There is a median line of small, dark spots starting on the neck and extending onto the tail, where the spots are fused into a continuous dark line that disappears toward the end of the tail. The spots, which are on the ends of the vertebral scales, are distinct and dark brown on the paratype but are faint and blackish on the holotype, where they are rather blurred so as to give the impression of a gray vertebral streak. A blackish brown (holotype) or brown lateral line extends along the body principally on scale row 4 and disappears toward the end of the tail. This line is several scales wide where it originates behind the head, but posteriorly the line narrows to the middle of row 4 (holotype), or to the top of row 3 and all but the upper edge of row 4. The sides below the lateral line are brown in the paratype and grayish brown in the holotype and are somewhat darker than the dorsum. The median seven scale rows of the dorsum are medium brown, which fades to pale brown on each side, thus forming a pale streak that extends along the body on row 5 and the upper part of row 4 above the lateral dark line; the widening of the dark line forces the pale stripe upward on the side of the neck, to the upper half of row 5 and row 6 and, on the holotype, on the lower half of row 7. The light stripe is most conspicuous on the holotype and on both specimens is palest (whitish) and most vivid on the neck; the holotype has a weak, dark line edging the top of the pale stripe on the neck.

The top of the head is brown and there is a pair of pale parietal dots with dark rims. The canthus rostralis is pale but without a discrete line. A whitish, wedge-shaped mark originates at the upper rear edge of the eye as a horizontal line that is posteriorly widened, so that the back part of the marking covers approximately equal portions of the parietal plate and the temporal region. The pale wedge-marking includes a part of each temporal scale within its dark brown edges. Immediately behind the head, on each side, is a large white blotch that has broken dark edges and which is higher than wide and slightly tipped backward, so that the lower edge is close to the bottom temporal and the upper edge is at the paravertebral row on the nape. The pair of markings has the appearance of an incomplete collar; each half of the collar is discrete on the paratype but on the holotype is posteriorly confluent with the white stripe on the neck and ventrally confluent with the white throat color. A black line crosses the rostral and widens on the nasal plate to form a horizontal brown-centered stripe that extends through the eye and onto the last supralabial, where it either terminates (holotype) or is narrowly continuous with the brown sides of the body. All the supralabials, the mental, and the first four pairs of infralabials are conspicuously marked with small black spots on

the holotype, but the paratype has fewer spots that are pale brown. The venter is immaculate except for brown edging that forms a serrated pattern across the ends of the ventrals and a continuous dark line across the ends of the subcaudals. The ventral edging is darkest under the neck, where each little extension of color forms a small blackish spot on the tip of each scute. The color in life is not known.

The right maxilla of the holotype was removed and that of the paratype was examined *in situ*. Both have 21 subequal teeth followed by a sizable diastema and two ungrooved fangs, which are noticeably less than one and one-half times larger than the prediastemal teeth. The last fang is offset laterad. The ultimate prediastemal tooth lies anterior to the front edge of the ectopterygoid process in the holotype and posterior in the paratype.

The left retracted hemipenis of the juvenile paratype is single and extends to the end of subcaudal 5. The retractor muscle originates at the level of subcaudal 16. Little detail can be seen because of the size and state of development of the organ, but the capitulum appears to comprise about half the length of the organ on one side. The unossified spines, of which I could discern less than a dozen, lie close to the capitulum well above the base.

REMARKS: The specific epithet is a Latin adjective meaning wedge-shaped, in reference to the postocular marking that presumably characterizes the species. The paratype of *Rhadinaea cuneata* was originally catalogued together with a series of six specimens of *Rhadinaea decorata*, indicating that these two species occur sympatrically.

Rhadinaea decorata (Günther)

Figures 1B, 10A, 11J, 12A, 14–16; map 6

Coronella decorata GÜNTHER, 1858, pp. 35, 36; 1893 (1885–1902), p. 111.

Diadophis decoratus (Günther): COPE, 1860a, p. 250. BOCOURT, 1886 (1870–1909), pp. 624, 625, pl. 40, fig. 3 (scutellation and color pattern of head and neck, of specimen from Mexico).

E[nicognathus] vittatus JAN, 1863, pp. 266, 271, 272, 327 (pp. 56, 61, 62, 117, in reprint) (Syntypes [not seen] from Mexico, originally in Tübingen and Milan museums). JAN AND SORDELLI, 1866, (1860–1881), vol. 1, livr. 16, pl. 2 (part: fig. 2 only, color pattern and details of scutellation of the syntype from Tübingen Museum). Secondary homonym.

Rhadinaea decorata (Günther): COPE, 1863, p. 101; 1875a, pp. 138, 140; 1887, p. 80; 1895, pl. 25, fig. 8 (illustration of retracted hemipenis of Mexican specimen); 1900, p. 757, pl. 23, fig. 8 (reprint of 1895 illustration of hemipenis). BOULENGER, 1894b, pp. 176, 177, 359. WERNER, 1929, p. 119. DUNN, 1932, p. 1; 1942b, p. 6. SMITH, 1943, pp. 463, 464, pl. 32, fig. 3 (photograph of preserved specimen from Veracruz). SMITH AND TAYLOR, 1945, pp. 116, 117. ALVAREZ DEL TORO, 1960, pp. 170, 172, 176 (poorly reproduced photograph of whole specimen). STUART, 1963, p. 112. MILLER, 1968, p. 430, fig. 33 (drawing of cochlear duct). PETERS AND OREJAS-MIRANDA, 1970, p. 265.

Dromicus ignitus COPE, 1871, p. 201 (holotype: USNM 24501, obtained by T. O. Selfridge on Isthmus of Darién [eastern Panama]).

Rhadinaea ignita (Cope): COPE, 1875a, p. 140; 1887, p. 80.

Coronella ignita (Cope): GÜNTHER, 1893 (1885–1902), p. 111.

Rhadinaea decorata decorata (Günther): COPE, 1900, pp. 757, 758. BAILEY, 1940, pp. 7, 8, pl. 2, fig. 5 (midbody pattern of UMMZ 83180, from Costa Rica). TAYLOR, 1951, pp. 113–116, pl. 11 (photograph of preserved specimen, KU 25733, Costa Rica); 1954, p. 679.

Rhadinaea decorata ignita (Cope): COPE, 1900, pp. 757, 758. DUNN AND BAILEY, 1939, p. 10. BAILEY, 1940, p. 8.

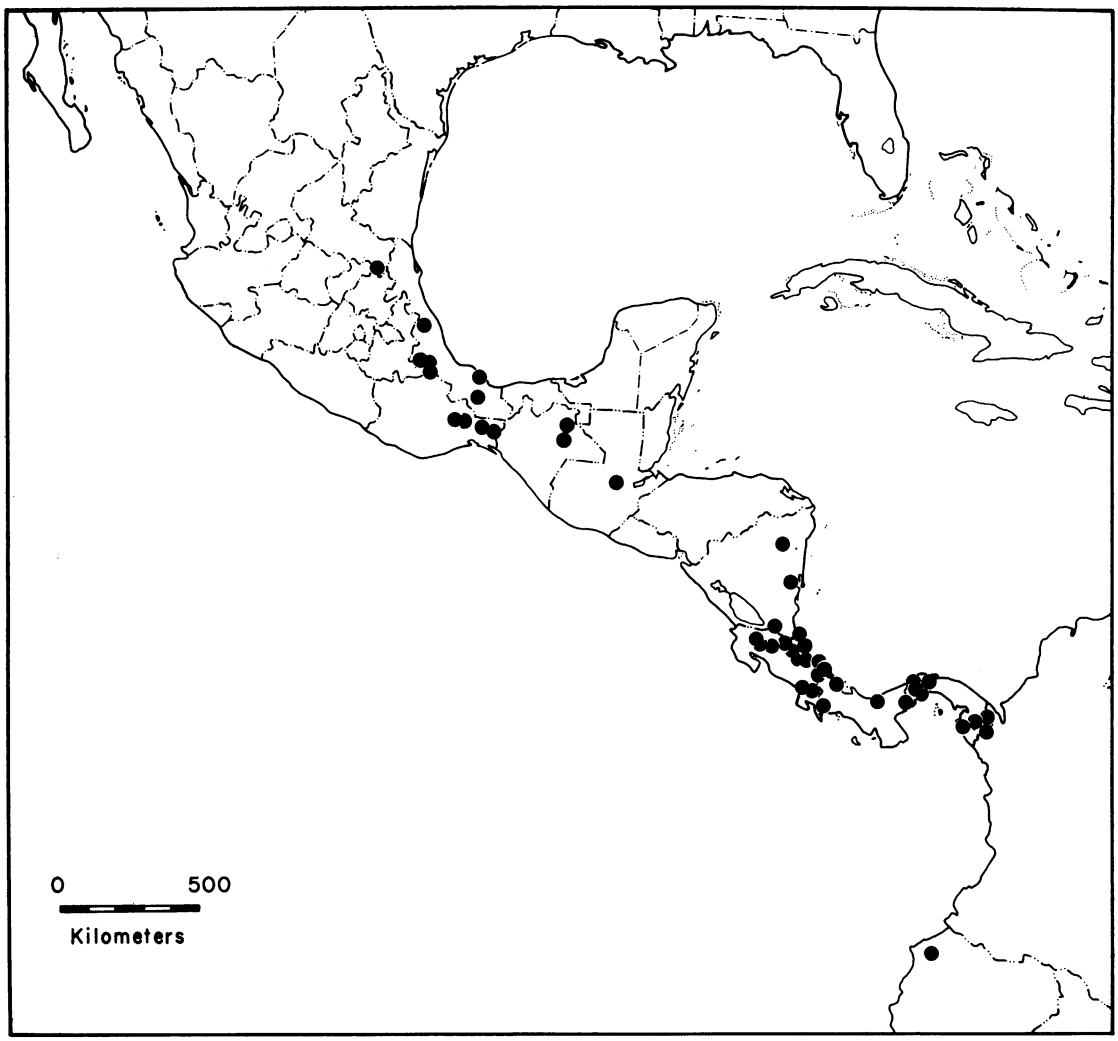
Erythrolamprus longicaudus WERNER, 1904, pp. 348, 349 (holotype [not seen]: originally Zoologische Sammlung des Bayerischen Staates No. 216/0, since lost or destroyed, *fide* Stuart, 1963, p. 112; obtained in Guatemala by Sapper).

Liophis decoratus (Günther): AMARAL, 1929b, p. 171.

Rhadinaea dorsata: UNDERWOOD, 1967a, p. 175 (*lapsus*, based on MCZ 53899 [=*R. decorata*] according to Underwood's unpublished appendix).

DESIGNATION OF LECTOTYPE: There are two syntypes, BMNH 1946.1.9.3 and 1946.1.9.4; both are from Mexico (no other data), collection of M. Sallé. Both specimens are adult females. BMNH 1946.1.9.4 is here designated lectotype because it is in the best condition, even though it is somewhat soft and has a stub tail. The head is of normal proportions (i.e., not aberrantly narrow; see Remarks), but this feature cannot be determined for the other syntype, whose head is in poor condition. The lectotype has 127 ventrals, 1 preventral, 10+ subcaudals, and 8/9 supralabials, with 4–5/5–6 bordering the eyes. The extra labial on the right is a tiny scale situated under the subpreocular.

DIAGNOSIS: This widely distributed snake is easily identified by its general color pattern (figs. 11J, 15). There is a dark lateral line on the



MAP 6. Locality records for *Rhadinaea decorata* in Middle America and northwestern South America.

lower edge of scale row 5, frequently overlapping onto row 4, below which the body is darker than it is above the line; a discrete vertebral dark line is lacking, although a dark streak (one to five scale rows wide) often is discernible. There is a vivid white postocular pattern, which, in the northern part of the range, almost invariably is comprised of discrete ocelli, but which is often a continuous line to the neck in southern specimens (compare fig. 15A–E). Other noteworthy characteristics of *R. decorata* include a long tail (35–47 percent of total length) and a low number of ventrals (110–134).

Mexican and Guatemalan specimens can be immediately separated from all other northern *Rhadinaea* by the conspicuously dark-margined white ocelli, one behind the eye and one on the side of the neck (fig. 15A, C). This pattern (including fig. 15B), when present, also readily identifies southern specimens of *decorata*; *R. guentheri* has similarly placed ocelli but a completely different body pattern (four white lines on a dark ground). Southern specimens of *decorata* having a continuous white line to the neck resemble in this regard the sympatric *R. sargenti* and *R. vermiculaticeps*, both of which, however, have a pale reticulum atop the head, as well as different body patterns.

Northern *Rhadinaea decorata* may be confused with *Coniophanes imperialis*, some specimens of

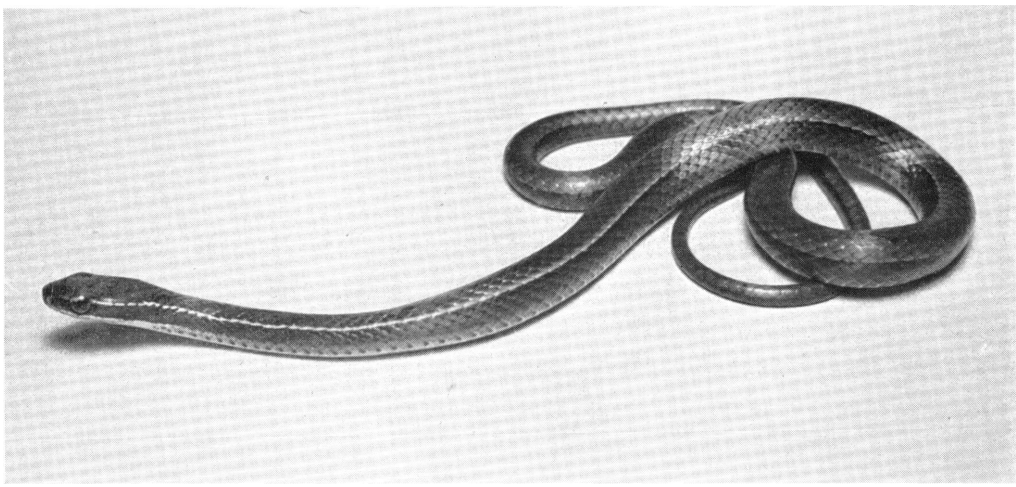


FIG. 14. *Rhadinaea decorata*, KU 112443, from Darién, Panama. Unbroken temporal line is seen only in specimens from southern part of range (compare fig. 15).

which have a color pattern similar to *decorata*; but *C. imperialis* is easily separated from *Rhadinaea* by its grooved fangs and 19–19–17(15) scale rows (17–17–17 in *decorata*).

DISTRIBUTION: Low and moderate elevations in humid, broadleaf forest, from southeastern San Luis Potosí, Mexico, south to northwestern Ecuador. The elevational range is about 0–1200 meters, with a majority of known localities being less than 500 meters.

Rhadinaea decorata is restricted to the Atlantic watershed from Mexico to Costa Rica, although it nearly crosses to the narrow Pacific drainage on the Isthmus of Tehuantepec. A few specimens have been taken on the headwaters of Pacific-drainage streams in northern Costa Rica, and the species occurs in both Atlantic and Pacific lowlands in southern Costa Rica and in Panama, and then only in the Pacific drainage in northwestern South America.

DESCRIPTION (195 SPECIMENS): The largest specimen is a male 470 mm. total length, 205 mm. tail length. The largest female is 444+ mm. total length (with an incomplete tail of 164+ mm.); two other large females each measure 417 mm. total length, with tail lengths of 175 and 182 mm. Specimens over 400 mm. are unusual, as only 11 specimens (five males, six females) exceed that length. The tail is 37.9–47.0 percent of total length in males, and 35.3–44.7 percent in females. The dorsal scales are in 17–17–17 rows (one specimen each with 15–17–17 and 17–17–16). The dorsal scales tend to be noticeably striated, especially posteriorly. In addition to the striations, a majority of specimens have weak keels on some of the body scales; these often are very faint, but occasionally they are moderately strong. Occasionally, the keels are few and confined immediately above the cloacal area, where they are not distinguishable from the anal ridges normally found in many other species of *Rhadinaea*, but more often the keeling extends some few dozen ventrals forward on the body and, on occasional specimens, may even extend more than 100 ventrals forward to the neck. Some specimens have apical "pits" on scales of the neck; the pits, when present, are either single (and positioned off center) or paired.

There are 110–134 ventrals (males, 110–127; females, 114–134), and 67–122 subcaudals (males, 85–122; females, 67, 88–120). There are eight supralabials, or in rare cases nine (five specimens) or seven (two specimens) on one side only; there are usually 10 infralabials, or occasionally nine, or in rare cases 11 or eight. There are one or two postoculars, frequently a subpreocular between the third and fourth supralabials, and two (rarely one or three) postoculars. Temporals are basically 1+2; occasional deviations (usually on one side only) include 1+1, 1+1+2, $1+^{2}_{1}$, and, especially, a fusion of the primary temporal with the upper secondary temporal.

The sides are darker brown than the top of the body and are delimited by a lateral black line, which extends along the lower edge of scale row 5, frequently overlapping onto the top edge of row 4 but less commonly being situated higher, toward the middle of the fifth row. A narrow, dorsolateral white or tan stripe on the neck is bordered by the lateral black line below and by another black line above, on the sixth or seventh row. The latter marking disappears posterior to the neck and the white or tan stripe turns pale brown, in some cases fading into the brown of the dorsum and in some remaining discernible as a poorly defined light stripe for the length of the body. The middorsum is brown, either uniform light brown or with a dark brown or grayish brown median streak, which may be the width of one, three, or five scale rows. The median dark streak, when present, lacks sharply delimited edges (except occasionally on the neck); it is very obvious in some cases but often it is vague and shades almost imperceptibly into the dorsal ground color. These linear markings disappear before reaching the end of the tail. A white streak originates in the pale throat and extends on the first scale row along the lower side of the neck, usually disappearing posteriorly but occasionally extending faintly for the length of the body.

The brown head is conspicuously marked with a black-edged, vivid white postocular pattern of considerable variability (see Geographic Variation). The basic types of head pattern are shown in figure 15; these differ first of all in whether there are discrete ocelli (fig. 15A–C) or a continuous stripe (fig. 15D, E). Figure 15A–C shows the pattern of a somewhat elongated white ocellus behind the eye, followed after a gap by another ocellus that is situated between the temporal plates and the anterior end of the white stripe on the neck. The discrete postocular marking may be aligned horizontally (fig. 15A) or slanted upward (fig. 15C), in both of which cases it usually lies mainly on the parietal plate, or it may slant downward to lie mainly on the temporals (fig. 15B); this marking may include the postocular plate in any of the above situations. In some populations there is a solid white stripe that extends posteriorly from the eye to fuse with the dorsolateral white or tan stripe on the neck. This stripe may be aligned horizontally (straight or slightly wavy; fig. 15D) or it may have a conspicuous dip in the temporal region (fig. 15E). Occasional modifications occur on the basic patterns shown in figure 15. Thus, there may be an essentially continuous stripe except for a short break in the temporal region or on the neck, or the posterior ocellus and neck stripe may be fused although the postocular marking remains well separated; but the great majority of specimens fit one of the patterns illustrated. A pair of white parietal dots may be present or absent. Sometimes there is a vague whitish streak on the canthus rostralis, but it is never well defined. The side of the head is darker than above and a blackish line edges the anterior supralabials, passes under the eye, and extends

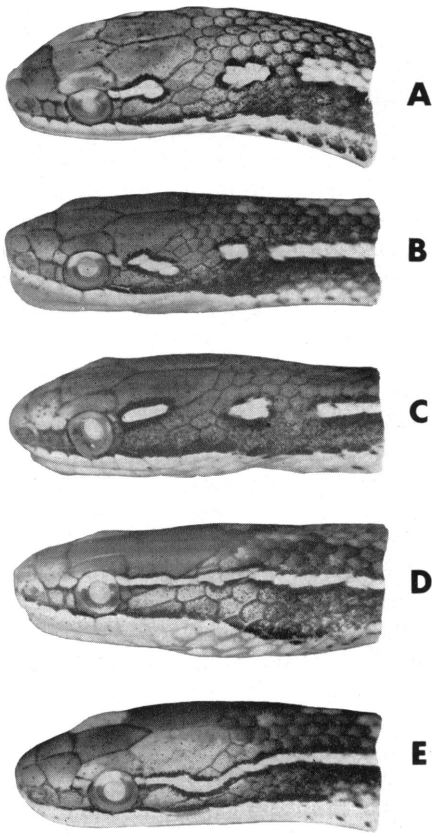


FIG. 15. Variation in head pattern of *Rhadinaea decorata*. A. Postocular and neck markings discrete and in straight line (USNM 30610). B. Postocular and neck markings discrete, with downward slant to postocular mark (KU 75741). C. Postocular and neck markings discrete, with upward slant to postocular mark (UIMNH 48762). D. Continuous, straight line from eye to body (KU 75745). E. Continuous line from eye to body, with depression in temporal region (KU 75740).

across the posterior labials to the lower side of the neck. The supralabials are white below the dark line, and may be immaculate or weakly dotted with black or with dark pigment along the common sutures. The underside of the head is white, with or without some black dots near the chin. There is usually a row of small black spots or elongated dashes, sometimes confluent, across the ends of the ventral plates, and a solid black line across the subcaudal tips; a few individuals have irregular dark speckling on the subcaudal surfaces. The venter is otherwise white in preserved material (but see the following section, Color in Life).

The maxillary teeth vary geographically from 17+2 to 24+2. The majority of specimens have the ultimate prediastemal socket lying posterior to the ectopterygoid process, but this socket occasionally lies anterior to the process in specimens with the lower numbers of teeth. Some of the specimens with higher numbers of teeth additionally have all or part of the penultimate prediastemal socket lying posterior to the ectopterygoid process. There is normally a diastema (fig. 1B), but it may be short in specimens having the higher numbers of teeth; a few specimens examined completely lacked a diastema, evidently because of their large number of teeth. The last fang is offset laterad.

The hemipenis shows remarkable variation, largely geographic, in shape and size and in the number of spines. It varies particularly in length, extending to the levels of subcaudals 5–14 in retracted organs of 57 specimens and to subcaudals 5–12 in everted organs of 15 others. The everted hemipenis ranges from short and bulbous to long and slender (fig. 16). The retractor muscle originates at the levels of subcaudals 21–32 in 14 specimens with varying sized hemipenes; the retractors tend to originate further posteriad in specimens having the longer hemipenes although the correlation is not perfect. The capitulum on its sulcate side comprises from about half of the length of the shorter organs to a fourth or a fifth of the length of the long, slender organs (fig. 16). The distal calyces are papillate, whereas those around the basal part of the capitulum and on the asulcate fold are spinulate. The sulcus spermaticus forks at a point about one-third of its length up the capitulum; the branches stop short of the tip of the retracted hemipenis and extend little more than halfway up the capitulum when the organ is everted. The wall of the capitulum forms a single large fold on the asulcate side of the retracted hemipenis. The edge of the capitulum is fused to the underlying stalk below the asulcate fold, and this fusion is obvious on the everted hemipenis (fig. 12A). There are about 15–50 small to large, recurved spines below the capitulum; several large spines lie on the asulcate side and varying numbers of smaller spines are situated laterally and on the sulcate side. The basal half to three-fourths of the organ (depending on its total length) is free of spines and is ornamented solely with spinules. Variation in length was determined by examination of hemipenes from 72 specimens. Details of structure are based primarily on everted hemipenes from KU 75740, 75741, 75745, 80239, 80601, 112442–112444, 112446 (illustrated), TCWC 21391 (illustrated), and USNM 120832 (illustrated), and on retracted hemipenes from MCZ 15304, 15310, and UIMNH 25959 and 37160.

Color in Life: I have made color notes from life of specimens collected in northwestern, central, and extreme eastern Panama (KU 112442–112447, 112450, 112452). The postocular stripe or ocelli were usually white, although the stripe was pale tan in one individual. On the neck, the anterior part of the dorsolateral stripe was white in most, but pale tan in a few, turning tan farther back on the neck, and orangish brown or light orange on the body; this marking faded into the brown of the body in one individual, but on most it remained distinct as a narrow orangish region between the brown middorsum and grayish brown side. The labials and underside of the head and throat were white, turning pale orange under the neck (pale yellow in one) and then becoming uniform red or reddish orange by ventral 28–45; one small juvenile was pale orange under the body and tail, rather than the usual reddish orange color. The upper sector of the iris was pale tan to pale orange-red, and the lower part varied from dark brown through orange-brown to reddish brown.

The specimen (KU 112442 from extreme eastern Panama) mentioned above as having pale tan rather than white head markings is the same one in which the underside of the neck was yellow rather than pale orange. A Costa Rican specimen (Taylor, 1951, p. 115) and another from Nicaragua (collector's field notes for AMNH 12717) also were pale yellow under the neck, between the white chin and red belly; the

Nicaraguan specimen also had pale yellow rather than white head markings and a pale yellow dorsolateral area. Cope ("1893" [1894], p. 344) emphasized that an individual from Boruca, Costa Rica had a yellow rather than red venter, but it is not known whether this represented the condition in life. Taylor (1954, p. 737) stated that a specimen from Tenorio, Costa Rica had a pink venter. Boruca (Puntarenas Province) and Tenorio (Guanacaste Province) are both on the Pacific drainage of Costa Rica, and additional color notes on Pacific-side specimens are needed; specimens from the Atlantic drainage of Costa Rica had red bellies (Taylor, 1951, p. 115; and collector's field notes for UF 10190).

A specimen from Veracruz was said to have a bluish white belly (W. E. Duellman, field notes for UMMZ 114657).

GEOGRAPHIC VARIATION: *Rhadinaea decorata* is a wide-ranging species and, not surprisingly, undergoes geographically correlated variation in a number of features, including color pattern, scutellation, number of teeth, and hemipenis. Nonetheless, interpopulational differences are not so great as might be expected within such a large geographic area (map 6) and involve average rather than absolute differences between populations. A sparsity of material from many areas, upper Central America for example, prevents meaningful conclusions about possible intraregional differences or whether apparent clines are smooth or stepped. Such knowledge would be of evolutionary interest but probably is of no great taxonomic importance in the present case, because the degree of difference between populations seems too slight to arouse suspicion that there might be more than one species, or even to warrant recognition of subspecies.

The most obvious variation occurs in the vivid white markings on the rear of the head. There are several distinct types of patterns, which were coded A through E, as shown in figure 15 and as tabulated below. A very few specimens have different patterns on the left and right sides. A Costa Rican snake was coded B/E and the single Ecuadoran specimen is E/D; these are arbitrarily tabulated according to the condition on the left side. Other relatively rare variants usually agree more closely with one of the major pattern types than another and were not difficult to classify. One Mexican specimen, for example, has elongated, nearly connected markings, which, however, are still discrete and more like pattern A than D. Several individuals coded B or C have the neck marking fused with the pale line behind, but the postocular mark is discrete and well separated. A Costa Rican snake coded D has a slight break in the line on the side of the neck, but there is no hint of discrete markings in the white line that extends anteriorly to the eye.

		Head Pattern				
Region	No.	A	B	C	D	E
Mexico	106	14	—	92	—	—
Guatemala	2	—	—	2	—	—
Nicaragua	6	6	—	—	—	—
Costa Rica–W. Panama	47	38	1	5	3	—
Central–E. Panama	33	3	5	—	17	8
Ecuador	1	—	—	—	—	1

It is seen that the variation is slight in the northern part of the range, where there are only two major types of head pattern and only one that is common; but there is considerable variation in the southern part of the range, where the common Mexican type of pattern (C) becomes rare and then seems to disappear. The fusion of the markings into a continuous line (types D and E) is the basis for the name *Dromicus ignitus* Cope, type locality Isthmus of Darién; this sort of pattern is common in central and eastern Panama but it is variable and not sufficiently predominant to warrant recognition of a separate subspecies. More than one-third of the specimens coded D or E have a break in the line at the rear of the temporal region.

Normally the supralabials are nearly immaculate or only weakly spotted with dark pigment (fig. 10A, upper head; fig. 15). Therefore it is probably of geographic significance that the only known Ecuadoran specimen has conspicuous extensions of dark pigment along the common labial sutures (fig. 10A, lower head).

A middorsal dark streak, one, three, or five scale rows wide, may be present or absent in any part of the range. This marking frequently is weak and diffused and consequently difficult to code, but it seems to vary regionally as follows. It is absent in half (51 of 100) of the Mexican-Guatemalan specimens coded, and absent in about 36 percent (29 of 81) of the specimens from Nicaragua to Panama. The streak is one scale row wide in about half of the northern specimens possessing it, and three or five rows wide in equal numbers of the remaining specimens. By contrast, the streak is three rows wide

in more than half (69 percent) of southern specimens possessing it, less commonly the width of one row (27 percent) or five rows (4 percent). The single Ecuadoran specimen has a middorsal streak that is three rows wide.

There may be significant geographic variation in coloration, particularly of the ventral surfaces (see Color in Life). Specimens from Panama through Nicaragua have reddish venters (turning yellow and/or white anteriorly), whereas a Mexican specimen had a bluish white venter. More color descriptions are needed, especially of northern individuals.

Not counting the subpreocular, there is normally but a single preocular in northern specimens; there are two preoculars on one or both sides of the head in only nine of 107 specimens from Mexico and Guatemala. Individuals from Nicaragua and Costa Rica also usually have a single preocular, there being two in only seven of 45 specimens. But the situation is quite different in Panama, where more than half of the sample (22 of 40) has two preoculars on one or both sides.

Another geographically variable aspect of scutellation is the presence or absence of weak keels on the body scales. Although easily overlooked, keels seem completely absent on only 17 percent of 109 specimens from Mexico and Guatemala, in contrast to 46 percent of 85 specimens from Nicaragua to Panama. The single Ecuadoran specimen also lacks keels.

Mexican specimens have, on the average, several more ventral plates than do individuals from lower Central America, but the differences seem small considering the distance involved.

Mexico	
Males (20)	Females (30)
114.6±1.01 (105–123)	106.5±0.84 (100–120)
Costa Rica	
Males (14)	Females (7)
102.4±1.67 (85–109)	95.3±1.85 (88–101)
Panama	
Males (16)	Females (10)
100.1±0.74 (95–105)	96.1±1.60 (89–105)
Ecuador	
—	Females (1)
—	67

The female specimen from Ecuador has 119 ventrals and so falls within the ranges of the above samples.

As with the ventrals, Mexican specimens have more subcaudal plates than do specimens from lower Central America, but the differences between the means are much more pronounced and there is little overlap between the ranges. In addition, the Ecuadoran specimen has 21 fewer subcaudals than the next lowest number for a female (from Costa Rica), although the ventral count of the Ecuadoran snake lies within limits of variation of the northern populations.

Mexico	
Males (50)	Females (54)
119.7±0.45 (112–127)	126.4±0.51 (116–134)
Costa Rica	
Males (22)	Females (17)
116.0±0.55 (111–120)	121.1±0.71 (114–125)
Panama	
Males (21)	Females (19)
114.0±0.36 (110–116)	121.1±0.63 (115–126)

The number of maxillary teeth ranges from 17+2 (total =19) to 24+2 (total =26). There is a decided tendency for northern specimens to have more teeth than southern ones, as shown by the following tabulation:

		Number of Teeth								
Country	N	19	20	21	22	23	24	25	26	Mean
Mexico	60	–	–	–	1	19	17	17	6	24.1
Guatemala	2	–	–	–	–	–	2	–	–	—
Nicaragua	3	–	–	1	1	1	–	–	–	—
Costa Rica	22	1	2	11	6	2	–	–	–	21.3
Panama	31	–	–	6	13	10	2	–	–	22.3
Ecuador	1	–	–	–	–	1	–	–	–	—

It is my impression that northern specimens usually have a smaller diastema on the maxilla than is seen in southern individuals; a diastema was completely lacking in a few Mexican specimens. The size of the diastema seems correlated with the number of tooth sockets, but it might also be influenced by differences in the length of the maxilla.

There is striking variation in the length and shape of the hemipenis, which ranges from the short, bulbous organ to the long, slender one (fig. 16). If extreme examples are compared, as in figure 16, it appears that two distinct species must be involved, but there is a continuous gradation in size of the organ, as shown by the following tabulation of the lengths of 57 retracted hemipenes from as many individual snakes. These data further indicate the existence of geographic variation in length of the hemipenis:

Country	N	Subcaudals Spanned 5	6	7	8	9	10	11	12	13	14
Mexico	32	1	5	16	10	–	–	–	–	–	–
Nicaragua	2	–	–	1	1	–	–	–	–	–	–
Costa Rica	13	–	1	2	1	3	–	3	1	2	–
Panama	10	–	5	2	–	1	1	–	–	–	1

Variation in hemipenial length is relatively slight in the northern part of the range but is obviously great in lower Central America. Unfortunately, it is not now possible to estimate the extent of variation within single populations or to determine adequately the nature of interpopulational variation in lower Central America; the sample is too small and several Costa Rican specimens lack adequate locality data. But it appears that the longest and most slender hemipenes (i.e., those 11 or more subcaudals in length) are to be found in specimens of the Atlantic rain forest, from as far north as La Lola, Limón Province, Costa Rica, to at least the Río Concepción, Veraguas Province, Panama. Specimens from outside of the aforesaid region have hemipenes either the same size as, or longer than, the organs of Mexican specimens, and it is possible that additional data will reveal a complex pattern of variation. For example, four specimens from the Serranía de Pirre region, extreme eastern Panama, have hemipenes 6–7 subcaudals in length, whereas in three individuals from the nearby Serranía del Darién the range is 7–11 subcaudals; the range in several specimens from central Panama is 5–7 subcaudals.

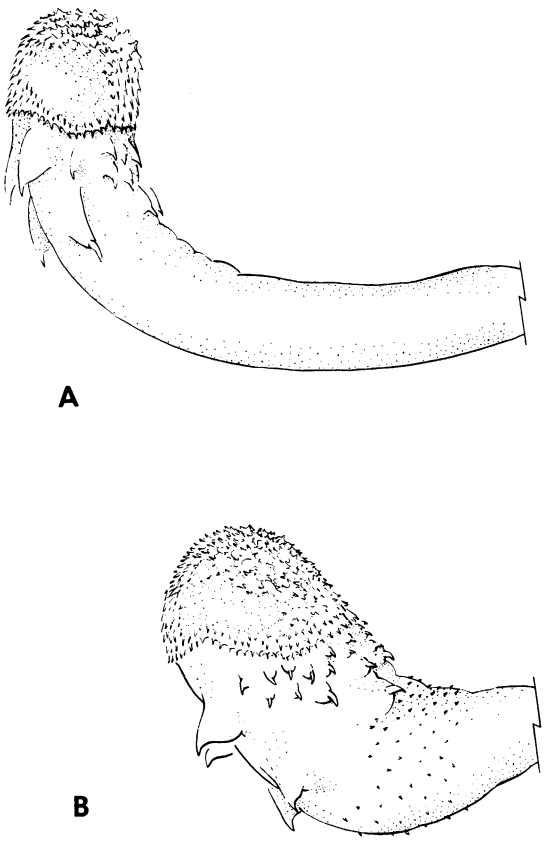


Fig. 16. Variation in hemipenis of *Rhadinaea decorata*. A. Right everted organ (11 subcaudals long) of USNM 120832 from Costa Rica. B. Right everted organ (seven subcaudals long) of TCWC 21391 from Veracruz, Mexico. Both are drawn to same scale.

There also is considerable variation in the number of spines present on the hemipenis but, again, no clear picture emerges from the available data. On the shorter hemipenes, I have counted 21–50 spines in Mexican specimens and 15–18 spines in Costa Rican and Panamanian specimens; I obtained counts of 28–33 spines on several long, slender hemipenes of specimens from the Atlantic rain forests of southern Costa Rica–western Panama.

Remarks: Specimens of *Rhadinaea decorata* recently have been taken close to the international border in extreme eastern Panama, and so the species certainly occurs at least in the immediately adjacent parts of Colombia. Nevertheless, there seem to be no acceptable records for Colombia. Werner (1899) described a snake from the Magdalena Valley in sufficient detail to show that it was not *decorata* as claimed, although it might have been a specimen of *Rhadinaea fulviceps* (*q.v.*). The Chocó specimen that Boulenger (1914) hesitantly identified as a young *decorata* is really the rare *Rhadinaea dumerilii* (*q.v.*), and Rendahl and Vestergren's (1940, p. 6) record for southwestern Colombia is based on a misidentified *R. fulviceps*; I have examined the last two of the foregoing specimens. The only authentic South American specimen, therefore, seems to be one from northwestern Ecuador, and I am grateful to Dr. James A. Peters for permission to report on it. The peculiarities of the specimen (USNM 166933), namely a low subcaudal count and the labial pigmentation (fig. 10A), presumably are a reflection of the geographic distance between it and known populations in Central America (map 6). But there is the possibility that this

snake represents an unnamed species, and so it will be instructive to examine the hemipenis when a male specimen becomes available from Ecuador or adjacent Colombia; caution will of course be required in the interpretation of penial data because of the great variation already known to be present in the hemipenis of *R. decorata*.

Rhadinaea decorata is expected in the Atlantic drainage of Honduras but does not yet seem to have been found in that country. A specimen in the National Museum of Natural History that was reported by Dunn and Emlen (1932, p. 31) has been reidentified in the collections as *Coniophanes imperialis* (*fide* George R. Zug, *in litt.*).

A few Mexican specimens examined by me seemed to have unusually narrow heads, but no record was kept of this condition which at first was thought to have resulted from desiccation of poorly preserved specimens. But a specimen (UAZ 26579) recently obtained by Robert L. Bezy and Charles J. Cole near Catemaco, Veracruz, is well preserved. Its head appears very slender compared with the usual condition in specimens from the same region and elsewhere, the difference being approximately of the magnitude shown in figure 24, which illustrates normal and abnormally shaped heads in specimens of *Rhadinaea taeniata*. The cause of aberrantly narrowed heads in these two species is not known, although the condition in *taeniata* is associated with an intraspecific hybrid.

The National Museum of Natural History has two specimens of *Rhadinaea decorata* listed as syntypes of *Dromicus ignitus* Cope (Cochran, 1961, p. 174). I consider one of these, USNM 24501, to be a holotype, as it is the only one described by Cope (1871, p. 201), who did not mention the existence of a second specimen (hence there is no proof that it figured in his concept of *ignitus*, even though both specimens bear identical collection data). The measurements of USNM 24501 are similar to those given by Cope, and the specimen has 128 ventrals (including two preventrals) and 62+ subcaudals, thus matching Cope's counts exactly.

Rhadinaea decorata is a diurnal snake. I have found 11 Panamanian specimens that were prowling in leaf litter by day, mostly in late morning and midday when the maximum amount of sunlight was filtering through the forest canopy, but I know of none having been found at night. Several other individuals were found concealed, two under pieces of wood and one under a leaf.

Rhadinaea decorata was included by Miller (1968) in a study of the cochlear duct of snakes.

The specific epithet is an adjective meaning decorated or adorned, in reference to the white markings on the head.

Rhadinaea forbesi Smith

Figures 10D, 11D; map 7

Rhadinaea forbesi SMITH, 1942, pp. 188, 189, fig. 3 (anterior body pattern of holotype). SMITH AND TAYLOR, 1945, p. 117. TAYLOR, 1950, pl. 6, fig. 1 (photograph of a preserved paratype).

HOLOTYPE: USNM 110365 (original number S-13212), an adult male in good condition, from Tequeyutepec, Veracruz, Mexico, obtained by Hobart M. Smith on March 23, 1940. The type locality, Tequeyutepec, is said to be "seven miles west of Jalapa" in the original description and in Smith and Taylor (1950a), but it is listed as "10 miles northeast of Jalapa" in a later gazetteer (Smith and Taylor, 1950b, p. 11). I have not found the locality on a map but have not searched extensively.

DIAGNOSIS: *Rhadinaea forbesi* is one of several species in the *decorata* group characterized by a sharply inclined white line, extending from the upper rear edge of the eye to behind the corner of the mouth (sometimes fusing with the pale throat color or with a white line on the side of the neck). *Rhadinaea forbesi* differs from *R. marcellae* in lacking a white line across the nape and in having fewer spines on the hemipenis, and it differs from *R. macdougalli* in having more ventrals. It differs from both of the aforesaid species in a bolder color pattern on the body, including usually a wide, vertebral dark line and conspicuously dark ventral tips. *Rhadinaea bogertorum*, aside from having a less sharply inclined postocular line, has more ventrals than *forbesi*.

DISTRIBUTION: Southern end of the Sierra Madre Oriental, in central Veracruz. KU 23963 was taken at an elevation of 1700 feet (518 meters) according to the field tag.

DESCRIPTION (10 SPECIMENS): The largest specimen examined, a male, is 420 mm. total length, of which 116 mm. is tail; a female specimen probably would have been larger had its tail not been broken (414+ mm. total, 97+ mm. tail). The tail is 24.8–29.0 percent of total length in males; the only two females have incomplete

tails. The dorsal scales are in 17–17–17 rows; anal ridges are present on the adult males. Ventrals are 136–149 (138–144, males; 136, 149, females) and subcaudals are 59–67 (males only). There are eight supralabials (seven in one), and 10 (five specimens), nine (two), or eight (two) infralabials (8/9 in one other). There is one preocular, usually a subpreocular between the third and fourth labials, two postoculars, and 1+2 temporals.

A blackish vertebral line overlaps slightly onto the paravertebral rows and extends from the neck to the end of the tail; this line is reduced to a series of dark dots on the apexes of the vertebral scales in one specimen (KU 23963). A blackish lateral line or narrow stripe extends from the neck to the end of the tail and is somewhat variable in position and width, but it includes at least part of row 4 and the adjacent edge(s) of row(s) 3 and/or 5. The ground color below the lateral line tends to be darker brown than on the dorsum, and in some individuals the median three or five scale rows may themselves be darker brown than the dorsolateral ground color. There is a linear white marking above the lateral dark line: It starts as a short white stripe on the side of the neck on rows 5 and 6, and posteriorly becomes limited to row 5, as a series of white dashes that extends along the body and well onto the tail, although the dashes are inconspicuous in some specimens. There is a short, longitudinal white line on the nape, in front of the vertebral dark line.

The head is brown above, with a pair of white parietal dots and in some individuals, with faint indication of a pale scroll-like pattern. A black-edged, white postocular line slants from the upper rear edge of the eye to behind the corner of the mouth, where the line tends to widen somewhat and where it may fuse with the front end of the white stripe on the side of the neck (in KU 26732). A blackish brown stripe is narrowly continuous around the rostral plate and extends through the eye alongside of the head, usually terminating against the postocular white line but sometimes connecting with the lateral dark stripe on the neck. The supralabials below the lateral head stripe, and the infralabials, are immaculate white, except for black dots on the anterior plates of some specimens. The venter is white, except that the ventrals and subcaudals are narrowly and conspicuously (except in KU 26732) tipped with blackish brown pigment, which forms a ventrolateral line that may have either a serrated or a straight edge. The color in life has not been recorded.

Maxillary teeth vary from 15+2 to 17+2, with the prediastemal teeth all lying anterior to the front edge of the ectopterygoid process. The last fang is offset laterad.

The retracted hemipenis extends to the end of subcaudal 7, and the retractor muscle originates at the level of subcaudal 24 or 25. The capitulum comprises nearly half the length of the organ on its sulcate side. The calyces are spinulate in a band around the periphery of the capitulum and papillate elsewhere. The sulcus spermaticus forks about one-third of its distance on the capitulum and the branches extend nearly to the tip of the retracted hemipenis. The wall of the capitulum forms a single fold on the asulcate side of the organ. There are 20 or more small to relatively large, slightly recurved spines below the capitulum. The basal fourth of the organ bears only minute spinules. This description is based on uneverted hemipenes of the holotype and USNM 29124.

REMARKS: The holotype and two topoparatypes were found under stones and logs in a grassy area in the mountains, after a heavy rain in the dry season (Smith, 1942, 1943). *Rhadinaea forbesi* is named for Mr. Dyfrig McH. Forbes, who aided in the discovery of the type series.

Rhadinaea gaigeae Bailey

Figures 10C, 11B, 17; map 7

Diadophis decoratus (not of Günther): GARMAN, 1883, pp. 71, 158; 1887a, p. 127.

Liophis decorata (not of Günther): BARBOUR AND AMARAL, 1924, p. 130 (part, MCZ 4539 [now UMMZ 90668]).

Rhadinaea gaigeae BAILEY, 1937, pp. 118, 119; 1940, pp. 12, 13, pl. 1, fig. 2 (midbody pattern of MCZ 24984). SMITH AND TAYLOR, 1945, p. 117.

Rhadinaea crassa SMITH, 1942, pp. 190, 191, pl. 3, figs. 4, 5 (anterior body pattern, and scutellation and color pattern of head of holotype: E. H. Taylor-H. M. Smith No. 5526 [now FMNH 100123], from Durango, Hidalgo, Mexico; E. H. Taylor collector); 1943, pl. 32, fig. 1 (photograph of preserved holotype). SMITH AND TAYLOR, 1945, p. 116. New synonymy.

HOLOTYPE: MCZ 24983, an adult male in good condition, from Alvarez, 8800 feet, San Luis Potosí, Mexico, obtained by W. W. Brown on June 9, 1926. The specimen has 161 ventrals

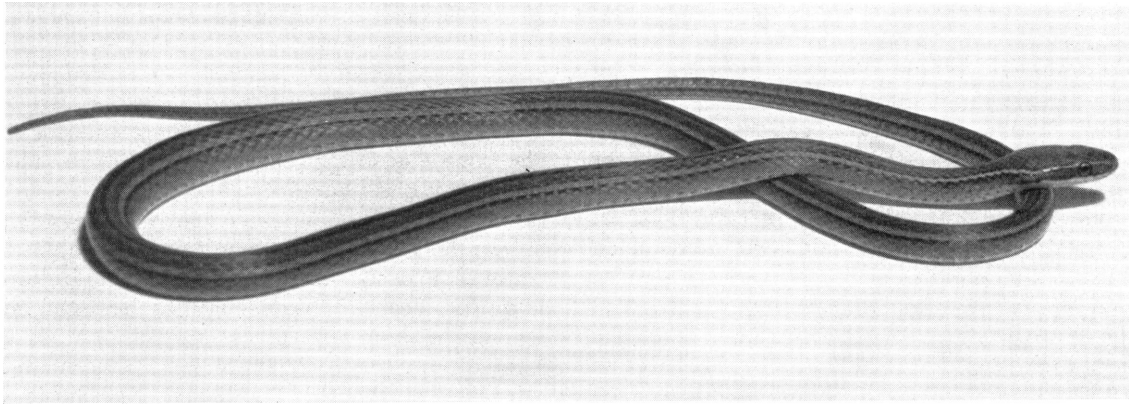


FIG. 17. *Rhadinaea gaigeae*, AMNH 102490, from Tamaulipas, Mexico. (Photograph by Isabelle Hunt Conant.)

(and one preventral) rather than 160 as given in the original description, and the infralabials are 11/10 by the present method of notation (rather than "10/11").

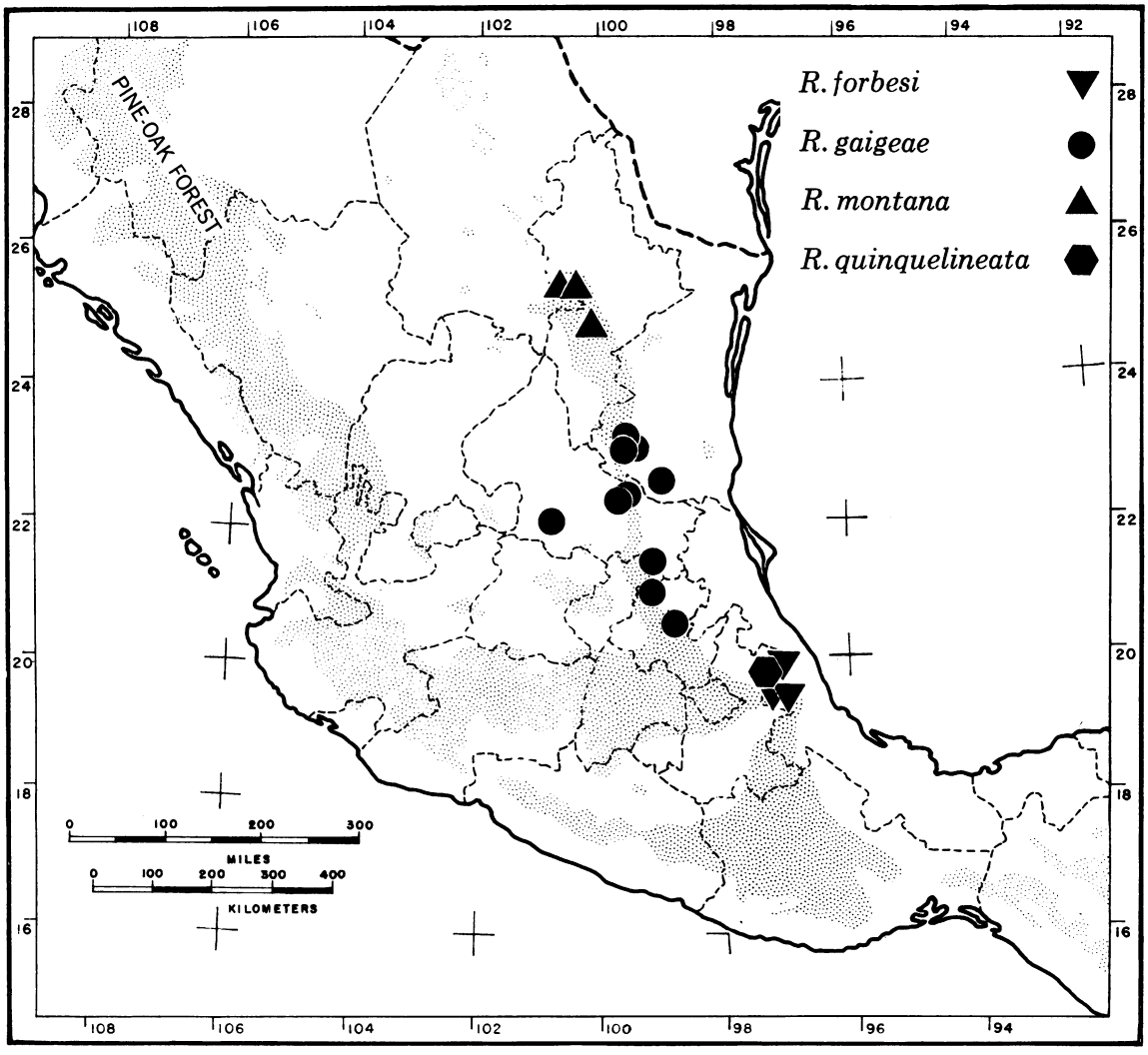
DIAGNOSIS: *Rhadinaea gaigeae*, a member of the *decorata* group, usually has a grayish streak along each side of the vertebral dark line, thus causing it to somewhat resemble *R. montana* and *R. quinquelineata*. The pale paravertebral areas are delimited by brown or blackish brown pigment, which is not confined within darker edges as in *montana*, and which includes the bottom part of row 7 unlike in *quinquelineata*. In some cases the grayish streaks are lacking and, except for the vertebral dark line, the middorsum is uniformly brown between the inner edges of the sixth scale rows.

A pale tan or cream lateral stripe is conspicuous; it occupies most of row 6, all of row 5, and usually the upper half of row 4, and so tends to be intermediate in width between the lateral light markings of *montana* (row 5 and adjacent halves of rows 4 and 6) and *quinquelineata* (all of rows 5 and 6 and adjacent halves of rows 4 and 7).

DISTRIBUTION: Pine-oak and cloud forest (occasionally tropical deciduous forest and possibly even thorn forest) in the Sierra Madre Oriental of southern Tamaulipas, eastern San Luis Potosí, and northern Hidalgo, and a mountainous area to the west, in southern central San Luis Potosí. The known elevational range is 610–2683 meters in southern central San Luis Potosí, and *ca.* 200–1829 meters in Tamaulipas (i.e., *ca.* 200 meters at El Pachón, and 1006–1829 meters in the Gómez Farías region).

DESCRIPTION (96 SPECIMENS): Some specimens attain lengths in excess of 600 mm. The largest male measured 568 mm. total length, of which 191 mm. is tail; the largest female measured 650+ mm. total length, of which an incomplete tail accounts for 179+ mm. The tail is 28.6–34.2 percent of total length in males and 27.5–33.0 percent in females. The dorsal scales are in 17–17–17 rows; anal ridges are present on most adult males and on occasional females. Ventrals are 156–184 (156–175, males; 161–184, females), and subcaudals are 81–112 (87–112, males; 81–104, females). There are constantly eight supralabials (8/7 in one) and usually 10 infralabials, or occasionally nine or 11 (10/8 in one). There is one preocular, or in rare cases two, and usually a subpreocular between the third and fourth labials. There are constantly two postoculars (2/1 in one) and a basic pattern of 1+2 temporals, with rare deviations such as 1+1+2 or $1+^{2}_{1}$.

The middorsum varies from light brown to dark brown or even blackish brown (an ontogenetic change, at least in part), except for a black vertebral line that usually is emphasized on each side by a light gray streak. The vertebral line starts several scales behind the head and extends back onto the tail, where it becomes very thin and either disappears or continues faintly to the tip. The light gray streak on each side of the vertebral line usually is confined to the paravertebral row and edge of the vertebral row, but occasionally it is unusually pale and is broader, extending from the paravertebral row onto the adjacent (seventh) row where it is bordered by a blackish brown line on the edges of rows 7 and 6.



MAP 7. Locality records for four species of the *decorata* group in eastern Mexico. Stipple pattern indicates approximate distribution of pine-oak forest.

The pale streaks often extend in front of the anterior end of the dark vertebral line, thus fusing and forming a short whitish line on the nape. A black-edged white line passes along the canthus rostralis and through the upper edge of the eye, behind which it becomes a little wider and more vivid. This white line may terminate on the temporals, but usually it makes a dip and is posteriorly continuous with a dorsolateral pale tan or cream stripe that occupies row 5 and adjacent parts of rows 4 and 6 [rows 5 and 6 only in UAZ 26582] and which extends nearly to the end of the tail. A black line crosses the rostral plate and splits into diverging lines that edge a brown to blackish stripe, which passes alongside of the head and through the eye and fades on the brown side of the neck, except that the upper edge is continuous with a black or blackish brown lateral line or narrow stripe. The lateral line may be narrow and confined to the middle of row 4 or the edges of 4 and 5 [on edge of 5 only in UAZ 26582], or it may be broader and cover the lower half or three-fourths of row 4 and the upper edge of row 3; the lateral marking is much broader in a specimen (LSU 11010) from Hidalgo, on which it is a stripe covering most of

rows 3 and 4. The lateral line usually disappears before it reaches the tail tip. The sides below the lateral dark line are light brown in small individuals and become progressively darker grayish brown with age, except that the first row occasionally remains pale.

The head is brown or grayish brown above, with a pair of pale parietal dots absent or inconspicuous. A dorsolateral pale marking and a lateral dark one are usually contiguous with the body stripes as already stated. The supralabials below the lateral dark stripe are white and range from being immaculate to having a bold black dot on all but the last few. The ventral surfaces are white, with dark specks on the infralabials of some individuals and, occasionally, a few scattered dark specks on the belly or tail or a dusky median streak under the tail. Each ventral tip has a small, discrete blackish spot, tiny dot, or a dark smudge that is contiguous with the lateral body color. These markings tend to fuse into a continuous line along the edges of the subcaudals.

The maxillary teeth vary from 16+2 to 19+2, with the ultimate prediastemal tooth usually lying anterior to the front edge of the ectopterygoid process. The last fang is offset laterad.

The retracted hemipenis extends to the level of subcaudals 7–9 and the everted organ to subcaudal 6. The retractor muscle originates at the level of subcaudal 23 or 26. The capitulum comprises half or more of the length of the hemipenis on its sulcate side. The calyces are ornamented with papillae, except over most of the asulcate side and on a strip along the base of the sulcate side, where the papillae are replaced by tiny spines. The sulcus spermaticus forks at a point one-third or less of its length on the capitulum, and the branches extend nearly to the end of the uneverted organ, but no more than about halfway to the end of the capitulum of the everted hemipenis. The wall of the capitulum forms a single fold on the asulcate side of the retracted organ. There are 11 (LSU 11010) or 15–18 small to medium, slightly recurved spines below the capitulum, with a longitudinal bare space between those on the asulcate side, where most of the spines occur. Approximately the basal fifth to fourth of the organ has only spinules. The preceding description is based on seven everted hemipenes of AMNH 102490, LSU 11009, 11010, UAZ 26582, UMMZ 102991, and four retracted organs of AMNH 102490, KU 28086, MCZ 24982, and UAZ 26582.

Geographic Variation: I did not find any obvious, geographically correlated variation in this rather wide-ranging species, although I did not look at all of the available specimens at one time. The type specimens from south-central San Luis Potosí seem to have somewhat paler dorsums than the average of adult specimens from elsewhere; this may be a geographic difference, but also might partly be due to fading (the types were collected in 1879 and 1926). A single mutilated specimen (LSU 11010) from 1.5 miles north of Zacualtipán, Hidalgo, might represent a locally differentiated population, although the few other Hidalgo specimens (including the types of *R. crassa*) resemble northern *gaigeae*. The Zacualtipán individual has very dark linear markings, the lateral of which is unusually broad, covering virtually all of scale rows 3 and 4, which is to say that it is a "stripe" rather than a "line." Also, the dark spots on the ventral tips are relatively large and the entire venter is conspicuously speckled with dark pigment. There are only about 11 spines on each everted hemipenis, rather than 15–18 spines as on the hemipenes of several northern specimens.

Remarks: I compared the type series of the nominal *Rhadinaea crassa* Smith with the types of *R. gaigeae* and found no significant differences that would suggest the presence of two species. According to Smith (1942, p. 191), *R. crassa* differs from *gaigeae* in the presence of dark spots on the ventral tips and in having light lines bordering the vertebral dark line. But the types of *gaigeae* also have these characteristics, although the ventral spots are restricted to the anterior part of the body and are posteriorly reduced to one or more dots or specks on each ventral tip; the paravertebral light streaks are also most obvious anteriorly on the *gaigeae* types. Smith's concept of *gaigeae* evidently was based on the brief description and midbody illustration in Bailey (1940). Smith (*loc. cit.*) suggested that *crassa* might have more maxillary teeth than *gaigeae*, but Bailey's (1937, 1940) count of 14+2 teeth for the holotype of *gaigeae* is in error, as there actually are 18 prediastemal sockets on each maxilla. Therefore, *Rhadinaea crassa* Smith, 1942, is here relegated to the synonymy of *R. gaigeae* Bailey, 1937, an action that was anticipated by Martin (1958, p. 73).

The only substantial information on the

habits and habitats of this common species is given by Martin (1958, pp. 72, 73), under the name *Rhadinaea crassa*:

"Represented by specimens from a variety of localities, *Rhadinaea* [*gaigeae*] is virtually the only snake in the Gómez Farías region of [southern Tamaulipas] that is common enough to restrict zonally with some confidence. It is found through the belt of humid montane forest between 1000 and 1800 m., mainly on the eastern side of the Sierra Madre. Individuals were found in all types of terrestrial habitats, on trails, truck roads, dry leaves of the forest floor, grass in clearings, inside or under logs, beneath stones or bark, and in one instance about 10 m. inside the mouth of a cave (Walker and Heed). Cloud forest and humid pine-oak forest are the typical habitats; the La Joya record indicates that drier oak-pine woods may also be occupied.

"Salamanders may constitute the major item of diet. Although the stomachs of most specimens were empty, Walker forced one to regurgitate a *Pseudoeurycea scandens*, and another ate the tails of two *P. scandens* which were confined with it. Parts of three *Chiropterotriton* were found in stomachs of two other specimens, with a *Pseudoeurycea* tail and complement of 12 salamander eggs enclosed in a jelly mass in the stomach of a third."

As indicated by Martin (see above, and 1955, p. 355), *Rhadinaea gaigeae* quite obviously is a montane species, with a dispersal center primarily in the pine-oak zone, but it also occurs at low elevations, if only rarely. Robert L. Bezy and Charles J. Cole found a specimen at about 200 meters elevation, in a cave at El Pachón, near Antiqua Morelos, Tamaulipas. "The area is in general of low relief with thorn scrub which is now [August 6, 1967] already somewhat leafless; along the stream and near the cave however, the trees seemed somewhat taller and better leafed, perhaps approaching short-tree [tropical deciduous] forest" (Robert L. Bezy, field notes). Hillsides near the cave are covered with tropical deciduous forest according to Walker (1955, p. 9), on the basis of information from Paul S. Martin. The specimen of *gaigeae* presumably represents a fringe population (or possibly a chance stray) that reached the area by way of tropical deciduous and gallery forest, but it does not seem likely that populations are maintained in the thorn forest proper.

The name *Rhadinaea gaigeae* is a patronym honoring Helen Thompson Gaige, formerly herpetologist at the University of Michigan Museum of Zoology.

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Figures 10G, 11K–M; map 5

Rhadinaea vittata (not of Jan): BOULENGER, 1894b, p. 179 (part, specimens *k–m*, *fide* Bailey, 1940, p. 8); 1896, p. 635 (part, specimens *p* and *q*?, *fide* Bailey, *loc. cit.*). OLIVER, 1937, p. 20.

Rhadinaea hesperia BAILEY, 1940, pp. 8–10, pl. 2, fig. 3 (midbody pattern of BMNH 94.5.17.5).

Rhadinaea hesperia hesperia Bailey: SMITH, 1942, pp. 185, 186. SMITH AND TAYLOR, 1945, p. 117. New synonymy.

Rhadinaea hesperia baileyi SMITH, 1942, pp. 187, 188, pl. 3, fig. 2 (anterior body pattern of holotype, E. H. Taylor-H. M. Smith No. 5444 [now FMNH 100028], from El Treinte, Guerrero, Mexico; E. H. Taylor collector). SMITH AND TAYLOR, 1945, p. 117. New synonymy.

Rhadinaea hesperia hesperioides SMITH, 1942, pp. 186, 187, pl. 3, fig. 1 (anterior body pattern of holotype, USNM 67373, from Magdalena, Jalisco, Mexico; C. C. Elliott collector). SMITH AND TAYLOR, 1945, pp. 117, 118. New synonymy.

HOLOTYPE: MCZ 42661, an adult male from Omilteme, Sierra de Burro, Guerrero, Mexico, obtained by W. W. Brown in 1936. The type locality is on the Río Balsas drainage of the Sierra Madre del Sur. The specimen is in fair condition except that the tail is incomplete and the right maxilla is broken. The holotype differs slightly from the original description in having a maximum of 162 ventrals (not "163") if two preventrals are included, and in that there are two preoculars excluding (not "including") a small subpreocular.

DIAGNOSIS: This is a slender, long-tailed species (more than 100 subcaudals, and tail comprising about 32–42 percent of total length). Color pattern is variable, but the species can be distinguished from all other members of the *decorata* group by the combined presence of narrow dark lines on at least the vertebral row and fifth lateral rows; there is a white line on the canthus rostralis and behind the eye, but it does not extend onto the neck. *Rhadinaea decorata* has a line on row 5 but lacks a definite, narrow vertebral line, although there may be a wider vertebral streak; Mexican populations of *R. decorata* also are characterized by a distinctive

head pattern. Other members of the *decorata* group have the lateral marking lower on the body (fig. 11).

Rhadinaea hesperia is geographically isolated from other species of the *decorata* group but occurs at least macrosympatrically with members of the *taeniata* group. These are larger snakes that have a dark stripe (not a narrow line) on the side and their ventral plates are basically pale from one side to the other, although dark dots may be present on the tips of the ventrals. *Rhadinaea hesperia* has an encroachment of the brown or blackish body color onto the ends of the ventrals.

Although the presence of a dark, thin lateral line on row 5 is stressed as being diagnostic, the following points should be noted: the lateral line may be obscure on some individuals, but in these the sides are dark up to the middle of row 5, or else the line is low on row 5 and interrupted by the tops of the scales in row 4. Other individuals show a slight intensification of brown pigment between the blackish line on row 5 and a dark brown line on row 4, and thus give the appearance of having a dark-edged, lateral brown stripe; such specimens should not be confused with some members of the *taeniata* group (*R. fulvivittis* and some juvenile *R. omiltemana*) that have broader, dark-edged brown stripes on rows 3–5.

DISTRIBUTION: Western Mexico, from Sinaloa southward into Guerrero and Morelos, in the Sierra Madre Occidental, Cordillera Volcánica, Sierra de Coalcomán, and the Sierra Madre del Sur. The elevational range for a dozen specimens with complete data is 884–1982 meters. The primary habitat is probably the lower part of the pine-oak zone, but in Michoacán specimens also have been found in tropical semideciduous forest, arid scrub forest, and mesquite-grassland (*fide* Duellman, 1961, p. 107; 1965, pp. 655, 656, 659). Hardy and McDiarmid (1969, p. 194) stated that the habitat in Sinaloa is "tropical deciduous forest of the southern highlands and foothills," but the specimens for which elevations were given (two of three specimens) came from localities higher than the 1000 meters that these authors (p. 56) regarded as the approximate upper limit of "tropical dry forest" (including "tropical deciduous forest"). The elevations of 1200 and 1890 meters attached to their Sinaloan *hesperia* seems to place the specimens in the zones of "subtropical dry forest" (1000–1500 meters) and/or "lower montane dry forest" (including oak forest, 1000–2000 meters, and pine-oak forest, 1500–2400 meters), as defined by Hardy and McDiarmid (*op. cit.*, pp. 57, 58). A recent specimen (AMNH 102518) from Sinaloa was collected by Tim Walker at about 6000 feet (1829 meters) in pine-oak woods.

Rhadinaea hesperia has been recorded from as far inland as Guanajuato, but no recent specimen is available (see Remarks). Specimens have not yet been taken in Nayarit, but are expected because of the species' occurrence to the north and south.

DESCRIPTION (50 SPECIMENS): The largest individuals are a pair from Chilpancingo, Guerrero. The female is 592 mm. total length, of which 212 mm. is tail, and the male is 479 mm. total, 198 mm. tail length. The tail is 35.4–41.6 percent of total length in males and 32.3–39.0 percent in females. The dorsal scales are in 17–17–17 rows; anal ridges are usually present on adult males and occasionally on females. Ventrals number 139–177 (139–164, males; 147–177, females) and subcaudals 104–137 (110–137, males; 104–118, females). There are nearly always eight supralabials (8/9 in one specimen); infralabials are more variable, being usually 10 but not infrequently nine (on one or both sides in 12 specimens). There is one or occasionally two preoculars, and two postoculars (2/1, one specimen). A subpreocular is usually present between the upper edges of the third and fourth supralabials. The temporals are basically 1+2, with occasional deviations (most often on only one side) such as 1+1, 1+1+2, 1+2+2, 2+2, and $1+^{3}_{1}$.

There is considerable variation in color pattern, both within and between populations. The only constant markings on the trunk are a median black line that is confined to the vertebral row and a lateral black or blackish brown line near the middle or on the lower half of the fifth row of scales. However, the lateral line may be obscured by encroachment of dark pigment from below, in which case it seems like a dark edge to a broader stripe (see below). Immediately above the lateral line is a dorsolateral tan or pale brown stripe (or less definite streak) that varies in width and intensity but invariably includes the upper part of row 5 and, usually, at least the lower part of row 6; this stripe becomes white on the neck. The top of the body is

medium brown. Many specimens have additional thin black lines on each side of the vertebral line, on the centers of rows 8 (paravertebral) and/or 7. The dark line on row 7, when present, usually delimits the upper edge of the pale dorsolateral stripe, which is then centered on row 6 and overlapping onto adjacent parts of rows 5 and 7. When the dark line on the seventh row is absent, the medium brown middorsal region is usually widened to include all of the seventh and part of the sixth rows; the dorsolateral pale stripe is then not only narrowed but often less distinct, because its upper edge is sharply defined only on the neck. Individuals from most populations have light or medium brown sides, often with somewhat darker brown lines along the centers of some or all of the lower four rows of scales. These lines are most commonly present on the second and/or fourth rows. Often there is an intensification of brown pigment between the brown line on row 4 and the blackish line on row 5, resulting in the appearance of a dark-edged, lateral brown stripe occupying the adjacent parts of rows 4 and 5. The sides below the blackish line on row 5 are uniformly dark brown, or even black, in individuals from some populations. Dark sides seemingly are the result of ontogenetic change, because juveniles (e.g., FMNH 38350 and 105093) from populations of dark adults have lighter brown sides, on which there is a tendency for a brown line on each of the lower four scale rows; the blackish line on row 5 is sharp and discrete in these juveniles. The edges of the ventrals are brown or black, like the lower sides. The tail is weakly marked, with the sides being darkest; the linear markings do not continue distinctly to the tip.

None of the stripes and lines extends from the body onto the head, which is brown and usually has a pair of dark-edged white parietal dots. There invariably is a conspicuous, black-edged white line along the upper side of the head. The white line starts on the rear of the nasal plate and extends along the canthus rostralis and through the top of the eye, then crosses the upper postocular and parietal edge and terminates on the temporals; the postocular part of the white line is in many cases wavy, in some broken, and may be aligned either horizontally or with a slight downward slant. The white line does not connect with a variably shaped white marking on the neck, where the anterior segment of the pale dorsolateral body stripe has become white and turned downward, toward the corner of the mouth. This anterior segment of the pale body stripe in some cases runs into the white color of the throat, but usually it terminates abruptly, above and behind the mouth, often after enlargement into a black-edged ocellus that is in some cases disconnected from the stripe. A juvenile from Jalisco (KU 73619) is unusual in having on each side of the neck a large white blotch extending from the white throat up onto the paravertebral scale row; each blotch, which might be described as half a broken collar, probably represents the terminus of the pale dorsolateral stripe but is disconnected and much enlarged, being about two scales wide and completely edged in black except at the throat. A blackish line crosses the rostral and the top edges of the anterior supralabials, then crosses the posterior labials and corner of the mouth, and fades out on the side of the neck. The lower parts of the supralabials are white, being nearly immaculate or having a horizontal black line or row of dots. The infralabials, especially the anterior ones, may be lightly dotted with dark pigment. There is encroachment of the brown or blackish dorsal pigmentation onto the ends of the pale ventrals and subcaudals; the venters of occasional individuals are sparsely dotted with black.

In life the venter is white anteriorly and reddish posteriorly, at least in specimens from north of Guerrero: A specimen (AMNH 102518) from Sinaloa died in shipment to the museum, where I noted that the venter was whitish to ventral 30 and graded to orangish red posteriorly. I saw a relatively fresh specimen (KU 73619) from Jalisco after it had been in formalin for two weeks; the venter was whitish to ventral 58, then graded to salmon. Duellman (1954) stated that a specimen from Volcán Jorullo, Michoacán, had a pink belly and cream dorsolateral stripes; he evidently was referring to the posterior part of the venter and the anterior part of the dorsolateral stripe, which turns pale brownish posteriorly. Specimens from the Sierra de Coalcomán, Michoacán, had, "bright cream-colored temporal stripes and dorsolateral stripes on the anterior part of the body. The chin and anterior one-sixth of the belly was white; posteriorly the venter was bright orange-red" (Duellman, 1961, p. 107).

The maxillary teeth vary from 18+2 to

23+2. The last one-half, one, or two prediastemal sockets lie posterior to the front edge of the ectopterygoid process, except in specimens having only 18 or 19 prediastemal teeth in which case all are anterior to the process. The last fang is offset laterad.

Retracted hemipenes extend to the level of subcaudals 5–7 and one pair of everted organs to the end of the sixth pair of subcaudals. The retractor muscle originates at the level of subcaudals 23 or 24. The capitulum comprises well over half the length of the organ on its sulcate side. Papillae on the calyces are replaced by tiny spinules on the periphery and over most of the asulcate folds of the capitulum. The sulcus spermaticus forks at a point about half of its length up the capitulum; the branches stop short of the tip of the retracted hemipenis and extend only halfway up the capitulum when the organ is everted. The wall of the capitulum forms a double fold on the asulcate side of the retracted hemipenis. There are 27–33 small to medium, slightly hooked spines below the capitulum; the spines on the sulcate side originate closer to the base than any on the asulcate side. Approximately the basal fourth of the hemipenis is free of spines but is rather densely ornamented with large spinules, which are conspicuous because of their abundance. The preceding description is based on retracted hemipenes from TCWC 7000, UIMNH 18933, and UMMZ 84708, and the everted hemipenes of AMNH 102518. These specimens are from localities throughout the range of the species.

Geographic Variation: *Rhadinaea hesperia* has a relatively large geographic range, and the available sample of 50 specimens is not sufficient for a detailed analysis of variation. Nonetheless geographic trends are evident in the number of ventrals and in color pattern.

The number of ventrals increases in a southerly direction, as shown by the data (mean and range) below:

Sinaloa and Jalisco	
Males (5)	Females (4)
144.0 (139–154)	153.5 (147–158)
Colima and Michoacán	
Males (7)	Females (4)
152.9 (148–155)	162.0 (158–165)
Guerrero	
Males (15)	Females (6)
156.3 (147–163)	165.7 (161–169)
Morelos	
Males (2)	Females (4)
162.0 (160, 164)	174.8 (172–177)

A trend similar to that of the ventrals possibly occurs in the number of subcaudal plates but, if so, is less evident, as seen by inspection of the following data:

Sinaloa and Jalisco	
Males (4)	Females (3)
119.0 (112–131)	109.0 (106–111)
Colima and Michoacán	
Males (6)	Females (3)
118.3 (110–126)	112.0 (110–117)
Guerrero	
Males (10)	Females (4)
123.7 (119–132)	111.5 (109–114)
Morelos	
Males (0)	Females (4)
—	109.5 (104–118)

The trend in ventrals is obviously clinal, and a similar but less evident cline questionably is present in number of subcaudals. There is no evidence that this pattern is influenced to any great extent by changes in elevation, inasmuch as a few specimens from Sinaloa were taken at about the same elevations (1830–1890 meters) as a few specimens from Morelos. This is not to say that local differences might not exist if the species has an extensive vertical range at any one area; unfortunately, few specimens are available from a given area and fewer still have the elevation recorded. One local difference masked in the tabulations above is discernible by comparison of specimens from the northern (Río Balsas drainage) and southern (Pacific side) slopes of the Sierra Madre del Sur of central Guerrero. The samples are small but there is no overlap in numbers of ventrals and subcaudals, indicating that the number of these plates is correlated with regional factors as well as sexual and latitudinal ones.

Northern Slopes	
Ventrals:	154–163 (12 males); 164–169 (5 females)
Subcaudals:	121–132 (8 males); 109–114 (4 females)
Southern Slopes	
Ventrals:	147–151 (3 males); 161 (1 female)
Subcaudals:	119, 119 (2 males); —

Northern specimens may have, on the average, slightly more maxillary teeth than southern specimens, but the data are too few to be conclusive. Eight specimens from Sinaloa, Jalisco,

Colima, and Michoacán have 19–23 prediastemal teeth, mean 21.5, whereas six individuals from Guerrero and Morelos have 18–23 teeth, mean 20.8.

Variation in color pattern is considerable and is not readily explained by the assumption of simple clines, albeit clinal factors are probably present. Obvious, regional differences led Smith (1942) to propose the recognition of three subspecies. The feasibility of applying trinomens to definable groups of populations is examined in the following brief analysis of geographic variation in color pattern.

Populations from the upper Río Balsas drainage, in the Sierra Madre del Sur of Guerrero and the Cordillera Volcánica of Morelos, are characterized by an ontogenetic change that produces uniformly darkened sides, although juveniles have a tendency for brown lines on lighter brown flanks. The pale dorsolateral stripes, which are clearly defined between the dark sides and the middorsum (which is often gray in preservative), are centered on row 6 and overlap on rows 5 and 7 throughout the body. Usually, but not invariably, there is a fine dark line down the center of each paravertebral and/or seventh row of scales; the line on row 7, when present, delimits the top edge of the pale dorsolateral stripe. The holotype of the species fits this description in all particulars, and so the name *Rhadinaea hesperia hesperia* Bailey is applicable if subspecies are recognized.

Most of the specimens on which the above description is based are from the vicinity of Chilpancingo and Omilteme (the type locality), on the north-facing slopes of the Sierra Madre del Sur in Guerrero. A few specimens of a completely different aspect are available from a short distance across the divide to the south, on the Pacific slopes in the area of Acahuizotla and Agua del Obispo (Davis and Dixon, 1959, localities on map). These specimens (TCWC 7489, 7490, 11574) are lighter and are not vividly striped like those from north of the divide; in size, they appear to range from subadult to adult. The sides are relatively light (medium brown) but lack darker lines on the lower scale rows. The lateral dark line is on the lower edge of row 5 (rather than near the middle) and is interrupted by the tops of the scales in row 4. Dark lines are lacking on rows 7 and 8 on each side of the vertebral line. The pale brown dorsolateral stripe is reduced in width and is sharply defined only on the neck, where it is confined to the adjacent halves of rows 5 and 6 (rather than on 6 and each adjacent half-row). These specimens, which were called *R. h. hesperia* by Davis and Dixon (1959, p. 86), resemble the holotype and only assigned specimen of *R. h. baileyi* Smith, which has a type locality some 60 or 70 kilometers southward and closer to the coast of Guerrero. Thus, the population of *Rhadinaea hesperia* from the Pacific slopes of the Sierra Madre del Sur is quite different in color pattern from the one immediately north of the divide; but the latter is very similar to a population in the Cordillera Volcánica across the basin of the Río Balsas. The Pacific-side specimens of *hesperia* also have fewer ventrals and subcaudals than do those from north of the divide, as mentioned previously.

Proceeding northwestward, there are two evidently disjunct populations in Michoacán, one in the isolated Sierra de Coalcomán (a northern segment of the Sierra Madre del Sur) and one on the Río Balsas drainage of the Cordillera Volcánica. The available specimens agree with the populations of the upper Balsas drainage in having the dorsolateral light stripe centered on row 6, at least on the neck (the adjacent part of row 7 is darkened on most of the body in UMMZ 104494 from the Cordillera Volcánica). An ontogenetic darkening of the sides may occur, at least in the Cordillera Volcánica, but seemingly at a larger size than in the populations of the upper Balsas. An individual 479+ mm. total length has dark sides and is from the Cordillera Volcánica; the three next largest specimens (354–364 mm.) represent both mountain areas and have relatively light sides, although they are no larger than some dark-sided individuals from farther east. It remains to be determined whether the ontogenetic darkening occurs in populations in the Sierra de Coalcomán or in adjacent Colima (where only two juveniles have been collected).

Samples are small from the northern part of the range (Sinaloa and Jalisco), but apparently there is no pronounced ontogenetic darkening of the sides of the body, inasmuch as several specimens exceed 400 mm. total length and show little or no intensification of pigment. Usually a brown line is present on rows 4 and/or 2 (and occasionally on 3 also), but such lines are lacking on one juvenile (KU 73619) collected near Purificación, Jalisco, and also on two juveniles

(UMMZ 80226, 80227) from Queseria, Colima. Lines on the lower scale rows are present on some specimens from Michoacán and absent on others, regardless of size; one juvenile (UMMZ 104502) from the Sierra de Coalcomán has a brown line on each of the lower four rows, as do some juveniles from the dark-sided populations of the upper Balsas. A dark line on row 2 was considered by Smith (1942, p. 186) as being diagnostic of a northern subspecies, *R. h. hesperioides*. The other characters thought to be diagnostic are also variable. Thus, the dorsolateral light stripe may occupy row 6 and half of each adjacent row well onto the neck (KU 75629, Sinaloa), rather than have the upper edge restricted to row 6. The blackish line on row 5 may lie near the middle of the row (KU 80870, Sinaloa) rather than on the bottom edge; the appearance of a wider, dark-edged brown stripe (resulting from a slight intensification of pigment between the brown line on row 4 and the blackish one on row 5) occurs throughout the range, except possibly on the Pacific slopes of Guerrero.

Any worker wishing to apply the trinomen *R. h. hesperioides* conceivably might base his concept on the absence of dark-sided adults in the northern populations but, because of the total variation, there would remain problems in formally dealing with the highly variable populations in Michoacán and elsewhere. These populations would have to be considered as more than simple intergrades between "*R. h. hesperia*" and "*R. h. hesperioides*," because some individuals from as far north as Jalisco (e.g., KU 73619) have the weak body pattern of "*R. h. baileyi*." It would seem simplest to drop the concept of subspecies in *Rhadinaea hesperia* and to recognize it as a geographically variable species in need of further study. Any such study should ideally be based on considerably more specimens than now available and should attempt to account for the historical factors that have caused present patterns of differentiation.

REMARKS: A few old specimens (USNM 15429, 15430) from "Guanajuato" are not mentioned in the foregoing analysis of geographic variation. Both are paratypes of *Rhadinaea hesperia* and one (15430) also was designated a paratype of *R. h. hesperioides* by Smith (1942), who decided that it was, "in all probability from the vicinity of Guadalajara (from Dugès)." Smith did not elaborate on this remark, but presumably he was influenced by the presence of a dark line on the second row of scales; thus, the specimen—a juvenile—fit his concept of *hesperioides*. The other specimen is an adult with dark sides and was considered by Smith as belonging to the nominate subspecies. However, Smith was unaware of the ontogenetic pattern change in some populations and, seeing that one specimen is a juvenile and one an adult, there is no evident reason to suppose that both are not from the same locality. Nonetheless, the occurrence of *Rhadinaea hesperia* from as far inland as the state of Guanajuato needs verification.

Specimens have been found under rocks (Davis and Smith, 1953; Peters, 1954). Duellman (1954, p. 16) provided the following information on specimens from Volcán Jorullo, a locality on the fringe of the Cordillera Volcánica in Michoacán: "One specimen was found after a rain crawling across an ashy flat on the malpais. The other was under a log imbedded in the ash at the base of the cone. Another specimen, under a log halfway up the north slope of the cone, escaped into the loose ash and debris." A Sinaloa specimen (AMNH 102518) was "on the move among rocks in pine-oak woods . . . 3:15 p.m.," according to a field tag written by Tim Walker.

This species was described relatively recently, considering that it has a rather large distribution and was first collected in the 1800s. Bailey (1940, p. 8) gave the Greek equivalent of *hesperia*, which is an adjective meaning "western" a self-evident allusion to the geographic range in western Mexico.

Rhadinaea macdougalli Smith and Langebartel

Figures 10I, 11F; map 5

Rhadinaea macdougalli SMITH AND LANGEBARTEL, "1949" [1950], pp. 413–415, fig. 1 (photograph of preserved holotype).

HOLOTYPE: UIMNH 3775, a male in fair condition, from near Buena Vista, at crest of Sierra Madre, 4000–4500 feet, directly north of Río Grande, Oaxaca, Mexico. This locality is about 70–80 kilometers northeast of the town of Tehuántepec. The specimen was obtained by Thomas MacDougall on March 7, 1949.

DIAGNOSIS: *Rhadinaea macdougalli*, a small member of the *decorata* group, is perhaps most likely to be confused with the geographically

adjacent *Rhadinaea bogertorum*. There are differences in color pattern, but not enough is known of the variation to say which features are most diagnostic. Probably the most useful features at present are differences in numbers of ventral plates and maxillary teeth—low in *macdougalli* and higher in *bogertorum*. *Rhadinaea macdougalli* might also be confused with *R. myersi*, another species of the Oaxacan highlands, but *macdougalli* has a sharply inclined postocular white line (compare illustrations), and the capitulum comprises nearly half the length of the hemipenis on its sulcate side (about two-fifths in *myersi*).

Other species with sharply inclined, postocular white lines (from the upper rear edge of the eye to behind the mouth), are *Rhadinaea marcellae*, which additionally has a white line across the neck and more spines on the hemipenis, and *R. forbesi*, which has more ventrals and usually has a conspicuous vertebral line and blackish ventral tips.

DISTRIBUTION: Known definitely only from two localities in eastern Oaxaca—in the Sierra Madre de Chiapas and in the Sierra Madre del Sur (on the Cerro Zempoaltepec ridge), east and west of the Plains of Tehuántepec, respectively. Estimated elevations are 4000–4500 feet (1220–1372 meters) for the holotype, and 3750 feet (1143 meters) for a specimen from Yelagago, a locality about 160 kilometers northwest of the type locality.

DESCRIPTION (THREE SPECIMENS): The holotype is a male 292 mm. total length, of which 104 mm. is tail; two females have total lengths of 291 mm. (91 mm. tail) and 297 mm. (87 mm. tail). The tail is 35.6 percent of the total length in the male, and 29.3 and 31.3 percent in the females. The dorsal scales are in 17–17–17 rows; anal ridges are absent. Ventrals are 119–131 (119, male; 124, 131, females) and subcaudals are 60–74 (74, male; 60, 64, females). There are eight supralabials and 10 infralabials (10/8 in UIMNH 37163). There is one preocular (1/2 in the holotype), a subpreocular between the third and fourth labials, two postoculars, and 1+2 temporals.

The dorsum is medium brown. Although there is formation of small pigment spots on some of the vertebral scales, a dark vertebral line is essentially absent, except for a faint line atop the tail. There is a narrow, rather diffuse, black lateral line involving row 4, and the sides below the lateral line are several shades darker brown than the dorsal surfaces. The sides of the tail remain dark virtually to the tip, but in AMNH 89618 there is a vague whitish line along the side of the tail on the first scale row. The position of the lateral black line varies slightly. On the holotype and UIMNH 37163, the line lies mainly on the top of row 4, with a slight overlap onto the bottom edges of scales in row 5; the line is in this same position on the neck of AMNH 89618, but posteriorly it is shifted down onto the middle of row 4. The lateral dark line may be bordered above by a whitish spot on each scale in row 5; these spots are not vivid (virtually absent in AMNH 89618) and become most conspicuous on the neck, where they merge to form a short, white line. The anterior termination of the white line, a few scales above and behind the ultimate supralabial, is black-edged and varies from a slight widening in the holotype to a distinct white spot in UIMNH 37163. On the holotype and AMNH 89618 there is a barely discernible indication of a median white line on the nape, on a few vertebral scales immediately behind the parietals.

The head is brown above, like the dorsum of the body, and there is a pair of pale parietal dots and some inconspicuous black flecking. A black-bordered white line extends posteroventrad from the upper rear edge of the eye to behind the last supralabial, where it either merges with the white throat color or is narrowly separated from the throat. AMNH 89618 has a short posterodorsad extension of this line that nearly connects it with the anterior termination of the white line on the side of the neck. A black line which crosses the rostral splits and diverges behind the naris, to form the dark edges of a brown stripe that passes through the eye and extends obliquely below the postocular white line to behind the corner of the mouth, where it may terminate or (in the holotype) have a narrow connection with the lateral body coloring. There is a conspicuous blackish brown dash or spot on each of the first six or seven supralabials, which otherwise are white below the bottom edge of the lateral brown stripe. There are dark dots on the mental, first several infralabials, last infralabial and, in two specimens, on the anterior genials. The venter is immaculate white except for the ventral and subcaudal tips. On the holotype and AMNH 89618, there is a small dark spot on the tip of each ventral; the spots are present only on the anterior ventrals of

UIMNH 37163, and the remaining ventrals have only a slight tinge of brown on each tip. The dark pigment forms a continuous line across the tips of the subcaudals. The color in life is not known.

I counted 14+2 teeth on a maxilla of UIMNH 37163, and 16+2 on a maxilla from each of the other two specimens. The prediastemal teeth are anterior to the front edge of the ectopterygoid process and the last fang is offset laterad.

The retracted hemipenes of the holotype extend to the middle of subcaudal 8 (left) and to the base of subcaudal 9 (right). The left retractor muscle originates at the level of subcaudal 18; the right retractor lacks an anchorage (see Remarks). The capitulum comprises nearly half of the length of the organ on its sulcate side. The calyces are papillate except on the asulcate fold and in a band around the base of the capitulum, where the papillae are replaced by tiny spines. The sulcus spermaticus forks about a third of its length up the capitulum and the branches extend nearly to the tip of the retracted organ. The wall of the capitulum forms a single fold on the asulcate side. There are 22 small- to medium-sized, recurved spines below the capitulum. The spines are mostly medium-sized and most lie close below the capitulum on the asulcate side; only a few spines originate slightly below the middle of the organ. Most of the basal half of the hemipenis is nude, except for spinules, and even these are absent on the basal sixth of the organ. The preceding description is based on the retracted organs of the holotype; the right hemipenis was removed after its length had been determined.

REMARKS: The right retractor muscle of the holotype lacks an origin. Its blunt end lies free at the level of subcaudal 14, four plates anterior of the normal origin of the left retractor. This condition seemed to be an aberration rather than the destruction from some previous dissection, judged by the appearance of the muscle and also by the position of the sulcus spermaticus in the right hemipenis. The sulcus was in a midventral rather than lateral position, indicating that the organ might have rotated due to the lack of posterior anchorage.

The species is named for Thomas MacDougall, who obtained the holotype. Additional comment on *Rhadinaea macdougalli* is to be found in the Remarks section of *R. bogertorum*.

Rhadinaea marcellae Taylor

Figures 10H, 11E; map 5

Rhadinaea marcellae TAYLOR, 1949, pp. 197, 198; 1950, p. 448, pl. 6, fig. 2 (photograph of preserved holotype).

HOLOTYPE: LSU 270 (original number R 246), a male in fair condition, from the Xilitla region, southeastern San Luis Potosí, Mexico, purchased from native by Marcella Newman, June 12, 1947.

DIAGNOSIS: The only known specimen of *Rhadinaea marcellae* is intermediate between *R. macdougalli* and *R. myersi* (both from Oaxaca) in its low number of ventrals and subcaudals, and is also similar to *R. forbesi* (Veracruz) in this regard. Assuming that the holotype is representative, *R. marcellae* differs from the aforesaid species (all in the *decorata* group) and from all other congeners in the head and neck pattern, the most distinctive element of which is a white line crossing the nape and connecting with a white line on each side of the neck. There are also pale vermiculations atop the head, and a white line from the upper rear edge of the eye to the side of the neck, and, although not diagnostic in themselves, these markings contribute to the unique appearance of the head. There are more spines on the hemipenis than in any other species of the *decorata* group for which the copulatory organ is known.

DISTRIBUTION: Known only from the type locality, in the Sierra Madre Oriental of extreme southeastern San Luis Potosí. The elevation of the type locality is not recorded. The town of Xilitla lies at about 2200 feet (671 meters), but some mountains in the region exceed 7000 feet (2134 meters), according to Taylor (1949, p. 172; 1950, p. 457).

DESCRIPTION (OF HOLOTYPE): The specimen is a subadult male 290 mm. total length; the tail is 95 mm., or 32.6 percent of the total. Dorsal scales are in 17–17–17 rows; anal ridges are absent. There are 128 ventrals and 77 subcaudals. There are eight supralabials, with the fourth and fifth touching the eye, and nine infralabials, with the first four touching the anterior genials. There is one preocular, a subpreocular between the third and fourth labials, two postoculars, and 1+2 temporals.

The holotype is medium brown above. A black vertebral line extends from the neck to near the end of the tail. The vertebral line is

nearly solid on the neck and tail but on most of the body it is light-centered, being formed by a pair of thin, broken lines, one on each side of the midline, on the border of the vertebral-paravertebral rows; pigment is most concentrated on the inner edge of each paravertebral scale, with a connection across the apex of each vertebral scale, giving the appearance of a tiny hourglass spot at the end of each vertebral scale along most of the body. A narrow, lateral black line is on the adjacent edges of rows 4 and 5, and is bordered above by an inconspicuous whitish spot on each scale in row 5; these spots merge to form a solid white line on the side of the neck. The brown sides of the body below the black line are a little darker than the middorsum.

There is a complex pattern of white markings on the head and nape: A black-bordered white line extends posteroventrad from the upper rear edge of the eye to a point behind the last supralabial, and from there it slants posterodorsad to fuse with the white line on the side of the neck. A black-edged white line crosses the nape, connecting each lateral line, and has an anterior projection that extends forward on two vertebral scales to the interparietal suture. There is a pale but vague scroll-like pattern atop the head, and a pair of white parietal dots. The upper tip of the snout and the canthus rostralis are whitish. The pale color of the canthus rostralis might be judged a diffused, anterior extension of the postocular white line. A black line crosses the rostral, splitting and diverging at the naris, to form the black edges of a brown stripe that passes through the eye and extends obliquely below the postocular white line to behind the corner of the mouth, narrowly fusing with the brown of the body. There is a dark brown dash on each of the first six supralabials, which otherwise are white below the bottom edge of the lateral head stripe; the mental and first several infralabials have dark dots. The venter is immaculate whitish, except for the ventral and subcaudal tips, which are a somewhat darker brown than the color of the lower sides. The color in life is not known.

There are 17+2 teeth on the left maxilla, with the prediastemal teeth all lying anterior to the front edge of the ectopterygoid process. The last fang is offset laterad.

The left retracted hemipenis extends to the base of subcaudal 7, and the retractor muscle originates at the level of subcaudal 22. The capitulum comprises nearly half of the length of the organ on its sulcate side. The calyces are adorned with papillae, some of which are presumably unossified spinules (see Remarks). The sulcus spermaticus forks at a point no more than one-fourth its length on the capitulum, and the branches extend nearly to the tip of the uneverted organ. The wall of the capitulum forms a single fold on the asulcate side. There are about 50 small to large, slightly recurved spines below the capitulum, mostly on the asulcate side. The uppermost spines are shortest, whereas the basal spines are long and relatively slender. No spines originate on the basal third of the hemipenis, although some spines overlap onto the distal part of this section, which is ornamented with minute spinules.

REMARKS: The uppermost spines on the hemipenis, and presumably the basal "papillae" of the capitulum, are unossified, indicating that the holotype had not attained sexual maturity. The species is named in honor of Mrs. Marcella Newman, who obtained the type specimen in the course of an expedition sponsored by the Louisiana State University.

Rhadinaea montana Smith

Figures 10B, 11A; map 7

Rhadinaea quinquelineata (not of Cope): BAILEY, 1940, pp. 11, 12, pl. 1, fig. 1 (part: ANSP 15355 [midbody pattern figured] = paratype of *R. montana*).

Rhadinaea montana SMITH, 1944, pp. 146–148. SMITH AND TAYLOR, 1945, p. 118.

HOLOTYPE: FMNH 30826, an adult female in good condition, from Ojo de Agua, near Galeana, Nuevo León, Mexico, obtained on August 11, 1938, by Harry Hoogstraal and party.

DIAGNOSIS: *Rhadinaea montana*, the northernmost representative of the *decorata* group, is a contrastingly striped snake that somewhat resembles specimens of *R. gaigeae* and *R. quinquelineata* in having a relatively pale area (usually grayish in preservative) along each side of a vertebral dark line. The dorsolateral stripes of brown that delimit the paravertebral pale areas have narrow dark edges in *montana*, which is thus distinguished from the other two species. In addition to the dark edges, the dorsolateral stripes are wider in *montana* (from the middle of scale row 6 to the middle of row 7 or to the edge of row 8), and adjacent pale lateral stripes are more narrow (compare illustrations).

The dark-edged, dorsolateral stripes are not always as dark-centered as illustrated herein; for comparison, see the midbody pattern given by Bailey (1940, pl. 1, fig. 1, under the name "*quinquelineata*").

DISTRIBUTION: The northern Sierra Madre Oriental, where the species is known only from central Nuevo León. Nothing is recorded concerning elevations or habitats.

DESCRIPTION (FOUR SPECIMENS): The only male examined measured 430 mm. total length, of which 142 mm. is tail; the largest female measured 580 mm. total and 188 mm. tail length. The tail is 33.0 percent of total length in the male and 28.1–32.4 percent in three females. The dorsal scales are in 17–17–17 rows; anal ridges are present on the male specimen and weakly present on the female holotype. Ventrals are 171–186 (171, male; 173–186, females) and subcaudals are 97–101 (100, male; 97–101, females). There are eight supralabials and 10 infralabials. There is one preocular and usually a subpreocular between the third and fourth labials. There are two postoculars and 1+2 temporals.

Preserved specimens of this species have contrasting stripes and lines of dark brown, gray, and white. A light gray or whitish middorsum (vertebral and paravertebral scale rows) is broken by a blackish brown vertebral line that overlaps slightly onto the paravertebral rows; this vertebral line extends from the nape well onto the tail, where it narrows and gradually disappears. On each side of the middorsal pale area is a dark-edged brown stripe, from the middle of row 6 to the edge of row 8 in width, or (in the holotype) from the middle of row 6 to the middle of row 7. The dorsolateral brown stripes are a posterior continuation of the brown head color, running the length of the body and gradually converging on the tail, on which they posteriorly form a median dark line after the disappearance of the vertebral line and middorsal pale gray area. A dark brown lateral stripe, which is narrowly continuous around the rostral plate, passes along the side of the head and through the eye, and slants posteroventrally across the corner of the mouth to the side of the neck, where the stripe narrows and continues caudad on row 4 (with slight extensions onto the edges of rows 3 and 5), going weakly but discernibly to the tip of the tail. The sides of the body below the lateral stripe are light brown. Between the lateral and dorsolateral dark stripes is a conspicuous white or brownish white stripe that runs from the rear of the head to the end of the tail and which may be anteriorly continuous with a white line on the head. The white line on the head is black-edged and tends to be continuous around the top of the rostral plate, extending conspicuously along the canthus rostralis and through the upper edge of the eye, behind which it crosses (either horizontally or obliquely) the upper postocular and parietal edge and slants posteroventrad across the temporals and onto the upper edge of the last supralabial. The white line usually stops short of the anterior end of the whitish body stripe, but these markings are continuous on one side of FMNH 40814. In the holotype only, there is a gap in the postocular part of the white line, leaving a discrete temporal marking (fig. 10B). There is a short white line, which may be nearly absent, on the nape, in front of the anterior end of the vertebral dark line. The top of the head varies from being uniformly dark brown to having a dense speckling of dark brown on a grayish background. A pair of pale parietal dots is present only on the holotype. A broken, dark brown line runs horizontally across the supralabials, which are white below the lower edge of the lateral dark stripe. The infralabials are dotted with dark brown. The other ventral surfaces are immaculate whitish except for a dark dot or irregular cluster of dark specks on each ventral and subcaudal tip. These markings, which are largest (tiny spots) on the first several ventrals, form a thin broken line across the ends of the subcaudals. The colors in life are not known.

The teeth are 17+2 on three maxillae and 19+2 on a fourth, with all the prediastemal teeth lying anterior to the front edge of the ectopterygoid process. The last fang is offset laterad.

The retracted hemipenis extends to the end of subcaudal 5 and the retractor muscle originates at the level of subcaudal 23. The capitulum comprises somewhat less than half the length of the organ on its sulcate side. The calyces are spinulate on the asulcate fold and on the periphery of the capitulum, and papillate elsewhere. The sulcus spermaticus forks about one-third of its length on the capitulum and the branches extend nearly to the end of the retracted hemipenis. The wall of the capitulum forms a single fold on the asulcate side of the organ. There are about 20 small to medium,

slightly recurved spines below the capitulum. Some of the medium-sized spines are arranged in two parallel rows of four spines each, on the asulcate side. Nearly the entire basal half of the organ is nude, except for some minute spinules. The preceding description is based on the retracted left organ of ANSP 15355.

REMARKS: Virtually nothing is known of this species, which lives farther north than any other montane *Rhadinaea*. The specific epithet is an adjective referring to an inhabitant of the mountains. One of the "paratypes" (ANSP 15355) seemingly was not examined for purposes of the original description, but it was correctly allocated (Smith, 1944) on the basis of the locality and an earlier description and illustration (Bailey, 1940, under the name *Rhadinaea quinquelineata*).

Rhadinaea myersi Rossman

Figures 10K, 11H, 12B; map 5

Rhadinaea myersi ROSSMAN, 1965, pp. 1–4, fig. 1 (photograph of side of head and neck of holotype).

HOLOTYPE: LSU 7566 (originally Laurence C. Binford No. 1137) an adult male in fair condition from the ecotone between pine and cloud forests, 5000 feet (1524 meters), 3 miles north of Pluma Hidalgo, Oaxaca, Mexico. The specimen was obtained by Laurence C. Binford on May 2, 1964.

DIAGNOSIS: *Rhadinaea myersi*, of the Pacific slopes of central Oaxaca, appears geographically isolated from other members of the *decorata* group. The white postocular line is only weakly diagonal and does not extend behind the corner of the mouth to the lower side of the neck, as in *R. macdougalli*, *R. marcellae*, and *R. forbesi*. The aforesaid white line normally terminates on the temporals, as in *R. hesperia*, which, however, has the lateral dark line on row 5 (row 4 in *myersi*) and many more subcaudals and ventrals (especially in the populations closest to the range of *myersi*). In color pattern, *Rhadinaea myersi* is close to *R. bogertorum*, which has considerably more ventrals; additional comparisons are given in the Remarks section under *bogertorum*.

The hemipenis of *Rhadinaea myersi* is a useful diagnostic feature, as the capitulum is very small, comprising only about two-fifths the length of the organ on its sulcate side (usually about half the length in other species of the *decorata* group).

DISTRIBUTION: Known only from the Sierra Madre del Sur in the vicinity of Pluma Hidalgo and La Soledad, near the Pacific coast of central Oaxaca. It remains to be learned whether the species is an inhabitant primarily of cloud forest or of the pine-oak zone. The holotype was taken in the ecotone, at 5000 feet (1524 meters) elevation.

DESCRIPTION (THREE SPECIMENS): Two adult males are 366 mm. and 386 mm. total length, with respective tail lengths of 120 mm. and 134 mm., or 32.8 and 34.7 percent of the total. A juvenile female is 187 mm. total length, with a tail of 54 mm., or 29.9 percent of the total. Dorsal scales are in 17–17–17 rows; anal ridges are present in the two males. Ventrals are 132–139 (132, 135, males; 139, female), and subcaudals are 72 in the female and 79 in both males. The supralabials are 8/8 or 9/8, and there are 10 infralabials. There is a subpreocular between the third and fourth labials, and there is one preocular, except in UIMNH 6317, which has two preoculars on the right (this specimen is also unusual in that the left loreal extends below a small preocular to touch the eye). There are two postoculars. Temporals are 1+2/1+2 in the holotype, and 1+1+2/1+2 in the other two individuals.

The body is light to medium brown, being darkest on the lower sides below row 5. Black pigment at the juncture of adjacent vertebral scales forms a median series of small spots, which fuse to form a continuous line on the tail. On the holotype, the vertebral and paravertebral scale rows are uniformly gray, except for the line of black vertebral spots; this middorsal region originally was "dark gray brown" (Rossman, 1965, p. 2), before loss of the stratum corneum in preservative, but the area is only slightly darkened in the other two specimens at hand. Two specimens have a lateral black line on row 4 and the extreme lower edge of row 5, this line being interrupted by a pale spot or dash on the dorsomedial part of each scale in the fourth row. The third specimen, the juvenile paratype, has the lateral dark line restricted to the lower edge of row 5 and lacks the line of pale dashes on the fourth row. On each side of the neck, close to the posterodorsal edge of the last supralabial, is a variable-sized, black-edged whitish spot that is posteriorly confluent with a dorsolateral pale stripe on the neck, on row 6 and the upper part of row 5. The pale stripe posteriorly tends to be

limited to row 5, becoming indefinite or indistinguishable, except in the juvenile paratype, on which there is a persistent pale line on the fifth row throughout the body and onto the tail. A thin line of brown ground color, low on the side of the tail (row 1), narrowly separates the lateral dark line from the dark subcaudal margins. These markings, and also the median dark line, become vague and diffused toward the end of the tail.

The head is brown above; a pair of pale parietal dots is evident in some cases. A black-edged white line extends along the canthus rostralis, where it is poorly defined, passes through the top of the eye, and with a slight downward slant crosses the edge of the parietals and the temporals. This pale line does not encroach onto the supralabials, although its lower dark edge may touch the ultimate and penultimate labials, and it ends short of the white ocellus behind the head, except on the left side of UIMNH 631, in which the line is confluent with the pale markings on the neck. A black line, which crosses the rostral, splits and diverges either before or behind the naris, to form the dark edges of a brown stripe that extends alongside of the head and above the corner of the mouth, to fade on the lower side of the neck. The supralabials and infralabials are whitish and are variably marked with a small number of black dots or (in the paratype) with clumps of dense brown speckling. The ventral and subcaudal plates are tipped with blackish brown, and UIMNH 6317 is sparsely dotted with black along the sides of the belly and under the tail. Otherwise the ventral surfaces are whitish in preservative. The color in life is not known.

There are 19+2, 20+2, or 21+2 teeth on a maxilla from each of the three specimens. The prediastemal teeth are anterior to the front edge of the ectopterygoid process and the last fang is offset laterad.

The hemipenis is fairly short and the sulcus spermaticus forks unusually high on the capitulum. The retracted organ extends to the base or middle of subcaudal 6, and the retractor muscle originates at the level of subcaudal 22 (holotype) or 28. The capitulum is small, comprising about the distal two-fifths of the length of the organ on its sulcate side. The calyces are papillate, except on the periphery of the capitulum, on the lips of the sulcus spermaticus below the fork, and on the asulcate folds (which would represent most of the asulcate side of the capitulum of an everted hemipenis). The sulcus spermaticus forks opposite the middle of subcaudal 5 in the organ *in situ*, more than half and as much as two-thirds (in UIMNH 6317) of its length up the capitulum, and the short branches extend nearly to the end of the retracted organ. The wall of the capitulum forms a double fold on the asulcate side of the uneverted hemipenis. There are 18 or 25 (holotype) small to large, slightly recurved spines below the capitulum. Two large spines flank a nude strip below the capitulum on the asulcate side. Most of the spines lie close under the capitulum, but a rather large spine originates slightly basad of the distal half of the organ, near the sulcus spermaticus. The basal half of the hemipenis is mostly nude except for minute spinules. The preceding description is based on the retracted hemipenes of the holotype (right organ illustrated) and UIMNH 6313. The right organ of the holotype and left organ of the other specimen were removed after preliminary examination *in situ*. Anyone wishing to verify the relative size of the capitulum should do so on the organs remaining *in situ*, as approximately the basal fifth of each organ removed was inadvertently left in place.

REMARKS: Bailey (1940, p. 17) declined to describe the present species because he had available only a poorly preserved juvenile (now the paratype) that had been collected in 1919. The catalogue entry for this specimen (AMNH 19783) notes that it was found on a brushy mountainside on a trail, which presumably means that it was abroad by day. The second specimen (LSU 7566) to become known was found in 1964, and, in the following year, Rossman named the species after me. A third specimen (UIMNH 6317) was collected in 1949 but was misidentified and has not been previously reported. The tag on this individual has the datum "El Soledad," but as *soledad* (a lonely place) is feminine, I presume that "La Soledad" was intended. A place with the latter name is situated some 60 kilometers west of the type locality.

Rhadinaea quinquelineata Cope

Figures 10E, 11C, 18; map 7

Rhadinaea quinquelineata COPE, "1885" [1886b], p. 277; 1887, p. 79. BAILEY, 1940, pp. 11, 12 (part: ANSP 15355, pl. 1, fig. 1 [midbody pattern]=*R.*

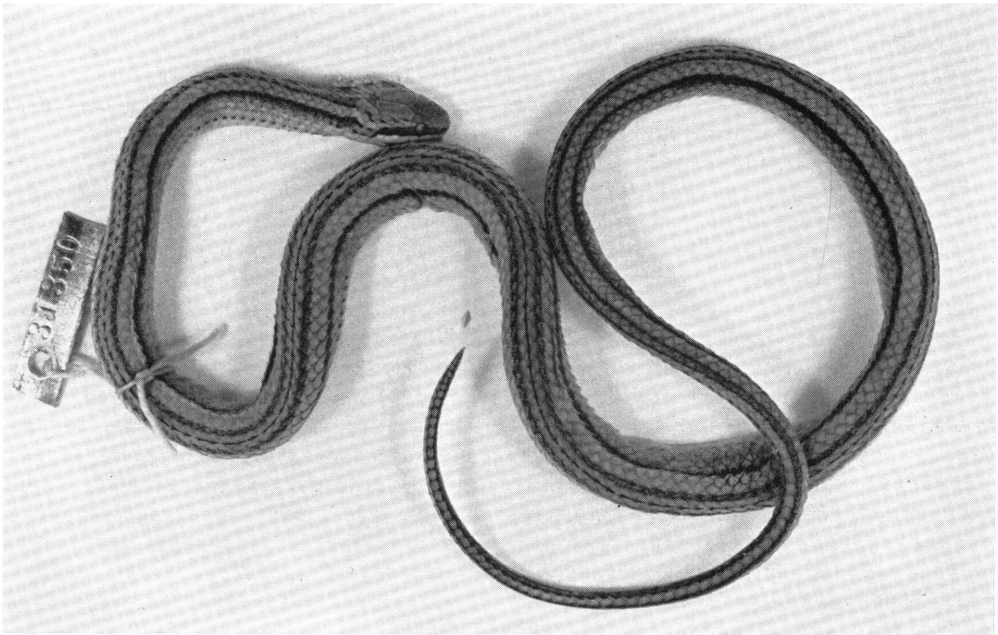


FIG. 18. *Rhadinaea quinquelineata*, USNM 31350, lectotype and only known specimen, from Teziutlán, Puebla, Mexico.

montana). SMITH, 1944, p. 148, fig. 19 (anterior body pattern of holotype). SMITH AND TAYLOR, 1945, p. 119.

Rhadinaea vittata (not of Jan): BOULENGER, 1894b, p. 178 (part). COPE, 1900, pp. 756, 757 (part).

LECTOTYPE: USNM 31350, a female (apparently adult), from [Teziutlán], Puebla, Mexico, obtained by Santiago Bernad. There were three syntypes, but the fate of two from Hidalgo is not known. The lectotype designation was made by Bailey (1940, p. 11), who almost certainly was correct in believing that Cope described the Puebla specimen, rather than one of the Hidalgo syntypes as would be inferred from remarks in the original description. Following are comparative data obtained from the original description and from the lectotype (in parentheses): Ventrals 179 (same), subcaudals 77 (76), infralabials 10 (10/8, but Cope usually counted one side only), total length 438 mm. (435 mm.), tail length 115 mm. (114 mm.). Cope gave only "State of Pueblo" as locality, but the USNM catalogue entry is more explicit.

DIAGNOSIS: The only known specimen of *Rhadinaea quinquelineata* is a contrastingly striped snake that resembles *R. montana*, and, to a lesser degree, specimens of *R. gaigeae* in having a pale area (gray in preservative) along each side of a vertebral dark line. The narrow, dorsolateral dark stripes that delimit these paravertebral pale areas lack sharply defined edges, thus distinguishing *quinquelineata* from *montana*, which has wider dorsolateral stripes with dark edges (compare illustrations). The dorsolateral dark stripe does not cover the bottom part of the seventh scale row in *quinquelineata*, whereas in *gaigeae* this marking covers all or at least the bottom part of row 7, and narrowly edges row 6. The dark markings of *gaigeae* are less well defined than in the holotype of *quinquelineata*; the latter specimen seems somewhat faded but it probably did have a relatively light ground color in life.

DISTRIBUTION: Sierre Madre Oriental. Known definitely only from the type locality (Teziutlán) in northern Puebla, near the Veracruz border. Cope did not originally give a specific locality for the Hidalgo syntypes, but later (1887, p. 79) he listed the locality Zacualtipán, possibly in reference to the syntypes, which are now lost and which conceivably might have represented another species (e.g., *Rhadinaea gaigeae*). Bailey's (1940) record for Nuevo León is based on a specimen of *R. montana*.

DESCRIPTION (OF LECTOTYPE): The specimen is a female 435 mm. total length; the tail length is 114 mm., or 26.2 percent of the total. Dorsal scales are in 17–17–17 rows; anal ridges are absent. There are 179 ventrals and 76 subcaudals. There are eight supralabials, with the third to fifth touching the eye, and 10/8 infralabials, with the first five (left) or four (right) touching the anterior genials. There is one preocular, no subpreocular, two postoculars, and 1+2 temporals.

The lectotype is pale brown, evidently faded, and has five longitudinal blackish brown markings: There is a thin, broken vertebral line that starts about a head's length behind the head and disappears just past the cloaca on the base of the tail; this is actually a line of dashes that are continuous only for a space at midbody. On each side of the vertebral line is an area of pale grayish ground color, which is limited by a dusky but discrete stripe that occupies slightly more than the upper half of row 7 and the adjacent edge of the paravertebral (eighth) row; each paravertebral dark stripe originates anteriorly as a faint, broken line extending from the upper, rear edge of the eye, and the pair of stripes posteriorly converge before the middle of the tail to form a single median line that continues weakly but discernibly to the tip of the tail. A lateral dark stripe, which is narrowly continuous around the rostral plate, runs along the side of the head through the eye and slants posteroventrally across the corner of the mouth to the side of the neck, from where it runs along the body on the lower two-thirds of row 4 and the adjacent edge of row 3, going weakly but discernibly to the tip of the tail. The pale ground color between the lateral and paravertebral dark stripes is too broad to appear as a definite light stripe, except on the neck and rear of the head, where it is narrowed and extends forward to the eye, after a dip on the temporal region; there is only the faintest indication of this pale stripe in front of the eye on the canthus rostralis. There is a short, partly dark-edged, median white line on the neck, several scales anterior to the start of the dark vertebral line. There is no indication of a pair of parietal dots. The supralabials are immaculate whitish below the lateral dark stripe, except for a few dark dots on the anterior plates. The ventral surfaces, including infralabials, are virtually immaculate white, except for a small dark brown spot on the tip of each ventral and for a dark line along the tips of the subcaudals. The labials and venter were yellow when Cope described the specimen.

There are 19+2 teeth on the left maxilla (the right maxilla is missing). The ultimate prediastemal tooth is anterior to the front edge of the ectopterygoid process. The diastema is short, being about the length of a prediastemal socket. The last fang is offset laterad.

REMARKS: The fact that this species has not been rediscovered since the original description indicates that it is rare and/or localized, and also suggests that the undescribed syntypes from Hidalgo might have represented a different species, perhaps *Rhadinaea gaigeae*. The specific epithet is formed from the noun *quinque* (five) plus the adjective *lineatus* (marked with lines), in obvious reference to the number of longitudinal dark markings on the body.

THE *taeniata* GROUP

The *taeniata* group is comprised of three species, one of which contains two remarkably distinct subspecies: *Rhadinaea fulvivittis*, *R. omiltemana*, *R. t. taeniata*, and *R. t. aemula*. They are strictly Mexican, occurring in the highlands north and south of the Balsas basin—in the Cordillera Volcánica, Sierra de Coalcomán, Sierra Madre de Oaxaca, and, principally in the Sierra Madre del Sur. The group is defined especially by the following combination of characters (see also table 3): The single hemipenis lacks notable, special features, except that spinules occur in a relatively wide and uniform band around the basal section of the distinct capitulum; the asulcate fold is doubled. Scutellation is generalized (except for 1+1 temporals in *fulvivittis*); a subpreocular is usually present. The head and body tend to be continuously and conspicuously striped with wide brown or black stripes that set off a narrow, dorsolateral pale stripe of ground color. The dorsal ground color does not extend onto the tips of the ventrals (or only minutely and inconspicuously so).

Rhadinaea fulvivittis is not especially large (less than 500 mm.), but some individuals of *R. omiltemana* probably exceed 600 mm. total length, and individuals of *R. t. taeniata* doubtlessly exceed 900 mm. (maximum known preserved length is 880 mm.). *Rhadinaea taeniata* is the largest species in the genus. *Rhadinaea fulvivittis* and *R. omiltemana* are closely related but evidently distinct species that, in their respective

TABLE 8

ASPECTS OF INTERSPECIFIC VARIATION[a] IN THE *taeniata* GROUP

Species	N	Ventrals		Subcaudals		Tail Length as a Percentage	
		Males	Females	Males	Females	Males	Females
fulvivittis	59	148–168 (31) 158.5±0.80	159–183 (28) 168.7±1.19	83–103 (29) 93.1±0.90	79–97 (21) 85.2±0.98	28.7–36.8 (28) 33.0±0.38	27.2–32.1 (20) 29.9±0.32
omiltemana	10	150–161 (4) 154.0	157–168 (6) 163.8	85–90 (4) 87.3	78–88 (6) 83.3	31.6–33.8 (4) 32.9	27.5–31.2 (6) 29.6
taeniata taeniata	12	168–180 (4) 172.8	178–197 (8) 188.1	106–110 (3) 108.0	95–105 (7) 101.1	31.0–32.7 (3) 31.7	27.6–35.1 (7) 29.6
taeniata aemula	40	150–170 (20) 157.3±1.24	160–178 (20) 167.5±0.89	100–121 (18) 107.4±1.29	97–114 (13) 103.9±1.23	30.4–36.8 (18) 33.8±0.38	28.7–33.3 (16) 31.2±0.31
t. taeniata × *t. aemula*	4	154, 166 160.0	170, 172 171.0	91+[b], 105 98.0	89, 89+[b] 89.0	31.2[b], 34.5 32.9	27.1, 28.5[b] 27.8
Combined ranges	125	148–180	157–197	83–121	78–114	28.7–36.8	27.1–35.1

[a]The following statistics are given if the sample is sufficiently large: Above, range followed by number of specimens in parentheses (if more than two); below, mean and standard error of the mean.

[b]Approximate figure; the extreme tip of the tail is missing.

ranges, occur macrosympatrically with *R. t. aemula*, but usually at higher elevations in the pine-oak forest.

Rhadinaea fulvivittis Cope

Figures 5, 19E, 20E, 21, 49B; map 8

Enicognathus vittatus, not of JAN: JAN AND SORDELLI, 1866 (1860–1881), vol. 1, livr. 16, pl. 2 (part: fig. 3, details of color pattern and cephalic scutellation of specimen in Paris Museum). Secondary homonym.

Rhadinaea fulvivittis COPE, 1875a, pp. 139, 140; 1887, p. 79; 1900, p. 756. WERNER, 1929, p. 119. BAILEY, 1940, pp. 10, 11, pl. 2, fig. 1 (midbody pattern of USNM 6333). SMITH, 1943, p. 464, pl. 32, fig. 2 (poor photograph of a preserved specimen).

Diadophis fulvivittis (Cope): GARMAN, 1883, pp. 71, 158.

Dromicus fulvivittis (Cope): GÜNTHER, 1894 (1885–1902), p. 113.

Rhadinaea vittata (not of Jan): BOULENGER, 1894b, p. 178 (part). COPE, 1887, p. 80. WERNER, 1929, p. 119. DUNN, 1932, p. 2. SMITH AND TAYLOR, 1945, pp. 6, 119.

Liophis vittatus (not of Jan): AMARAL, 1929b, p. 175.

HOLOTYPE: USNM 7075, an adult female in good condition, from the "Alpine region"

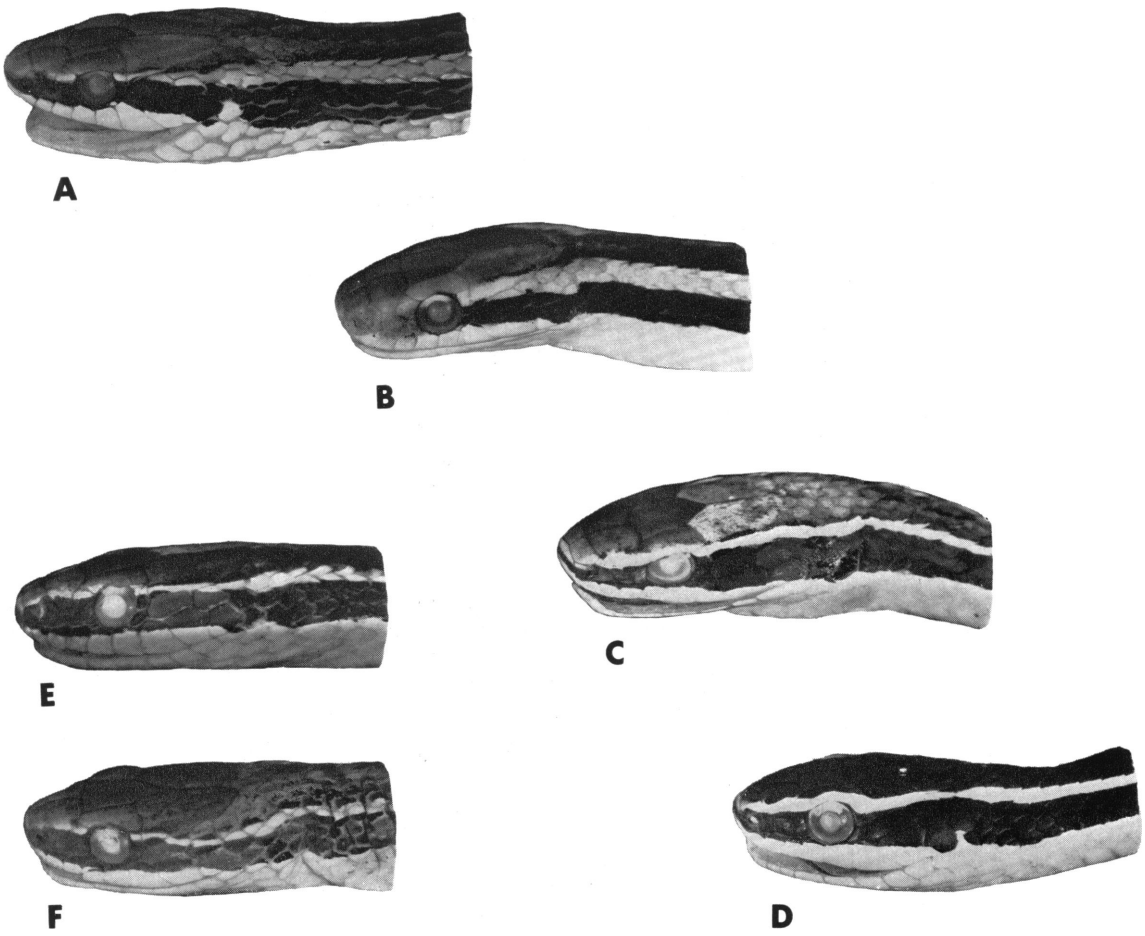


FIG. 19. Head patterns in the *taeniata* group. A–D. All *Rhadinaea taeniata*, as follows: A. *R. taeniata taeniata*, UMMZ 21522, Michoacán. B. Intraspecific hybrid, UMMZ 125731, Guerrero. C. Intraspecific hybrid (lectotype of species, hence type of nominate subspecies, but specimen is closer to subspecies *aemula*; note narrow dorsolateral line that continues above eye), SMF 2117-A, State of México?. D. *R. taeniata aemula*, AMNH 103688, Oaxaca. E. *R. fulvivittis*, UIMNH 60784 (right side of head, reversed), Oaxaca. F. *R. omiltemana*, BMNH 1946.1.1.7 (holotype), Guerrero.

TABLE 9
NUMBER OF MAXILLARY TEETH IN THE *taeniata* GROUP

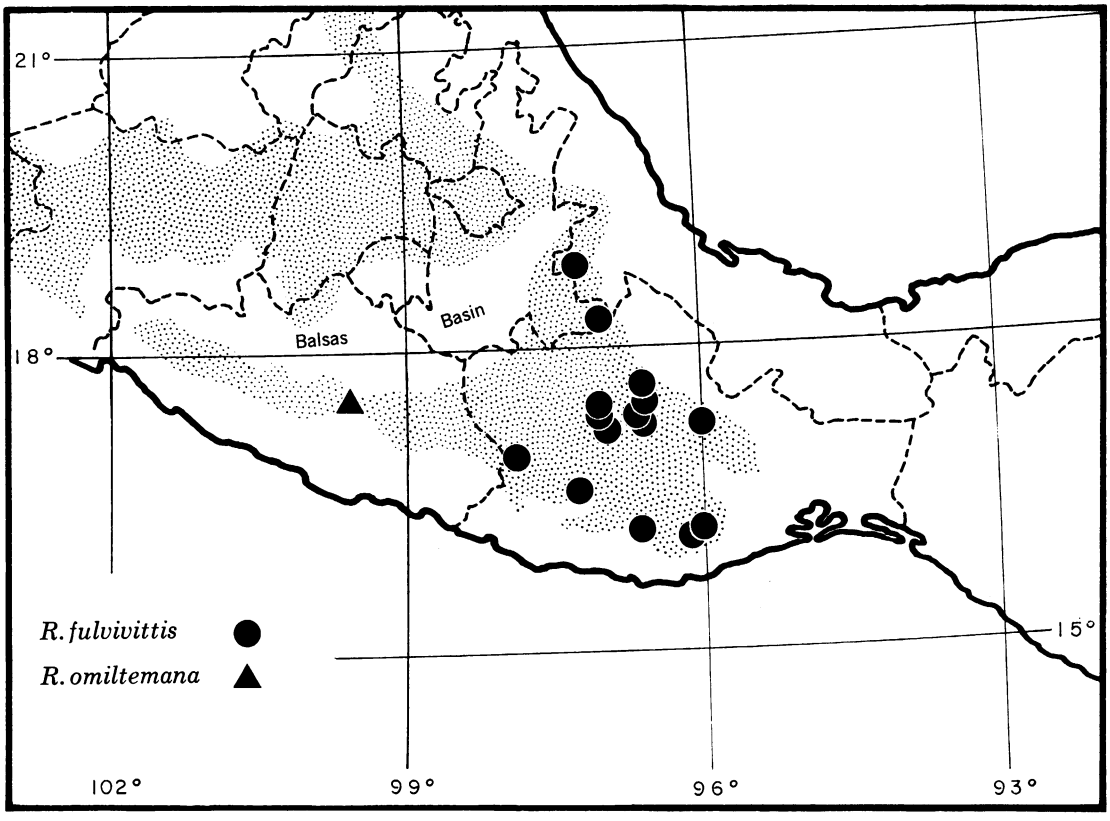
Species	N[a]	No. of Teeth 17+2	18+2	19+2	20+2	21+2	22+2	Range
fulvivittis	20	1	3	3	4	5	4	17+2–22+2
omiltemana	8	1	—	1	5	1	—	17+2–21+2
taeniata[b]	26	3	6	8	4	3	2	17+2–22+2
Combined	54	5	9	12	13	9	6	17+2–22+2

[a]A single maxilla from each specimen.
[b]A breakdown for subspecies and hybrids is given in the species account.

(according to catalogue entry) of [Cerro] Orizaba, Veracruz, Mexico; obtained by Sumichrast. Cope counted 177 ventrals and 91 caudals; my counts are 176 ventrals (plus 1 preventral=177) and 89 subcaudals. There are 10/9 infralabials, and the third to fifth supralabials touch the eye.

DIAGNOSIS: A member of the *taeniata* group that is distinguished from all other species of *Rhadinaea* by its three dark-edged brown stripes that run from the snout well onto the tail, on a lighter brown background. The lateral stripe of the related *R. omiltemana* is in the same position (row 4 and a part of each adjacent row) and may be dark-edged in young specimens, and even the dorsal stripe may have dark edges, but the dorsal stripe is broader in *omiltemana* (median five plus parts of two adjacent rows) than in *fulvivittis* (median three plus parts of two adjacent rows).

DISTRIBUTION: Pine-oak forest, in the Sierra Madre del Sur of Oaxaca and along the Sierra



MAP 8. Locality records for *Rhadinaea fulvivittis* and *R. omiltemana*, a pair of related species from Sierra Madre del Sur and Sierra Madre de Oaxaca. Stipple pattern indicates approximate distribution of pine-oak forest.

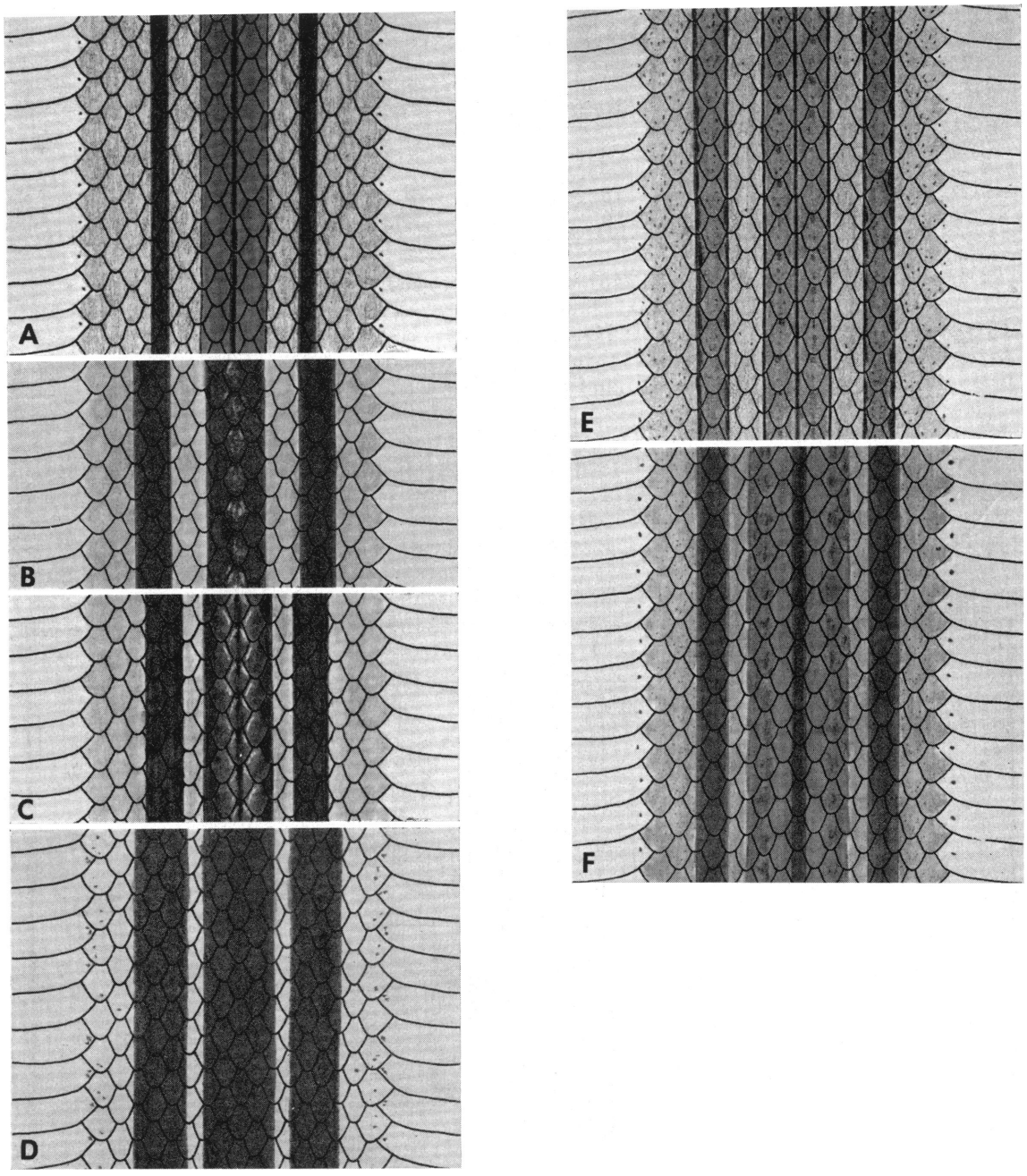


FIG. 20. Midbody color patterns in the *taeniata* group. A–D. All *Rhadinaea taeniata*, as follows: A. *R. taeniata taeniata*, TCWC 11585, Michoacán. B. Intraspecific hybrid, UMMZ 125731, Guerrero. C. Intraspecific hybrid, SMF 2117-A (lectotype), State of México?. D. *R. taeniata aemula*, AMNH 97970, Oaxaca. E. *Rhadinaea fulvivittis*, KU 70883, Oaxaca. F. *Rhadinaea omiltemana*, BMNH 94.11.14.14, Guerrero.

Madre de Oaxaca north to southeastern Puebla and central Veracruz. The known range of elevation is 2195 (?1738) to 3150 meters (see Remarks).

DESCRIPTION (62 SPECIMENS): This is the smallest species in the *taeniata* group, although some individuals probably attain lengths slightly

in excess of 500 mm. The largest male measured 473 mm. total length, of which 161 mm. is tail; the largest female is 478 mm. total, 131 mm. tail length. The tail is 28.7–33.8 percent of total length in males and 27.2–32.1 percent in females. The dorsal scales are in 17–17–17 rows; anal ridges usually are present on adult males and rarely on females. Ventrals are 148–183 (148–168, males; 159–183, females) and subcaudals are 79–103 (83–103, males; 79–97, females). There are eight supralabials (rarely seven or nine on one side) and 10 infralabials (occasionally nine or rarely eight). There is one preocular and usually a small subpreocular between the third and fourth labials. There are two postoculars (rarely 2/1 or 1/2) and a basic pattern of 1 + 1 temporals or, less frequently, 1 + 2.

The ground color is tan or light brown, on which there are three black-edged, brown or grayish brown (gray under stratum corneum) stripes that run from the tip of the snout well onto the tail, where they tend to fade toward the end. The dorsal stripe is a posterior continuation of the brown head color and its dark edges extend from the upper rear margins of the eyes. This stripe occupies the median three scale rows and the adjacent third to three-fourths (usually one-half) of a row on each side. In addition to the dark edges, the dorsal stripe contains one or three black lines: A narrow black line on the vertebral row may be either faint or distinct and, in addition, there is occasionally a line on each of the paravertebral rows. The lateral marking usually starts as a blackish stripe that is narrowly continuous around the rostral plate and runs through the eye and above the corner of the mouth, to cover the fourth and each adjacent half-row (more or less) of body scales. This stripe is conspicuously black-edged on the body, or it may be described as a dark stripe with a light center. The light dorsolateral ground color between lateral and middorsal dark stripes is itself a conspicuous stripe that lies on row 6 and part of each adjacent row and runs forward to the upper rear edge of the eye, beyond which it may be indicated by a narrow, pale line on the canthus rostralis. The dorsolateral light stripe is reduced in width on the rear of the head, where it may run horizontally or have a slight postero-ventrad slant; some individuals have an expanded portion of the stripe immediately behind the head and this may be connected to the white throat by a short, vertical white bar. The dorsolateral stripe is of nearly uniform lightness throughout the body, but somewhat paler on the head and neck. There is rarely a short break in the light stripe at the rear of the head. The lower sides are tan or light brown and may be punctated with dark pigment. In most individuals there are whitish dashes on the antero-lateral edges of the body scales; usually these dashes are inconspicuous and they may be concealed by adjacent, overlapping scales, but some specimens have a conspicuous line of white dashes along each edge of the vertebral scale row. The pale tan or brownish pigment of the lower sides may extend onto the ventral tips or not; there may be black specks on the ventral tips; otherwise the venter is immaculate white. Often there is an inconspicuous pair of pale parietal dots on the brown head. The supralabials are immaculate white below the dark lateral stripe, except for a rare, dark speck. The underside of the head is immaculate except for the frequent occurrence of black dots on the mental and first few labials.

Charles M. Bogert obtained a large series of *R. fulvivittis* at Tejocotes, about 40 kilometers northwest of the city of Oaxaca, in 1968, and kindly took the trouble to carry four living specimens to New York, for my examination. The dorsum of the head is brown in life and the body is light orangish brown, except that the dorsolateral strip of ground color turns pale tan on the neck and white on the rear of the head. The upper quarter sector of the iris is pale orangish tan and the lower three-quarters are dark brown. The tongue is orangish red, with black mottling at the base of the fork and gray on the tips. The supralabials and underside of the head are white, and the rest of the venter is pale yellowish green, except that a pale orangish suffusion extends from the lower sides onto the ventral tips. A single specimen obtained by Bogert about 35 kilometers west-northwest of the city of Oaxaca, in the Sierra de Cuatro Venados near Ojo de Agua, differs from the above description in having more orange in its coloration. The lower sides are strongly suffused with orange. The sides of the belly are medium orange in life, and the median part is yellow anteriorly, grading to light orange posteriorly. The lower three-quarters of the iris are orangish brown. Orange- or red-bellied individuals probably are characteristic of certain populations (see Geographic Variation).

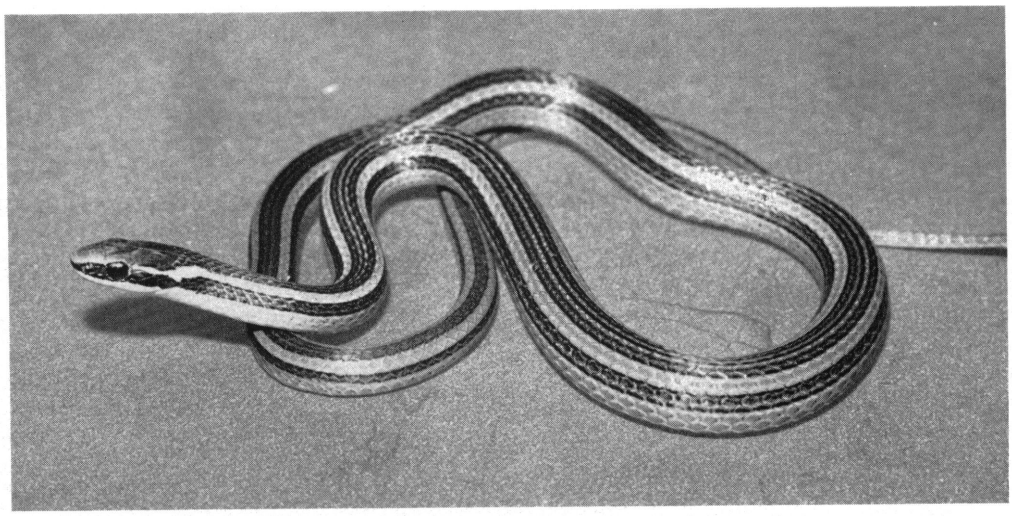


FIG. 21. *Rhadinaea fulvivittis*, specimen from Tejocotes, Oaxaca, Mexico.

The maxillary teeth vary from 17+2 to 22+2, with the ultimate prediastemal tooth often lying posterior to the front edge of the ectopterygoid process when there are 19 or more anterior teeth. The diastema may be virtually absent where the formula is 22+2. The last fang is offset laterad.

The retracted hemipenis extends to subcaudal 9 or 10 and the everted organ to subcaudal 7 or 8 (6 in one specimen). The retractor muscle in two specimens originates at the level of subcaudal 29 or 31. The capitulum comprises from about three-sevenths to about four-sevenths of the length of the hemipenis on its asulcate side. There are soft papillae on the calyces on the distal part of the capitulum, but these are replaced by tiny spines in a broad band around the basal part of the capitulum. The sulcus spermaticus forks rather high on the organ, at a point at least half and frequently two-thirds of its length up the capitulum; the short branches of the sulcus extend onto the distal half of the capitulum when the hemipenis is everted, but they do not reach the tip even of the retracted hemipenis. The wall of the capitulum forms a double fold on the asulcate side of the inverted organ. Below the capitulum is a zone of approximately 18 to 24 small to medium, slightly recurved spines; most of the spines lie on the asulcate side high above the base of the hemipenis, but toward the sulcate side the spines are lower (and larger). Below the zone of spines there is an ornamentation of spinules, which reach the capitulum in the region of the sulcus spermaticus. The preceding description is based on the retracted hemipenes of AMNH 91083 and USNM 110347, and the everted organs of ten AMNH specimens from Oaxaca.

GEOGRAPHIC VARIATION: There is interpopulational variation in the ventral coloration of *R. fulvivittis*, at least in the Sierra de Cuatro Venados, which is that section of the Sierra Madre del Sur that marks the western limits of the Valley of Oaxaca. All known specimens from this region were obtained by Charles M. Bogert, who noted that specimens (AMNH 97963 and 97964) from La Cofradía, at the south end of the Sierra de Cuatro Venados, had reddish bellies in life. A color transparency of one of these specimens shows that the lower sides were light orange. Seventy-one specimens from the north end of the range, in the vicinity of Tejocotes, had yellowish or greenish venters (see color description above) and, according to Bogert, so did two specimens (AMNH 103041 and 103042) from a locality some 20 kilometers south-southeast of Tejocotes ("5 miles northwest of Santa Inez del Monte"). An individual (AMNH 103140) with somewhat intermediate ventral coloration (see description above) was taken by Bogert 3 miles east of Ojo de Agua, which lies in the Sierra de Cuatro Venados between the Tejocotes and Santa Inez localities. The geographical position of the "intermediate" specimen precludes the

suggestion that a simple cline is involved. Bogert stated that specimens from Cerro San Felipe, to the northeast of the Valley of Oaxaca, have pale venters like those at Tejocotes.

REMARKS: *Rhadinaea fulvivittis* is found in pine-oak forest, usually concealed under rocks or logs or, sometimes, on the surface by day (C. M. Bogert, personal commun.). This species occurs in the same forests as another member of the *taeniata* group, *R. taeniata aemula*, but evaluation of available data indicates that there is a zonal partitioning of the environment, with *fulvivittis* usually occurring at higher elevations than *aemula*. *Rhadinaea taeniata aemula* is known from elevations between about 1707 and 2439 meters, whereas *fulvivittis* has been found from ?1738 or 2195 to 3150 meters. The lowest record (5700 feet=1738 meters) for *fulvivittis* is questioned by C. M. Bogert (personal commun.), for whom the specimen was collected; this specimen (AMNH 89590) was taken by a collector working up the slope of Cerro San Felipe, Oaxaca, and quite possibly came from a higher elevation than the collector indicated. Excluding this questionable record, there is overlap of about 700 meters between *aemula* and *fulvivittis*, which together range through a vertical zone of nearly 1450 meters. But this overlap is based on records from various localities and is not necessarily so broad at any one place, nor do *aemula* and *fulvivittis* necessarily occur side by side within the overlap. In the vicinity of Tejocotes, about 40 kilometers northwest of the city of Oaxaca, Bogert has obtained 18 specimens of *aemula*, at elevations of about 2195 to 2378 meters, and 71 specimens of *fulvivittis*, at about 2317 to 2500 meters. Thus, the known overlap near Tejocotes is only 61 meters, and both species have yet to be found in the same place, although at least limited microsympatry is anticipated (C. M. Bogert, personal commun.). Bogert suggested that populations of *R. fulvivittis* on the summits and slopes of the higher mountains are probably surrounded by populations of *R. t. aemula*, and that such populations of both forms are almost certainly disjunct from those on other mountains whenever the intervening country drops below about 1700 meters elevation. A similar zonal partitioning of the pine-oak zone seemingly occurs between *R. t. aemula* and *R. omiltemana* (*q.v.*), in Guerrero, the latter species being a close relative of *fulvivittis*.

Bailey (1940, p. 2) believed that the oldest name for *Rhadinaea fulvivittis* Cope, 1875a, is *Enicognathus vittatus* Jan, 1863. Bailey (1940, p. 1) correctly observed that a period of considerable confusion, "regarding the specific identities of Mexican . . . *Rhadinaea* . . . resulted from the uncritical 'lumping' of several forms under *vittata* Jan, by Boulenger." Bailey, following other authors, based his conclusions primarily on two specimens of "*E. vittatus*" illustrated in Jan and Sordelli [1866 (1860–1881), vol. 1, livr. 16, pl. 2, figs. 2, 3]. One of these specimens is the earlier named *Rhadinaea decorata* (Günther, 1858), as is obvious from Jan and Sordelli's figure 2, whereas the other, as correctly noted by Bailey, appears to be the same species as Cope's *Rhadinaea fulvivittis*. However, Bailey considered the prior name *vittata* to be inapplicable because Amaral (1929b, p. 175) had made a secondary homonym of *Rhadinaea vittata* (Jan) by casually synonymizing *Rhadinaea* under *Liophis*, which already contained the name *Liophis vittatus* (Hallowell, 1845) Cope, 1859. Bailey (1940, p. 2) concluded that, "the name *Enicognathus vittatus* Jan is therefore suppressed. This is a fortunate quirk of circumstance, for apparently the name has never knowingly been associated with the proper species." Unfortunately, Jan's *vittata* was not to be so easily disposed of, and the name *Rhadinaea vittata* (Jan) was continued in the literature as a senior synonym of *fulvivittis* because of the influential work of Smith and Taylor (1945, pp. 6, 119), who, among many taxonomists, did not believe in the permanent suppression of secondary homonyms. Indeed, the International Code (1964, art. 59c) now provides that names rejected after 1960 as secondary homonyms are to be restored whenever a zoologist believes that the two taxa in question are not congeneric. But, it seems to be the intent of the "Code" that names rejected prior to 1960 are to be permanently suppressed. Following the latter interpretation, Bailey's 1940 suppression of *vittata* in favor of *fulvivittis* seems proper.

In any case, the nomenclatural confusion described above not only is tedious but probably entirely unnecessary. All previous authors seem to have been mistaken in their belief that the two snakes illustrated as *E. vittatus* in Jan and Sordelli (*loc. cit.*) are both type specimens of the name. Jan's (1863, pp. 271, 272 [61, 62 in reprint]) two types of *vittatus* were from the museums of Milan and Tübingen, and both

specimens were said to have 129 ventral plates—far too low a number for *Rhadinaea fulvivittis* or any other member of the *taeniata* group (table 8). The two snakes in Jan and Sordelli were from the museums of Tübingen and Paris, according to the legend on the inside cover of livraison 16. The first of these specimens is a *Rhadinaea decorata* with a partial tail (36 pairs of subcaudals shown) and is presumably the Tübingen Museum syntype of *vittatus*, listed by Jan (*loc. cit.*) as having 33 subcaudals. Thus, the second specimen in Jan and Sordelli (their fig. 3) seems to be nothing more than a misidentified individual of the then undescribed *fulvivittis* from the collections of the Paris Museum. I have not attempted to ascertain if the Milan Museum syntype of *vittatus* is still extant, but I find nothing in Jan's original description to suggest that two species were involved. Therefore, it seems best to regard *Enicognathus vittatus* Jan as a simple, subjective synonym of *Rhadinaea decorata* (Günther).

The specific epithet of *Rhadinaea fulvivittis* is based on the adjective *fulvus* (tawny or yellowish brown) plus the noun *vita* (a ribbon or band) and evidently refers to the dorsolateral stripe of light brown.

Rhadinaea omiltemana (Günther)

Figures 19F, 20F; map 8

Dromicus omiltemanus GÜNTHER, 1894 (1885–1902), p. 113, pl. 40, fig. B (color pattern and details of cephalic scutellation).

Rhadinaea vittata (not of Jan): BOULENGER, 1894b, p. 178 (part, specimen *f*); 1896, p. 635 (part, specimen *n*). COPE, 1900, p. 756 (part).

Rhadinaea omiltemana (Günther): BAILEY, 1940, pp. 13, 14, pl. 2, fig. 2 (midbody pattern of BMNH 94.11.14.14). SMITH AND TAYLOR, 1945, pp. 118, 119.

HOLOTYPE: BMNH 1946.1.1.7, an adult male in good condition, from Omilteme, 8000 feet, Guerrero, Mexico. The collector is listed as H. H. Smith by Günther (1894 [1885–1902], p. 113) in the original description and as F. D. Godman by Boulenger (1894b, p. 178). This specimen does not agree completely with the original description. It has 151 ventrals (including a single preventral) and 86 subcaudals, rather than 154 ventrals and 94 subcaudals as stated by Günther (*loc. cit.*), or 153 ventrals and 88 subcaudals as given by Boulenger (1894b, p. 178). The internasals ("anterior frontals") are about half as long as the prefrontals ("posterior frontals"), rather than one-third as long. However, I obtained measurements of 389 mm. total length and 123 mm. tail length, which are close to Günther's figures of 15½ inches total length and 5 inches tail length.

DIAGNOSIS: A member of the *taeniata* group that can be distinguished from all other species of *Rhadinaea* by the positioning of its three brown or blackish stripes that start on the head and extend well onto the tail, on a lighter brown background. The dorsal stripe covers the median five rows plus an edge or larger part of an adjacent row on each side; the lateral stripe usually occupies row 4 and each adjacent half-scale row, or it may be almost confined to the fourth row. Some specimens have these stripes dark-edged like *R. fulvivittis*, which has a similarly positioned lateral stripe, but the dorsal stripe of *omiltemana* is broader than in any other member of the *taeniata* group.

DISTRIBUTION: The pine-oak(?) zone of the Sierra Madre del Sur in central Guerrero, where it is known only from Omilteme and the vicinity of Chilpancingo. The known elevational range is 2226–2439 meters, based on the only two specimens for which elevations are given.

DESCRIPTION (10 SPECIMENS): At least the female of this species probably attains lengths in excess of 600 mm. The largest male examined is 389 mm. total length, of which 123 mm. is tail; the largest female is 566 mm. total and 173 mm. tail length. The tail is 31.6–33.8 percent of the total length in males and 27.5–31.2 percent in females. The dorsal scales are in 17 rows and anal ridges are present on some females as well as adult males. Ventrals are 150–168 (150–161, males; 157–168, females) and subcaudals are 78–90 (85–90, males; 78–88, females). There are eight supralabials, and 10 (usually) or nine or 11 infralabials. There is one preocular, plus a subpreocular between the third and fourth labials. There are two postoculars and a basic pattern of 1+2 temporals.

The ground color is pale or light brown, on which there are three medium brown to blackish brown stripes that start on the head and run well onto the tail, where they may either fade toward the end or be discernible all the way to the tip. The dorsal stripe is a posterior continuation of the brown head color and is quite broad, occupying the median five scale rows and the adjacent edge, or up to one-half of an adjacent

row (the sixth) on each side. Superimposed upon this broad stripe is a black line that starts on the nape and occupies most of the vertebral scale row, often with a slight overlap onto the paravertebral rows, which may be somewhat paler than the rest of the middorsum, thus emphasizing the black line and causing further disruption of the dorsal stripe. The lateral dark stripe starts as a black line that is continuous around the rostral plate and runs through the eye and above the corner of the mouth, to cover the fourth and each adjacent half-row of body scales or, in some specimens, being nearly confined to the fourth row and lower edge of the fifth row. The lateral stripe normally seems rather uniformly dark, but in some individuals, especially young ones (e.g., KU 87754), it has dark edges and a lighter center very much like the usual situation in *R. fulvivittis*. In most there also is an accumulation of blackish pigment toward the outer edges of the dorsal stripe, on rows 6 and 7, and this may even give discrete dark edges (on the seventh rows) to the stripe. The pale, dorsolateral ground color between lateral and middorsal dark stripes is itself a conspicuous stripe that lies on adjacent parts of rows 5 and 6 and runs forward to the upper rear edge of the eye, beyond which it may be indicated by a whitish line on the canthus rostralis. This light stripe may run horizontally or have a slight posteroventrad slant on the rear of the head, and in some individuals the stripe widens behind the head to form an irregular blotch that may be connected to the white throat by a short, vertical white bar. The dorsolateral stripe usually is pale or light brown throughout, but on young individuals it may be whitish on the head and neck. One specimen has a slight break, behind the head, in each dorsolateral light stripe. The lower sides are pale or light brown and are punctated with dark pigment. The brown pigmentation of the sides does not extend onto the venter which is immaculate white except for a small blackish spot, dot, or dense cluster of specks on each ventral tip; these markings may fuse into a nearly continuous dark line along the edges of the subcaudals. A pair of dark-edged, white parietal dots usually is faintly indicated on the brown head, which also may have some irregular dark flecking. The lower parts of the supralabials and the underside of the head are white, often with some dark dots on the anterior supralabials and infralabials. The color of labial and ventral surfaces in life have not been recorded, but Bailey (1940) stated that freshly preserved specimens have pink bellies.

The maxillary teeth vary from 18+2 to 21+2, with the ultimate prediastemal tooth in some cases lying partly or entirely behind the front edge of the ectopterygoid process. The last fang is offset laterad.

The retracted hemipenis is a single organ that extends to subcaudal 9, with the retractor muscle originating at the level of subcaudal 30 or 31. The capitulum comprises two-sevenths to two-fifths of the length of the sulcate side of the organ. There are soft papillae on the calyces distally, but these ossify into tiny spines in a broad band around the basal part of the capitulum. The sulcus spermaticus forks at a point from one-third to one-half of its distance up the capitulum, and the branches of the sulcus extend virtually to the tip of the inverted organ. The wall of the asulcate side of the capitulum forms a double fold in the inverted hemipenis. Below the capitulum is a zone of about 27–31 medium, recurved spines, mostly on the asulcate side, plus a larger one. The tip of the largest spine extends to a point about a fifth of the length of the organ above the base, but the spines on the asulcate side are much higher. There is a dense zone of spinules below the spines; this zone is narrow toward the sulcus and broad on the asulcate side. The basal fifth of the organ is completely nude. The foregoing description is based on the left retracted hemipenis of AMNH 72499 and USNM 110374. The latter specimen is a juvenile and the spines and spinules of the hemipenis are not ossified.

REMARKS: Peters (1863) did not have a specimen of *Rhadinaea omiltemana* among the syntypes of *Dromicus taeniatus* (=*Rhadinaea taeniata*) as suggested by Bailey (1940, pp. 2, 13).

It would be interesting to know more precisely the vertical distributions and zones of maximum abundance of this and the other species of *Rhadinaea* (*R. taeniata aemula* and *R. hesperia*) that occur in the Sierra de Burro, which is a section of the Sierra Madre del Sur in the Chilpancingo region of central Guerrero, but unfortunately specific localities and elevations are known for only a few specimens. A brief account of the vegetation of this region, and a vegetational map, are given by Davis and Dixon (1959, pp. 79, 80). *Rhadinaea omiltemana* is known only from the Chilpancingo region, whereas

R. taeniata aemula and *R. hesperia* have much broader distributions. The holotype of *omiltemana* reportedly is from 8000 feet (2439 meters) at Omilteme (after which the species is named), and so evidently was caught either in pine-oak forest or in the cloud forest above Omilteme. KU 87754 was taken at 7300 feet (2226 meters) near Omilteme, which probably is in pine-oak forest. I suspect that several other specimens of *omiltemana* were caught in pine-oak forest above Chilpancingo, although one individual bears only the name of this town, which is in xeric tropical deciduous forest. Also, some specimens of *aemula* and *hesperia* bear the datum "Chilpancingo," but the only specimens with precise data are from higher elevations, in the pine-oak zone. Davis and his students (see Davis and Dixon, 1959) found no *Rhadinaea* in the deciduous forest, but *hesperia* was taken at 1006 and 1067 meters (3300 and 3500 feet) in the pine-oak forest, and *aemula* was found in pine-oak forest at 1707 meters (5600 feet). Another specific record for *R. t. aemula* is KU 87753, which comes from 2012 meters, 2 miles east of Omilteme. Excluding all specimens for which specific elevations are not recorded, the following picture emerges of *Rhadinaea* distribution in the pine-oak forests of the Chilpancingo region: *Rhadinaea hesperia* occurs up to at least 1067 meters elevation, *R. t. aemula* is known from between 1707 and 2012 meters, and *R. omiltemana* from 2226 and 2439 meters. There doubtless is much to be learned, but these few records suggest that *Rhadinaea omiltemana* is a high elevation replacement of *R. taeniata aemula*, just as *R. fulvivittis* (the closest relative of *omiltemana*) tends to replace *aemula* in the high pine-oak forests of Oaxaca.

Rhadinaea taeniata (Peters)

Figures 2C, 3, 19A–D, 20A–D, 22, 23–25; map 9

Dromicus taeniatus PETERS, 1863, pp. 275, 277.
Rhadinaea taeniata (Peters): COPE, 1875a, pp. 139, 140.

INTRODUCTION: *Rhadinaea taeniata* is here envisaged to consist of two strikingly different subspecies—the northern *R. t. taeniata* and the more southern *R. t. aemula*. These forms are similar in habitus and most aspects of scutellation, but the colors and patterns are so divergent that Bailey (1940, pp. 15–17) was led to believe that *aemula* was without very close relatives. I very gradually came to realize that *taeniata* and *aemula* belonged to the same species group, but I was unprepared to consider them conspecific until I saw the syntypes of *taeniata*, which appear to be hybrids (i.e., secondary intergrades)! Indeed, I was on the verge of describing as a new species another hybrid recently collected by Kraig Adler.

My interpretation of the taxonomic status of *aemula* and *taeniata* conceivably might require modification when the situation in the areas of contact is better known. The two forms occupy rather sizable ranges but possibly have only limited contact, and some workers might prefer to consider the intermediate specimens as hybrids between species rather than between subspecies. Partly for these reasons and partly because there is so little resemblance in color patterns, I have not attempted a combined description of *aemula* and *taeniata*. They are described in separate, following accounts, as if each were a different species. The present account is used for the designation of a lectotype and assignment of names, for a comparison of the two forms, and for an assessment of the evidence of hybridization.

DESIGNATION OF LECTOTYPE AND RESTRICTION OF NAME: There are three specimens of *Rhadinaea taeniata* in the Berlin Museum, all obtained by Ferdinand Deppe in "Mexico," most probably in the 1820s. The type locality is probably in the southern half of the state of México, as will be commented on under Hybrid Zones later in this account. A male and a female are catalogued under one number, ZMB 2117, and are evidently the two syntypes of *Dromicus taeniatus* Peters (1863, pp. 275, 276). For convenience, I attached a tag reading "2117A" to the male syntype and a tag "2117B" to the female. Specimen 2117A is 510 mm. total, 176 mm. tail length, and has 154 ventrals, one preventral, and 105 subcaudals, and so it closely matches Peters's measurements of 505 mm. total, 177 mm. tail length and his counts of 155 ventrals, 108 subcaudals. Specimen 2117B is 340 mm. total, 92 mm. tail length, and has 172 ventrals, one preventral, and 91 subcaudals, and is thus close to Peters's data of 325 mm. total, 91 mm. tail length, 172 ventrals, 91 subcaudals. The third specimen, ZMB 2115, was sent to me as a "syntype," but Peters seems to have described but two specimens and data taken from this one do not match the original description; the specimen is a female, 530 mm. total length, 151 mm.

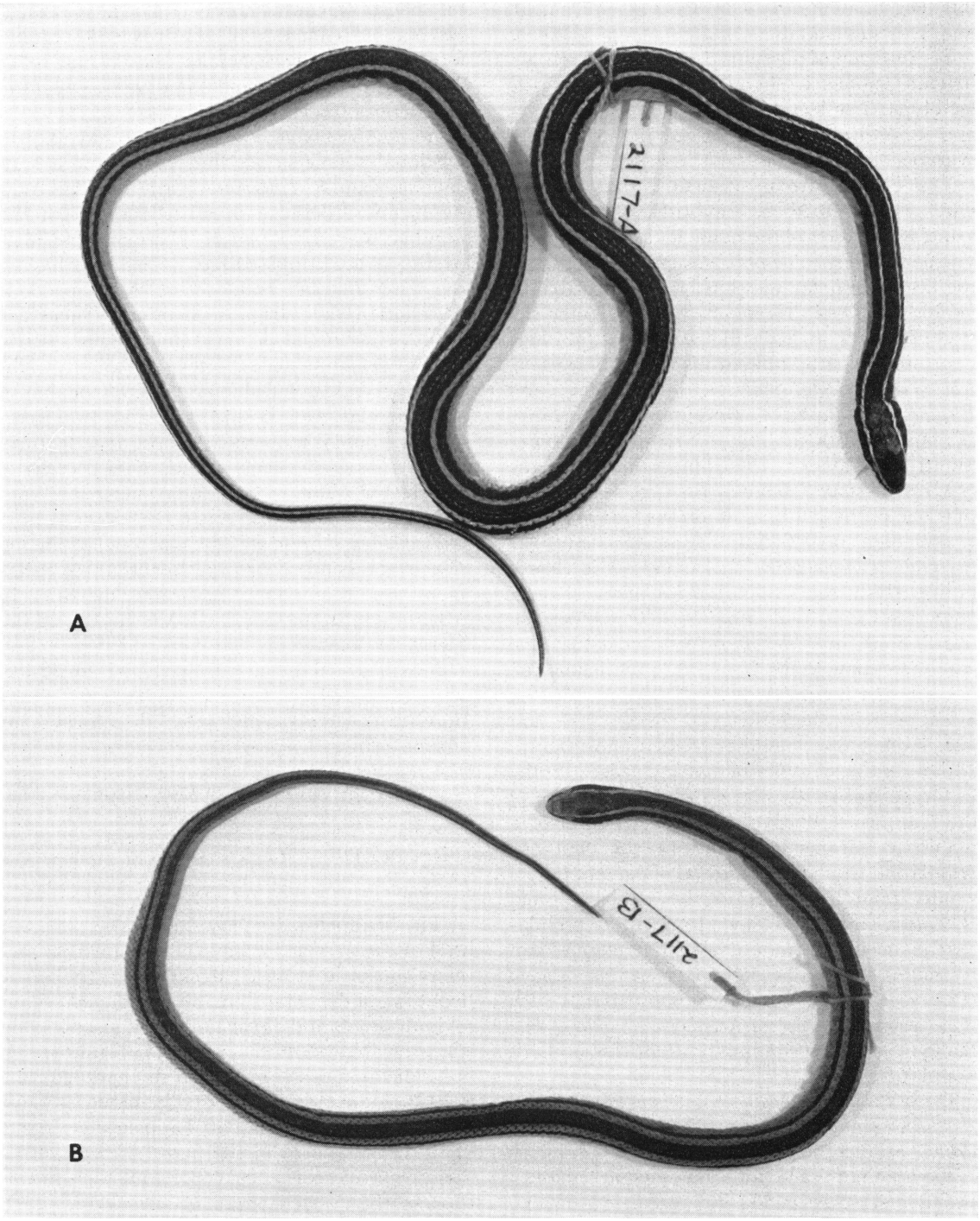


FIG. 22. Syntypes of *Rhadinaea taeniata*. ×0.9. A. ZMB 2117-A (lectotype). B. ZMB 2117-B.

tail length, with 170 ventrals, one preventral, and 89+ subcaudals.

Because one of the syntypes (ZMB 2117B) is a juvenile female, I select ZMB 2117 "A" as the lectotype. The lectotype is a male and is larger and somewhat better preserved than the other syntype.

The evidence to be presented that the two syntypes are intraspecific hybrids necessitates an arbitrary fixation of the name to one or the other subspecies. The concept of *Rhadinaea taeniata* over the last several decades has been that of Bailey (1940, pp. 2, 14, 15, pl. 2, fig. 4). Bailey described *aemula* as a distinct species in the same paper in which he offered his views on *taeniata*. *Rhadinaea taeniata* (Peters), *sensu* Bailey, and *Rhadinaea aemula* Bailey were insured a measure of nomenclatural stability by the publication of Smith and Taylor's (1945) important catalogue of Mexican snakes. Bailey (*op. cit.*, p. 2) indicated that one of the syntypes of *taeniata* was probably a specimen of *Rhadinaea omiltemana*, but the presence of *aemula*-like characteristics is clearly indicated in the original description (Peters, 1863; see Cope, 1900, pp. 756, 757, for English translation), in which it is mentioned that one specimen (now ZMB 2117 "A," the lectotype) has a broad lateral stripe that, "bis zur dritten Schuppenreihe herabsteigend zwei ganze und fast zwei halbe Schuppenreihen einnimmt." Although the syntypes of *taeniata*, especially the lectotype (table 10), have a high proportion of the features of Bailey's *aemula*, restriction of a nominate subspecific name to the southern population would be a reversal of current usage, would create a synonym of the well-established *R. aemula*, and would leave the northern population in need of a new name. Therefore, I am restricting the name *Rhadinaea taeniata taeniata* (Peters, 1863) to the northern population, which then permits the use of *Rhadinaea taeniata aemula* Bailey, 1940 (new combination) for the southern population.

COMPARISONS: *Rhadinaea taeniata taeniata* and *Rhadinaea taeniata aemula* are both large, but the former attains the greater size. Of 12 specimens of the nominate race (four males, eight females), two females exceed 800 mm. total length, one female is 791 mm. total length, and five specimens, including three males, exceed 600 mm. total length. The longest female (FMNH 39030) is the largest specimen of *Rhadinaea* that I have measured; it is 880 mm. total length, 243 mm. tail length. In contrast, only two of 42 specimens (22 males, 20 females) of *aemula* exceed 600 mm. total length; both are females, one 689 mm. total, 228 mm. tail length, and the other 690+ mm. total length (end of tail missing).

Rhadinaea taeniata aemula tends to have a proportionally longer tail and a few more subcaudals than *R. t. taeniata* (table 8). The most significant difference in scutellation is in the number of ventral plates. There is very little overlap of the sample ranges, with *aemula* having the lesser number (table 8). Other aspects of scutellation are virtually identical: There are 17–17–17 scale rows with anal ridges usually present on adult males. There are usually eight supralabials, 10 infralabials, one preocular, a subpreocular, two postoculars, and 1+2 temporals. There is more variation in these features in the sample of *aemula*, presumably because of the larger sample size. One variation that appears in *taeniata* but not in the larger sample of *aemula* is the presence of two preoculars on one side of the head of two specimens; these specimens are from widely separated localities in Michoacán (in the Cordillera Volcánica and the Sierra de Coalcomán).

Maxillary teeth vary from 17+2 to 22+2, with *R. t. taeniata* tending to have a greater number of prediastemal teeth than *aemula*, as shown below:

	NUMBER OF PREDIASTEMAL TEETH					
	17	18	19	20	21	22
aemula (N=12)	1	4	4	2	1	0
taeniata (N=10)	0	1	4	2	2	1

The hemipenes are very similar (fig. 23), but that of *aemula* seems to have more numerous and more conspicuous little ridges of tissue under the free edge of the capitulum. The retracted organs of both *aemula* and *taeniata* have a double fold on the asulcate wall of the capitulum, but in *aemula* an indication of the groove in the middle of the fold is retained on the everted hemipenis to give the organ a slightly bilobated appearance. These features are shown in the figure of the everted hemipenis of *aemula* (fig. 23D), but the illustration of the everted organ of *taeniata* (fig. 23B) was drawn from a more lateral aspect and is not directly comparable in these particulars.

It is in color and pattern that *R. t. taeniata* and *R. t. aemula* are most distinct, which gives them the appearance of being different, not even very

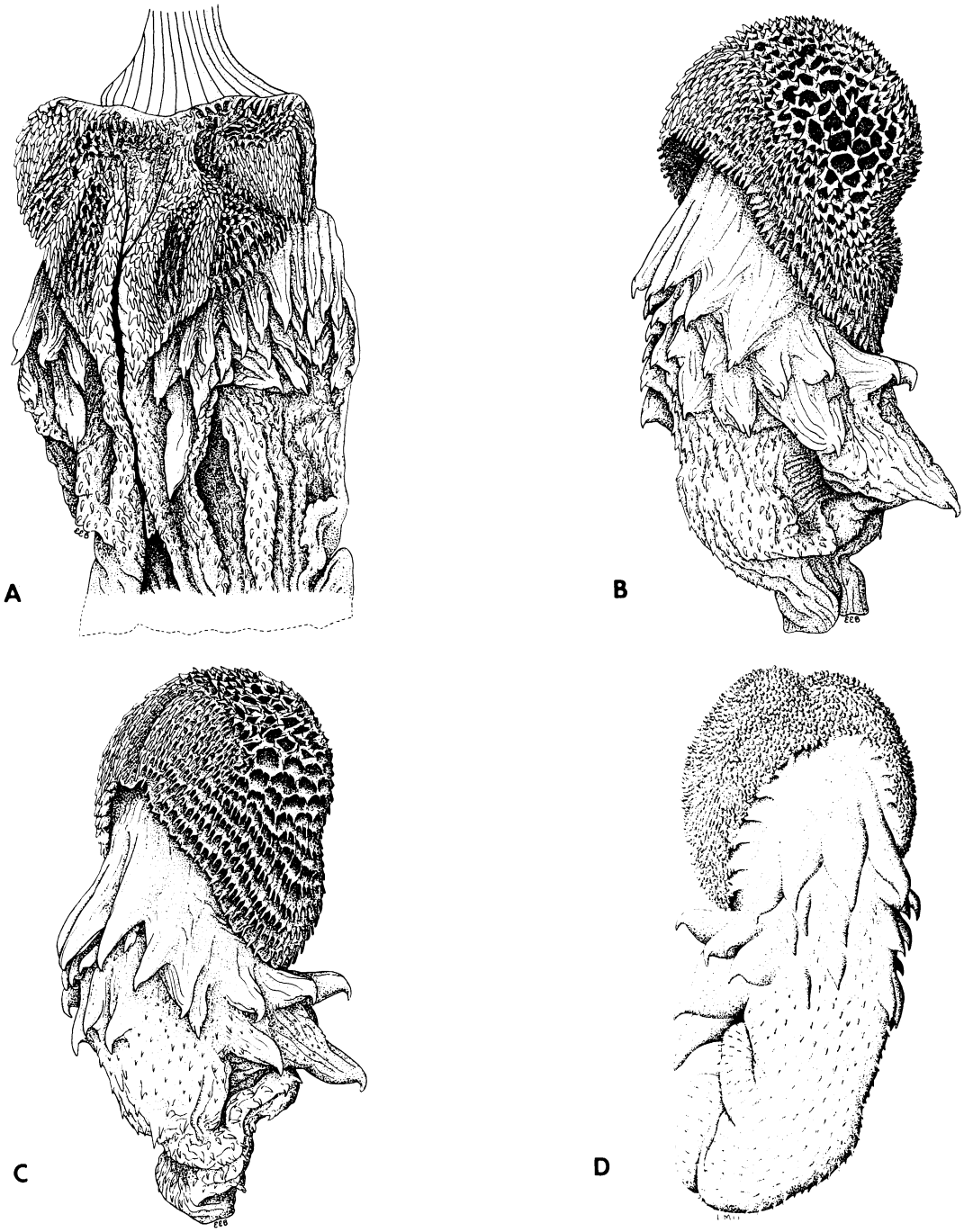


FIG. 23. Hemipenes of *Rhadinaea taeniata*. A, B. Left retracted and right everted organs of *R. t. taeniata*, UMMZ 121522, Michoacán. ×6. C. *R. t. taeniata* × *R. t. aemula*, right everted organ of UMMZ 125731, Guerrero. ×7. D. *R. t. aemula*, left everted organ of KU 116948. ×7.

Hemipenes of the two subspecies are actually more similar than indicated by comparison of B and D (see p. 106).

closely related species. *Rhadinaea taeniata aemula* has a whitish ground color (with no more than a pale tinge of orange in living examples from Oaxaca) on which there are three broad, black stripes that are continuous from the snout to the end of the tail. There is very little intrapopulational or interpopulational variation in the width and positioning of the black stripes, only slight expansion or contraction without a change in the scale rows occupied. The white dorsolateral ground color is a narrow stripe that is consistently continuous above and not broken by the eye. This snake is unique in the genus because of its nearly white ground color and the almost complete absence of brown (except on the tip of the snout) in the pattern.

Rhadinaea taeniata taeniata, on the other hand, is basically a light brown snake. There is a black lateral stripe but it is much narrower than in *aemula*, except immediately behind the head, where the stripe may be about as wide as in *aemula* for the space of a few scales. There is a dark median stripe about as wide as in *aemula*, but this stripe is brown and there is usually a black line down the vertebral row of scales; some individuals have the dorsal stripe blackened toward the sides, but not to the extent of obscuring the median black line. The nominate subspecies also differs from *aemula* in that the dorsolateral stripe of ground color is wider and broken by (passes through) the eye; the width of this marking is a function of the width of the lateral black stripe, but this has no bearing on whether or not the pale stripe is continuous above the eye. Another important difference is that the dark stripes of *R. t. taeniata* fade well before the end of the tail, which is uniformly light brown distally.

Individuals of both subspecies may have white dashes on the anterolateral edges of dorsal scales in certain rows, but I have not seen these nearly as conspicuous in *aemula* as on some specimens of *taeniata*. In several aspects of color pattern, including the vividness of the white dashes (when present), the presence or absence of black pigment in the dorsal brown stripe, and in the presence or absence of a break (close behind the head) in the lateral black stripe, the nominate subspecies is more variable than *aemula*, even though the sample size is smaller.

HYBRIDIZATION: Evidence for hybridization between these snakes exists primarily in four specimens—the two syntypes of *Dromicus taeniatus* (ZMB 2117[A, B]) and ZMB 2115, all of unknown locality, and UMMZ 125731, from 2.4 kilometers north of San Vicente de Jesús, 1000 meters, western Guerrero. These are described below and compared with normal *aemula* and *taeniata*. "Hybridization" is here used in the sense of secondary intergradation (Mayr, 1966, pp. 110, 380; Short, 1969).

The three Berlin Museum (ZMB) specimens seem to have had a ground color of pale brown and in this regard were probably closer to *taeniata* than to *aemula*, although most of the stratum corneum has been lost in preservative and the underlying color is now faded whitish (No. 2117A) or pale grayish; verification of the brown ground color was given by Peters (1863, p. 276), who examined the syntypes more than a century ago. All the top of the head is brown, except for a pair of pale parietal dots, and this also is unlike *aemula*, which has only a brown snout. The dorsal stripe occupies the median three and two half-scale rows on each specimen and, judged from a few remaining patches of stratum corneum, seems to have been very dark brown (gray under stratum corneum) turning blackish toward the edges. Within the broad stripe is a narrow, black vertebral line that is emphasized by a line of conspicuous white dashes on each edge of the vertebral row and a single line of dashes on the medial edge of each paravertebral row. Thus, the dorsal stripe is closer to the condition in *taeniata* than in *aemula*, in which the stripe tends to be uniformly black (at least anteriorly) except for white dashes that are less conspicuous than in *taeniata*. The lateral black stripes of two specimens (ZMB 2115, 2117B) agree with *taeniata* in occupying only the adjacent halves of rows 4 and 5, being expanded onto other rows for a distance of only five to six ventrals behind the head. The third specimen (2117A) is decidedly closer to *aemula* in that the lateral stripe occupies almost all of rows 4 and 5 and also the adjacent edges of rows 3 and 6 (this stripe is slightly wider in *aemula* and includes all of rows 4 and 5). The Berlin Museum specimens further agree with *aemula* in that the stripes extend to the end of the tail, most of which is uniform brown in *taeniata*. There is complete variation in whether the pale dorsolateral stripe is continuous above, or interrupted by, the eye: In ZMB 2115 the pale stripe is interrupted by the eye as in *taeniata*; in ZMB 2117B it is partly interrupted, with a narrow edge extending

above the eye; in ZMB 2117A the stripe extends wholly above the eye, as in *aemula*, and it is more conspicuous on the canthus rostralis than in the other two syntypes. The three specimens have a black dot on each tip of at least the anterior ventrals; these dots are most conspicuous on ZMB 2115 and least conspicuous on ZMB 2117A, which I think probably reflects resemblance toward the average conditions in *taeniata* and *aemula*, respectively.

The hybrids described above were possibly collected in the southern part of the state of México, as will be explained later. Another apparent hybrid (UMMZ 125731) from western Guerrero, differs in some important respects. The ground color of this specimen was pale salmon in life (grayish in preservative) according to the collector, and this would seem closer to the pale orangish of living *aemula* that I have seen than to the pale brown of preserved *taeniata*. The top of the head and sides of the snout are light brown; there is scarcely any indication of the dark lateral stripe in front of the eye, a condition that occurs in *taeniata* but not *aemula*. Although the dorsal stripe starts behind the head, it is nearly solid black as in *aemula*, except for some small gray areas that show through the black pigment on the vertebral scales, some of which also have relatively inconspicuous white dashes on their forward edges; there is no indication of a vertebral dark line. The stripes extend to the end of the tail as in *aemula* and the other hybrids. The lateral black stripe is intermediate between the two subspecies, as it occupies all of row 4 and the adjacent halves of rows 3 and 5. The dorsolateral pale stripe starts behind the upper rear edge of the eye and would be interrupted, as in *taeniata*, if it extended in front of the eye. The ventrals are unmarked.

In number of ventrals, all four hybrids are within the ranges (by sex) of *aemula* and outside the known ranges of *taeniata* (table 8). But in number of subcaudals, three of the four specimens fall below the observed ranges of both subspecies (table 8). The actual counts, double checked, are as follows (a plus sign indicates that possibly one or a very few pairs of subcaudals may be missing due to breakage of the extreme tip of the tail):

ZMB 2115	♀	170 ventrals 89+ subcaudals
ZMB 2117B	♀	172 ventrals 89 subcaudals
ZMB 2117A	♂	154 ventrals 105 subcaudals
UMMZ 125731	♂	166 ventrals 91+ subcaudals

The hybrid specimens in the Berlin Museum have low numbers of maxillary teeth (17+2, 17+2, 18+2), which is suggestive of *aemula*, whereas the UMMZ hybrid from Guerrero has a high number (22+2, fig. 2C), as is more common in *taeniata*. The left retracted hemipenis of one hybrid (ZMB 2117A) extended to the middle of subcaudal 7 and the retractor muscle inserted at subcaudal 29; there are 32 spines on this organ, which is virtually identical in appearance to the illustration (fig. 23A) of the retracted organ of *R. t. taeniata*. An everted hemipenis of the Guerrero hybrid (UMMZ 125731) extended to the end of subcaudal 6 and the retractor muscle originated at subcaudal 24; there are 22 spines on this organ, which is virtually identical with an everted organ of *taeniata* (compare figs. 23B, C). The hemipenes of both of these hybrids seem to agree with *R. t. taeniata*, and differ from *R. t. aemula*, in having fewer and less conspicuous little ridges of tissue under the free edge of the capitulum. However, the everted organs of the Guerrero hybrid have the slightly furrowed look (fig. 23C) on the asulcate side of the capitulum, which is suggestive of *aemula*, and so I would classify the hemipenes of this specimen as intermediate between *taeniata* and *aemula*. Conceivably, however, the asulcate furrow in figure 23C might merely be due to incomplete inflation of the organ. In any case, the evidence of dentition and hemipenis is only suggestive at best. Too few hemipenes have been examined to make positive statements about the taxonomic value of the asulcate furrow and ridges under the edge of the capitulum. Color pattern is a much better proof of the hybrid origin of the specimens.

The phenotypic characteristics that indicate a hybrid origin of the above specimens are summarized in table 10. There is a preponderance of *taeniata* characteristics in the specimens toward the left side of the table and a preponderance of *aemula* characteristics in the specimen to the right. All specimens have the top of the head brown as in *taeniata*, and all specimens have the diagnostic tail striping of *aemula*. The other characteristics in the table are variable in the sample, except that the numbers of ventrals fit only into the observed ranges (by sex) of *aemula*. The variability is sufficiently great that I doubt that the specimens represent areas of primary intergradation. I think that they are probably the result of secondary contact of populations that had diverged widely, especially in aspects of

TABLE 10
RELEVANT CHARACTERISTICS OF HYBRIDS (SECONDARY INTERGRADES) OF
Rhadinaea taeniata taeniata × *Rhadinaea taeniata aemula*

Character	ZMB 2115 ♀	ZMB 2117B ♀ (Syntype)	ZMB 2117A ♂ (Lectotype)	UMMZ 125731 ♂
Dorsal head color	*t*	*t*	*t*	*t*
Body gound color	*t*	*t*	*t*	*a*
Pigmentation of dorsal stripe	*t*	*t*	*t*	*a*
Dark vertebral line	*t*	*t*	*t*	*a*
Dorsolateral pale stripe at eye	*t*	*i*	*a*	*t*
Width of lateral black stripe	*t*	*t*	*a*	*i*
Tail pattern	*a*	*a*	*a*	*a*
Number of ventrals	*a*	*a*	*a*	*a*
Maxillary teeth	*a*	*a*	*a*	*t*
Hemipenis	—	—	*t*	*i*
Ratio of *taeniata* to *aemula* characteristics, followed by (number of intermediate features)	6:3 (0)	5:3 (1)	5:5 (0)	3:5 (2)

Symbols: *a*=identical or very close to *R. t. aemula*; *t*=identical or very close to *R. t. taeniata*; *i*=intermediate.

color and pattern. It is of interest to note the presence of a few features not observed in specimens from populations of "pure" *aemula* or *taeniata*. Three of the four hybrids have fewer subcaudals than observed in parent populations; unfortunately the extreme tip of the tail is missing in two of these, but even so the few (if any) missing subcaudals would still not bring the numbers into the observed ranges. The specimen from Guerrero has a peculiarly shaped head, the likes of which I have not noticed in any other specimen of the *taeniata* group of species. The head is narrow and the sides of the snout are nearly parallel, giving the snout a truncate appearance. The head of this specimen is illustrated with one of a specimen of *R. t. taeniata*, the habitus of which is similar to that of *aemula* (fig. 24).

Inasmuch as one collector (Deppe) accounted for three of the four hybrids, it seems that interbreeding between *aemula* and *taeniata* is not a rare event in areas where the ranges are contiguous. This is the primary reason why I am considering these forms as populations of a single species, rather than separate species that occasionally hybridize.

HYBRID ZONES AND POSSIBLE INTROGRESSION: *Rhadinaea taeniata taeniata* and *R. t. aemula* are creatures of montane, coniferous forest, and their ranges are largely separated by the inhospitable (to *Rhadinaea*) basin of the Río Balsas. *Rhadinaea taeniata aemula* occurs mainly south and southeast of the arid basin, in groups of mountains collectively comprising the Sierra Madre del Sur, but there is at least one population to the north, in the Cordillera Volcánica of Morelos. It is not known whether the Morelos *aemula* are presently linked to the rest of the range, but conceivably there might be a tenuous connection

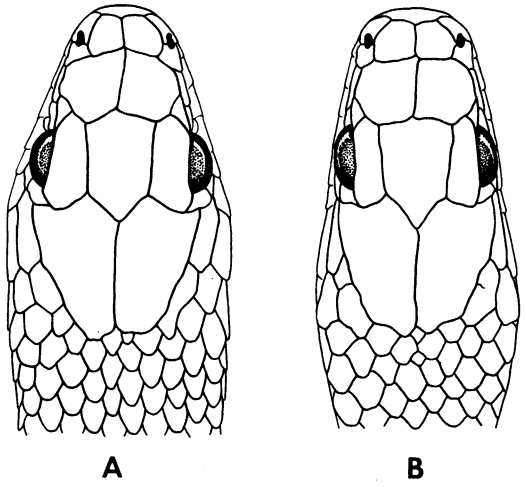
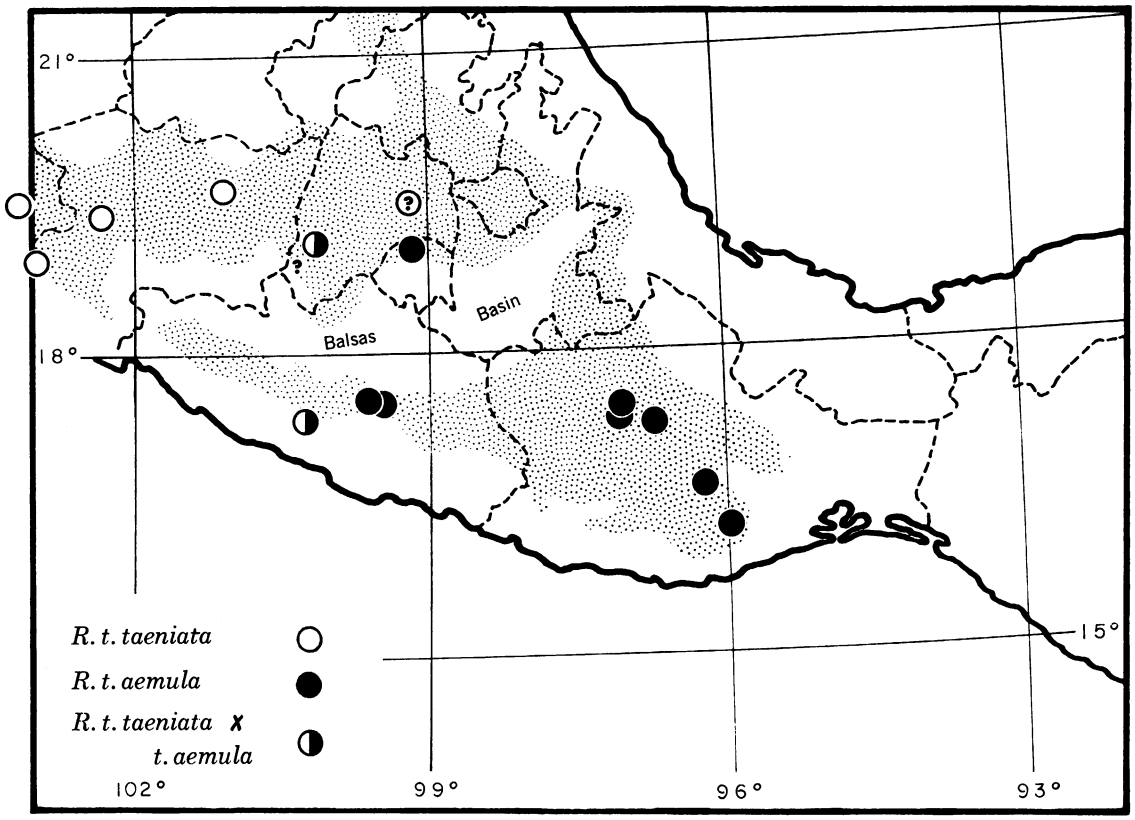


FIG. 24. Heads of *Rhadinaea taeniata* in dorsal aspect. A. *R. t. taeniata*, UMMZ 121522, Michoacán. ×7.7. Normal head shape for both subspecies. B. *R. t. taeniata* × *R. t. aemula*, UMMZ 125731, Guerrero. ×3.2. Unusual head shape, possibly associated with hybridization (?).



MAP 9. Locality records for *Rhadinaea taeniata*. Questioned record of nominate subspecies is for old specimens with datum "Mexico City"; questionable locality for hybrids is Temascaltepec-Real de Arriba area, which is suggested as being possibly the type locality (see text). Stipple pattern indicates approximate distribution of pine-oak forest in northern Cordillera Volcánica and in southern highlands of Sierra Madre del Sur and Sierra Madre de Oaxaca.

around the headwaters of the Balsas drainage. *Rhadinaea taeniata taeniata* occurs north of the Balsas basin, but its range evidently extends southeastward across the narrow, lower end of the Río Balsas, into the Sierra Madre del Sur of western Guerrero, where *taeniata* meets with *aemula* from eastern Guerrero. Guerrero is the only place for which there is definite evidence of hybridization, but there is circumstantial evidence that hybridization occurs (or occurred) in one other region where the ranges of the two subspecies might conceivably meet, namely in, or adjacent to, the southern half of the state of México, in the Cordillera Volcánica. The two probable zones of hybridization are discussed below, along with some weak evidence of introgression. See Short (1969), for a recent definition and discussion of hybrid zones.

Rhadinaea taeniata aemula is known from east-central Guerrero in the region of Chilpancingo, Sierra Madre del Sur. The only other specimen of *R. taeniata* from Guerrero seems to be the hybrid (UMMZ 125731) from 2.4 kilometers north of San Vicente de Jesús, also in the Sierra Madre del Sur. This locality is situated near 17° 15′ North Latitude, 100° 15′ West Longitude, and is shown on a few maps as being 89–90 kilometers southwest of Chilpancingo and 57–62 kilometers northwest of Acapulco. The specimen was found at 1000 meters elevation, "gliding through sparse grass in an open oak-pine forest, about noon on a warm day" (Kraig Adler, *in litt.*). Although no other specimens are known from the state, it seems likely that the nominate subspecies occurs in western Guerrero, assuming that the hybrid zone is a reasonably

narrow one. The Sierra Madre del Sur terminates at the western border of Guerrero, at the narrow gorge of the lower Río Balsas, beyond which the Sierra de Coalcomán extends westward along the coast of Michoacán (Duellman, 1961, pp. 10, 11). A single specimen (UMMZ 121522) of *R. t. taeniata* is known from toward the western end of the latter mountain range. The lateral black stripe of this specimen occupies all of row 4 and part of each adjacent row for a length of about 28 ventrals behind the head, and then it narrows to the lower half of row 5 and the top three-fourths of row 4, but isolated black edging is retained on the top of row three all the way to the tail. In other specimens of *R. t. taeniata*, the lateral stripe occupies parts of three rows for about five to 24 ventrals caudad, but then disappears completely from row 3 and is confined to about the adjacent halves of rows 4 and 5 along the rest of the body. Not only is the lateral stripe unusually wide in the Coalcomán specimen, but there is more black pigment in the dorsal stripe than I have seen in any other specimen of the nominate race. These characters possibly are involved in a clinal trend toward *aemula* in the Sierra de Coalcomán–Sierra Madre del Sur, but it also seems possible that the traits of the Coalcomán specimen are the result of introgression of genes from *R. t. aemula*. The problem cannot be settled with the few specimens at hand.

Specific locality data are not available for the three Berlin Museum hybrids obtained in "Mexico" by Ferdinand Deppe. However, Deppe evidently did not travel in Guerrero (Stresemann, 1954), so the specimens almost certainly came from the Cordillera Volcánica. Inasmuch as the nominate subspecies occurs in eastern Michoacán, and *R. t. aemula* occurs in Morelos, the only place left is the southern half of the state of México, assuming that there has not been a shifting of ranges since Deppe's time. Indeed, Deppe traveled into this region more than once to collect and to visit his friends William Bullock and son, who also collected natural history items (Stresemann, 1954). Important collections were made in the vicinity of Temascaltepec and Reál de Arriba and elsewhere in México and Morelos (Sibley and Davis, 1946; Stresemann, 1954). Therefore I suggest that Deppe's specimens were obtained in the Cordillera Volcánica in the southern part of the state of México, possibly in the Temascaltepec–Reál de Arriba area, in the 1820s (see Stresemann, 1954, for dates). New material from that region is much desired, although there can be no assurance that a hybrid zone of a century and a half ago would be still in existence. Deppe's having obtained not one but three hybrids is strong evidence that a real hybrid zone existed.

The dark stripes of some Morelos specimens of *R. t. aemula* tend to turn from black to dark brown on the rear of the body. As mentioned in the account of this subspecies, the brown color might represent a stage in the evolution of the unique coloring of *aemula*, or it might be the result of the introgression of genes from *R. t. taeniata*.

REMARKS: It seems important to place on record the living colors of the *Rhadinaea taeniata taeniata* × *R. t. aemula* hybrid from Guerrero (UMMZ 125731), as transmitted to me from the field notes of Kraig Adler (Charles F. Walker, *in litt.*). A comparable description of living specimens is available for the subspecies *aemula* (*q.v.*), but not for *taeniata*. The hybrid was "white below, pale salmon above with black stripes; labials pale yellow; top of head brown; small white flecks and/or edges of some scales on anterior half of body." A sketch of the iris shows the upper third "very pale yellow" and lower two-thirds "chocolate brown." Adler is to be commended for providing data that most collectors have not bothered with; color descriptions from life should prove extremely useful when additional material becomes available from the hybrid zone(s) and from the range of the nominate subspecies.

The specific epithet is derived from *taenia* (a head band) plus the suffix *-ata* (provided with), evidently in reference to the pale dorsolateral stripes (or possibly the lateral black ones) that extend from the body onto the head.

Rhadinaea taeniata taeniata (Peters), new combination

Figures 19A, 20A, 23A, B, 24A; map 9

Dromicus taeniatus PETERS, 1863, pp. 275–277. GÜNTHER, 1894 (1885–1902), p. 113.

Rhadinaea vittata (not of Jan): BOULENGER, 1894b, p. 178 (part, specimens *a–e*). COPE, 1887, p. 79 (part); 1900, p. 756 (part).

Rhadinaea taeniata (Peters): COPE, 1875a, pp. 139, 140. BAILEY, 1940, pp. 14, 15, pl. 2, fig. 4 (midbody pattern of BMNH 92.10.31.46). SMITH AND TAYLOR, 1945, p. 119.

LECTOTYPE: ZMB 2117 ["A," the male of a pair of specimens], as designated in the foregoing species account (*q. v.*). The specimen is seemingly a hybrid (secondary intergrade) between *Rhadinaea taeniata aemula* and the "nominate" subspecies.

DIAGNOSIS: A subspecies of *Rhadinaea taeniata* that is distinguishable from *R. t. aemula* and all other of its congeners in having a black (not brown) lateral stripe on the adjacent parts of rows 4 and 5, on a light brown ground color. A wide brown or blackish dorsal stripe occupies the median three rows plus part of an additional row on each side, and a darker vertebral line is usually present.

Rhadinaea taeniata aemula also has a black lateral stripe, but it is much broader and on a whitish or pale orange ground color. Other differences between *R. t. taeniata* and *R. t. aemula* are given in the foregoing account of the whole species. The pattern of *Rhadinaea omiltemana* is similar to that of *taeniata*, but the stripes are wider in *omiltemana* (compare figs. 20A, F).

DISTRIBUTION: The pine-oak zone (and possibly fir forest) in Michoacán and Jalisco and doubtfully in the vicinity of Mexico City, in the Cordillera Volcánica and the Sierra de Coalcomán, at known elevations of 1524–2835 meters. The Sierra de Coalcomán is separated by the gorge of the lower Río Balsas from the Sierra Madre del Sur of western Guerrero, where *R. t. taeniata* may also be expected to occur; this form evidently hybridizes with *R. t. aemula* in central Guerrero and possibly in southern México (map 9).

DESCRIPTION (12 SPECIMENS): Females of this, the largest kind of *Rhadinaea*, probably attain lengths in excess of 900 mm. The largest female examined is 880 mm. total length, of which 243 mm. is tail; the largest male is 670 mm. total and 219 mm. tail length. The tail is 31.0–32.7 percent of the total length in males and 27.6–35.1 percent in females. The dorsal scales are in 17–17–17 rows; anal ridges are present on adult males. Ventrals are 168–197 (168–180, males; 178–197, females) and subcaudals are 95–110 (106–110, males; 95–105, females). There are eight supralabials (8/7 in one), and 10 or occasionally nine infralabials. There is one preocular, except that two individuals have two preoculars on the right side, plus usually a subpreocular between the third and fourth labials. There are two postoculars and a basic pattern of 1+2 temporals.

Rhadinaea taeniata taeniata is a light brown snake, with three dark stripes that start on the head and disappear quickly on the tail, which distally is uniform brown. A black lateral stripe lies usually on the adjacent halves of rows 4 and 5 but may be shifted slightly up or down on either row. The lateral stripe is wider on the neck, where it occupies all of row 4 and adjacent parts of rows 3 and 5 for a distance of about five to 28 ventrals caudad. In some individuals the lateral black stripe is broken by a vertical white bar behind the mouth, but otherwise this stripe is continuous from the side of the head to the body; the stripe often has a brownish center on the head, especially in front of the eye where it may be weak and broken, and it is often contiguous with a black line across the rostral plate. The dorsal stripe is somewhat variable: It occupies the median three scale rows plus one-third, one-half (usually), or almost all (LACM 37325) of an additional row (the seventh) on each side. At least the anterior portion of the dorsal stripe has black edges that run forward onto the head as far as the upper rear edge of the eyes, and most specimens have superimposed on the dorsal stripe a narrow or wide black vertebral line that originates well back on the neck. The dorsal stripe is basically medium brown (gray under stratum corneum), a posterior extension of the dorsal head color, but a few individuals show a great intensification of black pigment on this stripe, which may have the brown coloring restricted to the vertebral and adjacent edges of the paravertebral scales. The dorsolateral ground color, on row 6 and parts of adjacent rows, appears as a light stripe that runs forward to the upper rear edge of the eye, beyond which it is only faintly indicated on the canthus rostralis. The dorsolateral light stripe in two specimens is broken by the width of one scale at the rear of the head, and in some specimens this stripe fuses behind the mouth with a vertical white bar that rises from the white throat and interrupts the lateral black stripe.

Most specimens have at least the anterior part of the trunk flecked with white, the result of small white dashes on the anterolateral edges of the scales in certain rows. The white dashes are most evident within the dark middorsal stripe, where there tends to be a pair of dashes on each scale in the vertebral row and a single dash on

the adjacent edge of each scale in the paravertebral row; the dashes are in some cases also present on the other anterolateral scale edges within the dorsal stripe. Elsewhere the dashes tend to occur every place except within the black lateral stripe and along the lower edge of the first row of scales. The dashes, when present, may be scarcely noticeable or very conspicuous.

There may be some sparse black speckling on the lower sides, the light brown coloring of which extends faintly or not at all onto the white ventrals and subcaudals. The undersides are unmarked except on a variable number of ventral plates, which have a black dot or small spot on each side. These markings disappear on the posterior part of the body and on some specimens are confined to the region of the throat. A few individuals have a pair of white parietal dots, but otherwise the only head markings are the anterior extensions of the body stripes, as already described. The supralabials are immaculate white below the lower edge of the lateral black stripe, and the white underside of the head likewise is devoid of markings. The colors in life have not been described.

The maxillary teeth range from 18+2 to 22+2, with the ultimate prediastemal tooth often lying posterior to the front edge of the ectopterygoid process when there are 20 or more anterior teeth. The last fang is offset laterad.

The retracted hemipenis extends to subcaudal 6 or 9 and the everted organ to the end of subcaudal 6. The retractor muscle originates at the level of subcaudal 32 or 33. The capitulum comprises from nearly half to more than half of the length of the hemipenis on its sulcate side. The calyces are spinulate in a wide band around the base of the capitulum, and papillate above. The sulcus spermaticus forks at a point one-half or more of its length up the capitulum, and the branches of the sulcus extend close to the end of the retracted hemipenis, but little more than halfway up the head of the everted organ. The wall of the capitulum forms a double fold on the asulcate side of the retracted organ (but this is not well indicated in the organ illustrated). Below the capitulum is a zone of approximately 28–40 medium, slightly recurved spines, most lying on the asulcate side high above the base of the hemipenis, but the largest lying on the sulcate side between one-third to one-fourth of the way above the base of the organ. The stalk is ornamented by minute spinules below the spinose region. The preceding description is based on the uneverted right hemipenis of BMNH 92.10.31.46, the left retracted and the right everted organs of UMMZ 121522 (both illustrated), and the partially everted right organ of LACM 37325.

GEOGRAPHIC VARIATION: See the species account, under Hybrid Zones.

REMARKS: Very little is known about *Rhadinaea taeniata taeniata* and few specimens have been collected, although it is the largest form in the genus and has been known for more than a century. *Rhadinaea taeniata taeniata* is known definitely only from the states of Michoacán and Jalisco; the old British Museum specimens reputedly from "Mexico City" must be viewed with suspicion, although I would not be surprised to see *R. t. taeniata* × *R. t. aemula* hybrids from the mountains of that region. *Rhadinaea taeniata taeniata* is presumably an inhabitant of pine-oak and possibly fir forest, judging from its known elevational range (1524–2835 meters) and from a comparison of Michoacán localities (see Specimens Examined) with remarks in Duellman's (1961, pp. 132–141) gazetteer for that state. According to Duellman (1961, p. 12; 1965, p. 641) pine-oak forest in Michoacán occurs at elevations between 1000 and 4000 meters and fir forest between 2400 and 4000 meters.

Rhadinaea taeniata aemula Bailey, new combination

Figures 19D, 20D, 23D, 25, 49A; map 9

Dromicus taeniatus PETERS, 1863, pp. 275, 276 (the syntypes are intermediate between *R. t. taeniata* and *R. t. aemula*; see discussion in the species account).

Henicognathus vittatus (not of Jan): BOCOURT, 1886 (1870–1909), pp. 630, 631, pl. 41, fig. 1 (scutellation, and color pattern of head and neck).

Rhadinaea vittata (not of Jan): BOULENGER, 1894b, p. 178 (part, specimens *h* and *i*).

Rhadinaea aemula BAILEY, 1940, pp. 4, 5, pl. 1, fig. 3 (midbody pattern of holotype). SMITH AND TAYLOR, 1945, p. 116.

HOLOTYPE: MCZ 42659, an adult female in good condition, from Omilteme, Sierra de Burro, Guerrero, Mexico, W. W. Brown collector.

DIAGNOSIS: A subspecies of *Rhadinaea taeniata* that differs from all its congeners in being vividly striped from tip of snout to end of tail with three wide black (not brown) stripes on a whitish or

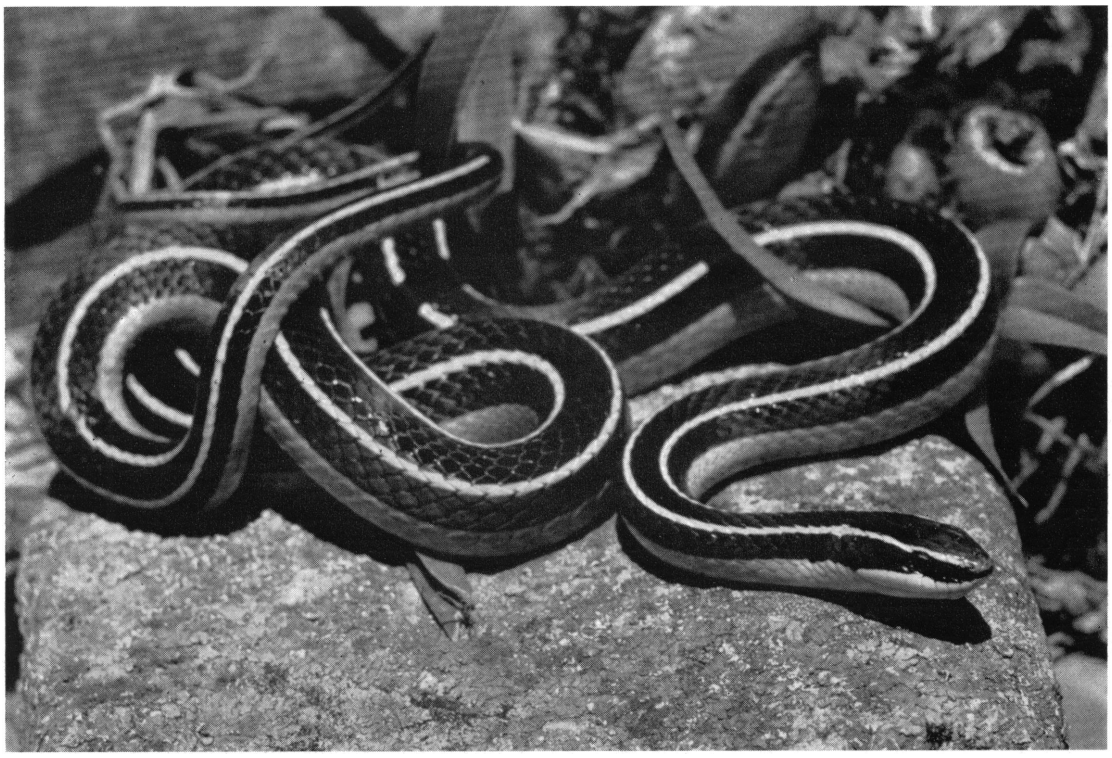


FIG. 25. *Rhadinaea taeniata aemula*, AMNH 89834, large female from Oaxaca. Vividly-striped subspecies is characterized by color, broadness of lateral black stripe, and by narrow whitish stripe that is continuous above the eye. *Rhadinaea taeniata aemula* is suspected to be a mimic of *Coniophanes piceivittis*, to which *aemula* bears much closer resemblance than to nominate subspecies. (Photograph by Charles M. Bogert.)

pale orange background. The lateral stripe occupies all of rows 4 and 5 plus adjacent parts of rows 3 and 6, and so is broader than in other species. Furthermore, the conspicuous dorsolateral stripe of whitish ground color, which is confined to adjacent parts of rows 6 and 7, extends from the snout to the tip of the tail, being anteriorly continuous above and not broken by the eye.

The various differences between this and the nominate subspecies are given in the species account. But specimens of *aemula* are as likely to be confused with *Coniophanes piceivittis* as with any kind of *Rhadinaea* (see Remarks at end of the present account).

DISTRIBUTION: The pine-oak zone, from central Oaxaca to central Guerrero in the Sierra Madre del Sur, and to Morelos (probably via the Sierra Madre de Oaxaca) in the Cordillera Volcánica, at known elevations of 1700–2439 meters. Hybridization with *R. t. taeniata* evidently occurs in the Sierra Madre del Sur of central Guerrero, and possibly in the state of México in the Cordillera Volcánica.

DESCRIPTION (41 SPECIMENS): This is a very large *Rhadinaea*, and females at least attain lengths in excess of 700 mm. The largest female measured 690+ mm. total length, of which 89+ mm. is tail; the largest male measured 586 mm. of which 207 mm. is tail. The tail is 30.4–36.8 percent of total length in males and 28.7–33.3 percent in females. The dorsal scales are in 17–17–17 rows; anal ridges are present on adult males. Ventrals are 150–178 (150–170, males; 160–178, females), and subcaudals are 97–121 (100–121, males; 97–114, females). There are eight supralabials, in few cases seven or nine, and 10 infralabials, in few cases nine. There is one preocular and usually a subpreocular between the third and fourth labials. There are usually two postoculars, or occasionally three. Temporals are normally 1+2, but the following formulae also occur: 1+1+2, 2+2, 2+2+2.

Rhadinaea taeniata aemula is unusual in normally lacking obvious brown pigmentation, except on the snout and in the iris. The color of preserved specimens is black and white. A broad dorsal black stripe and a broad lateral black stripe are continuous from the snout to the end of the tail; there may be tiny pale areas on the black scales, especially posteriorly on the body, but these usually are very inconspicuous except on close examination. The dark stripes are posteriorly more brown than black in a few specimens from Morelos. The dorsal stripe occupies the median three scale rows plus an adjacent half-row on each side. The lateral stripe covers rows 4 and 5 plus the adjacent one-third to two-thirds of rows 3 and 6. The pair of narrow, dorsolateral stripes of whitish ground color are vivid, and usually start from a common origin on the snout; each pale stripe extends along the canthus rostralis and passes unbroken above the eye to continue along the body, on the adjacent parts of rows 6 and 7, to the tip of the tail. An occasional individual has a slight break in the pale stripe on the rear of the head. The lower two and one-third or two and one-half scale rows are whitish, like the venter, and may be sparsely punctated with black. It is not unusual for individuals to have small, white dashes on the anterolateral edges of some scales. Such markings are most likely to occur within the dorsal black stripe, usually as an inconspicuous line of dashes on each edge of the vertebral scale row and, in some cases, as an additional line on the inner edge of each paravertebral row; similar dashes may also occur on some scales within the black lateral stripe and even on the pale ground color, where they are discernible as pure white dashes on whitish scales. Usually the venter is immaculate, except for the occurrence in many cases of a black dot on each ventral tip, especially on the anterior half of the body, but one specimen has conspicuous black dots clustered along the ventral midline on the basal two-thirds of the tail. Usually there is a pair of white parietal dots atop the black or blackish brown head. The tip of the snout is tinged with brown. The lower parts of the supralabials are immaculate white, as is the underside of the head.

The coloration in life can be described on the basis of five specimens, one of which I found about 20 kilometers northeast of the city of Oaxaca and four of which were collected by Charles M. Bogert at Tejocotes, Oaxaca. The narrow dorsolateral stripes are white with a very faint tinge of orange. The lower sides and tips of the ventrals are pale orange. The supralabials are orangish white. The underside of the head is white, turning pale, bright yellowish green over the rest of the venter. Approximately the upper third of the iris is tan and the lower two-thirds are dark brown. The tongue is bright orangish red except for black tips on the fork.

Maxillary teeth vary from 17+2 to 21+2, with the prediastemal teeth all lying anterior to the front edge of the ectopterygoid process. The last fang is offset laterad.

The retracted hemipenis extends to the base of subcaudal 9, and the everted organ to subcaudals 7 or 8. The retractor muscle of one specimen originates at the level of subcaudal 28. The capitulum comprises about half the length of the hemipenis on its sulcate side, and small connecting ridges of tissue are conspicuous under the free edge of the capitulum (fig. 23D). The calyces are spinulate in a wide band around the base of the capitulum, and papillate above. The sulcus spermaticus forks at a point one-half or slightly less than half of its length on the capitulum, and the branches of the sulcus extend close to the end of the retracted hemipenis but only about halfway up the head of the everted organ. The wall of the capitulum forms a double fold on the asulcate side of the inverted organ and the groove between these folds may be retained in the everted organ to cause a slightly bilobated appearance (fig. 23D). Below the capitulum is an area of about 23 to 30 medium, slightly recurved spines, most lying on the asulcate side high above the base of the hemipenis, but toward the sulcate side the spines are lower and there is a relatively large spine about one-third the way above the base of the organ. The hemipenis is ornamented by minute spinules below the spinose region. The preceding description is based on the right retracted and left everted (illustrated) hemipenes of KU 116948 and the everted organs of AMNH 93932, 102985, and KU 87753.

GEOGRAPHIC VARIATION: *Rhadinaea taeniata aemula* does not differ much from one locality to another. The most significant variation noted is that some specimens (e.g., FMNH 104995) from Morelos have the dark stripes less densely pigmented on the posterior part of the body, where the stripes take on a dark brown color rather

than black. The dorsal scales within the stripes on the posterior body seem to have more tiny pale areas showing through the darker pigment than is usual in other populations, and this has the overall effect of giving the stripes lighter (brownish) centers and darker (blackish) edges. The Morelos population is geographically isolated from the main part of the range of *aemula*, unless there is a tenuous connection around the headwaters of the Río Balsas drainage. The Morelos specimens possibly exhibit a late stage in the evolution of the highly distinctive *aemula* pattern, which is perfected in Oaxaca and eastern Guerrero. Or perhaps the brown coloration in the stripes is the result of introgression from *R. t. taeniata*, although this is not suggested by any other feature of color pattern, scutellation, or dentition.

An aberration in color pattern has been observed in material from one locality. Some individuals from Tejocotes, Oaxaca, have on the rear of the head a short gap in the white dorsolateral stripe. Five of 11 specimens from this locality have a break in the stripe on one (two specimens) or both (three) sides of the head.

REMARKS: *Rhadinaea taeniata aemula* is an inhabitant of pine-oak forest, where it usually is found concealed under rocks or logs or occasionally prowling on the surface by day (C. M. Bogert, verbal commun.). It occurs macrosympatrically with two other species of the *taeniata* group, but *R. t. aemula* seems to be replaced by these species at higher elevations in the pine-oak zone. For details of this apparent zonal partitioning of the environment by members of the same species group, see the discussions under *Rhadinaea fulvivittis* and *R. omiltemana*. Bogert twice found coral snakes (*Micrurus ephippifer*) that had preyed on *R. t. aemula*, at Tejocotes, Oaxaca.

The subspecific epithet is an adjective meaning emulous or rivalling in, in allusion to the resemblance between this form and *Coniophanes piceivittis* (*fide* Bailey, 1940). Bocourt [1886 (1870–1909), p. 631] also commented on the similarity between *R. t. aemula* (as *Henicognathus vittatus*) and *Coniophanes piceivittis* and illustrated both species (pl. 41, figs. 1, 2), although, as Bailey (1940) noted, the lateral dark stripe is drawn too narrow in the figure (dorsal view) of *aemula* (unless the specimen was an intergrade with the nominate subspecies). Aside from the generic characters, *Coniophanes piceivittis* differs from *Rhadinaea taeniata aemula* in possessing more rows of dorsal scales, broader black stripes, and dark-spotted supralabials and chin. But the resemblance between these snakes in dorsal aspect is indeed extraordinary and has led to the misidentification of some museum specimens. *Coniophanes piceivittis* is a lowland species that ranges from Costa Rica northward to the Isthmus of Tehuantepec, close to the southernmost limits of the highland *R. t. aemula*. There are specimens of both forms in the American Museum of Natural History, from localities less than 50 kilometers apart, near the juxtaposition of the Sierra Madre del Sur and the plains of Tehuantepec. There is an isolated population of *Coniophanes piceivittis* in the Sierra Madre del Sur in the Chilpancingo region of east-central Guerrero (Hall, 1951), or possibly the species occurs continuously but has just not been collected between Guerrero and Tehuantepec. In either case, it is perhaps significant that the specimens of *Coniophanes* were found at 800–1400 meters elevation, whereas *Rhadinaea taeniata aemula* has not been found below 1700 meters in the Chilpancingo region (or anywhere else). I doubt that the resemblances between this pair of snakes are fortuitous, and I suggest that the innocuous (nonbiting) *aemula* is a mimic of *Coniophanes piceivittis*, although whether the latter bites defensively is yet to be learned. Both species are presumably mildly poisonous, especially the grooved-fang *piceivittis*, but no species of *Rhadinaea* is known to bite, although some kinds of *Coniophanes* do so, at least on occasion (Brown, 1939; Myers, 1969a, p. 12). The apparent ecological separation of these species might be the result of past competition in a shared habitat and would not be a serious obstacle to a mimicry theory.

THE *godmani* GROUP

This is the only group of *Rhadinaea* in which some species have more than 17 rows of dorsal scales. There are 11 species.

21 SCALE ROWS:
R. godmani

19 SCALE ROWS:
R. hempsteadae
R. montecristi
R. serperaster

17 SCALE ROWS:
R. hannsteini

TABLE 11

ASPECTS OF INTERSPECIFIC VARIATION[a] IN THE *godmani* GROUP

Species	N	Ventrals		Subcaudals		Tail Length as a Percentage	
		Males	Females	Males	Females	Males	Females
godmani[b]	45	160–177 (31) 169.8±0.68	168–186 (13) 176.6±1.49	78–95 (28) 86.8±0.89	71–81 (11) 75.6±1.09	23.4–32.0 (28) 28.7±0.38	22.6–30.8 (12) 25.8±0.56
hannsteini	21	140–147 (10) 143.9±0.64	145–152 (11) 150.0±0.71	67–75 (8) 71.3±0.98	62–68 (9) 65.3±0.73	26.7–29.6 (8) 28.3±0.45	24.6–26.4 (9) 25.3±0.22
hempsteadae	13	162–174 (5) 168.4	168–189 (8) 178.9±2.59	89–94 (5) 91.6	74–82 (8) 77.1±0.89	30.6–32.8 (5) 31.9	24.3–29.4 (7) 26.3
kinkelini	5	136–148 (3) 143.0	161, 163 162.0	81–83 (3) 82.0	73 —	29.4–32.4 (3) 30.5	25.9 —
lachrymans	36	154–170 (18) 163.8±1.03	160–183 (17) 168.0±1.56	75–89 (19) 82.8±0.82	61–77 (16) 70.4±1.10	26.5–30.7 (18) 28.6±0.24	23.3–28.4 (16) 25.4±0.34
montecristi	32	158–165 (14) 161.0±0.52	164–176 (18) 167.2±0.70	79–87 (14) 82.9±0.61	71–79 (17) 74.6±0.55	28.3–31.2 (14) 29.4±0.20	24.9–27.6 (17) 25.9±0.20
pilonaorum	3	151 —	159, 164 161.5	— —	98 —	— —	33.3 —
pinicola[c]	1	150 —	— —	77 —	— —	[31.2] —	— —
posadasi	7	136, 139 137.5	143–146 (4) 144.3	92, 95 93.5	86–93 (5) 88.4	36.0, 37.4 36.7	33.3–35.8 (4) 34.5
schistosa	5	145–147 (3) 146.3	153, 154 153.5	40, 42 41.0	31, 34 32.5	16.5, 18.3 17.4	14.4, 15.3 14.9
serperaster	12	156–159 (5) 157.4	165–172 (7) 167.7	69–79 (5) 74.2	66–71 (7) 68.6	25.6–27.5 (5) 26.5	23.9–26.1 (7) 24.8
Combined ranges	180	136–177	143–189	40–95	31–98	16.5–37.4	14.4–35.8

[a]The following statistics are given if the sample is sufficiently large: Above, range followed by number of specimens in parentheses (if more than two); below, mean and standard error of the mean.

[b]A geographic breakdown of ventral and subcaudal counts is given in the species account.

[c]Data from original description (Mertens, 1952b).

TABLE 12
NUMBER OF MAXILLARY TEETH IN THE *godmani* GROUP

Species	N[a]	No. of Teeth 11	12	13	14	15	16	17	18	19	20	21	22	23	Range
godmani[b]	24	—	—	—	—	—	1	6	4	7	6	—	—	—	16–20
hannsteini	8	—	—	—	—	1	6	1	—	—	—	—	—	—	15–17
hempsteadae	8	—	—	—	—	—	—	2	3	3	—	—	—	—	17–19
kinkelini	4	—	—	—	—	—	4	—	—	—	—	—	—	—	16
lachrymans	14	—	—	—	—	—	—	—	2	5	5	2	—	—	18–21
montecristi	22	—	—	—	—	—	—	—	—	4	13	3	1	1	19–23
pilonaorum	2	2	—	—	—	—	—	—	—	—	—	—	—	—	11
pinicola[c]	1	—	—	1	—	—	—	—	—	—	—	—	—	—	13[c]
posadasi	5	5	—	—	—	—	—	—	—	—	—	—	—	—	11
schistosa	5	—	—	—	—	—	4	1	—	—	—	—	—	—	16–17
serperaster	6	—	—	—	—	—	1	5	—	—	—	—	—	—	16–17
Combined	99	7	0	1	0	1	16	15	9	19	24	5	1	1	11–23

[a]A single maxilla from each specimen.
[b]A geographic breakdown is given in the species account.
[c]Datum from Mertens (1952b, p. 135), who counted "Etwa 13 Maxillarzähne."

R. kinkelini
R. lachrymans
R. pilonaorum
R. pinicola
R. posadasi
R. schistosa

These are montane snakes, primarily of upper, or "Nuclear," Central America and adjacent Chiapas. There are outlying species in Veracruz (*R. schistosa*) and Costa Rica (*R. serperaster*), and one species (*R. godmani*) ranges from eastern Oaxaca to western Panama.

The *godmani* group is defined especially by the following combination of features (see also table 3): The last maxillary tooth is in line with the others, not offset laterad, and usually more than the last two teeth are noticeably enlarged; a diastema is absent or else small and variable in position (before the antepenultimate and/or before the penultimate tooth). The hemipenis usually is slightly bilobated, although this is not necessarily evident when the organ is everted, and there is a basal naked pocket. About one-third of the species have more than 17 scale rows. A subpreocular is absent; anal ridges are at least occasionally present in a majority of the species. Usually there is an oblique, pale bar, from the lower part of the eye to the corner of the mouth, a ∩-shaped dark marking on the rostral, and a tendency for the anterior supralabials to have dark edges and pale centers. Pale temporal lines or ocelli are never present, but in many there is evidence of a broken, pale collar on the neck, and a pair of pale blotches on the frontal plate.

This is essentially the "*lachrymans* group" of Stuart and Bailey (1941, pp. 6–9), with the addition of some species formerly included in the genera *Rhadinella* and *Trimetopon*, as commented on below.

The nominal *Rhadinella* was proposed with *schistosa* as its sole member (Smith, 1941). The proposal of a separate genus for this curious little snake seemed quite justified at the time. Certainly, *schistosa* does not look like a rhadinaea, for it is very small, has a relatively short tail, and it is very *Tantilla*-like in habitus; the describer of *Rhadinella schistosa* emphasized its remarkable similarity in color and habitus to a sympatric species of *Tantilla*. Nonetheless, the other diagnostic characters given by Smith are now seen to be invalid: The maxillary dentition agrees well with the basic pattern of the *godmani* group. The temporal formula 1+1 occurs normally in several species of three other groups, and other aspects of scutellation are in agreement with the variation seen in the *godmani* group (except for a low number of subcaudals). Most importantly, the hemipenis of *schistosa* bears remarkable resemblance to that of *Rhadinaea vermiculaticeps*, the type species of *Rhadinaea*. The organs of both species have virtually straight spines, an unusual

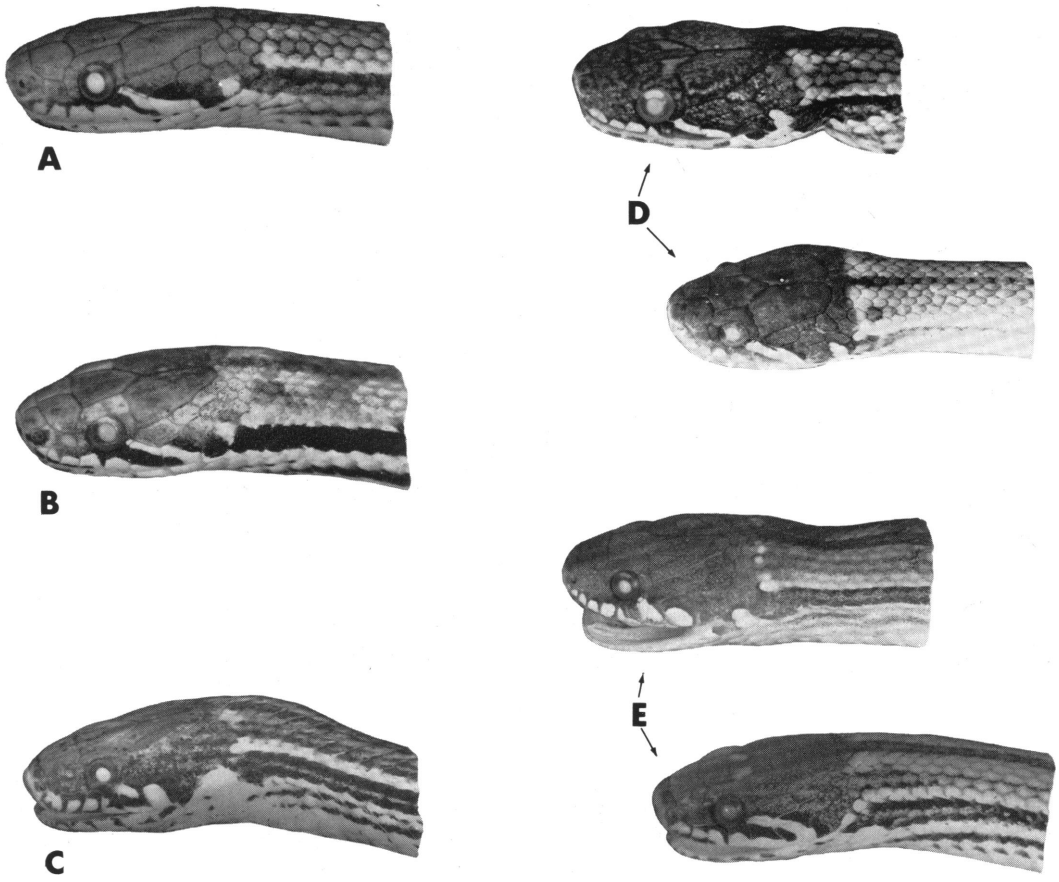


FIG. 26. Head patterns in large species of the *godmani* group. A. *Rhadinaea lachrymans*, CAS 67016, Guatemala. B. *R. montecristi*, KU 63869, El Salvador. C. *R. serperaster*, KU 30958, Costa Rica. D. *R. hempsteadae*—upper, UMMZ 127273, Guatemala; lower, JFC 66-60, Chiapas. E. *R. godmani*—upper, BMNH 1946.1.9.14 (syntype), Guatemala; lower, LSU 7565 (holotype of *R. binfordi*), Oaxaca.

feature that was stressed by Smith in his diagnosis of *Rhadinella*, and the general appearance of the organs is much the same (compare figs. 30G, 39). But spinules have been lost from the calyces of the hemipenis in the *vermiculaticeps* group, and this assemblage of snakes is well differentiated in terms of color pattern and more advanced maxillary dentition. I think that the pronounced hemipenial similarities between *schistosa* and the *vermiculaticeps* group probably are evidence of early radiation from common stock, but *schistosa* is demonstrably closer to members of the *godmani* group in details of dentition and color pattern (see below). Consequently, I regard *schistosa* as a specialized (in size and habitus) member of the *godmani* group. It is noteworthy that although *schistosa* has an undivided hemipenis, the slightly divided retractor insertion is evidence of ancestry from a bilobed condition. The name *Rhadinella* is referred to the synonymy of *Rhadinaea*.

The genus *Trimetopon* seemingly represents an offshoot from early *godmani*-group ancestry, and the several species in lower Central America represent a natural, definable group (Myers, MS). But I believe that several northern (Guatemala–El Salvador) species referred to *Trimetopon* are representative of a different line and should not be considered congeneric with *T. gracile*, the type species. The northern "*Trimetopon*" *hannsteini* and "*T.*" *veraepacis* are perfectly adequate members of the *godmani* group of *Rhadinaea* in my opinion [*T. veraepacis* was first described as a *Rhadinaea* and is tentatively

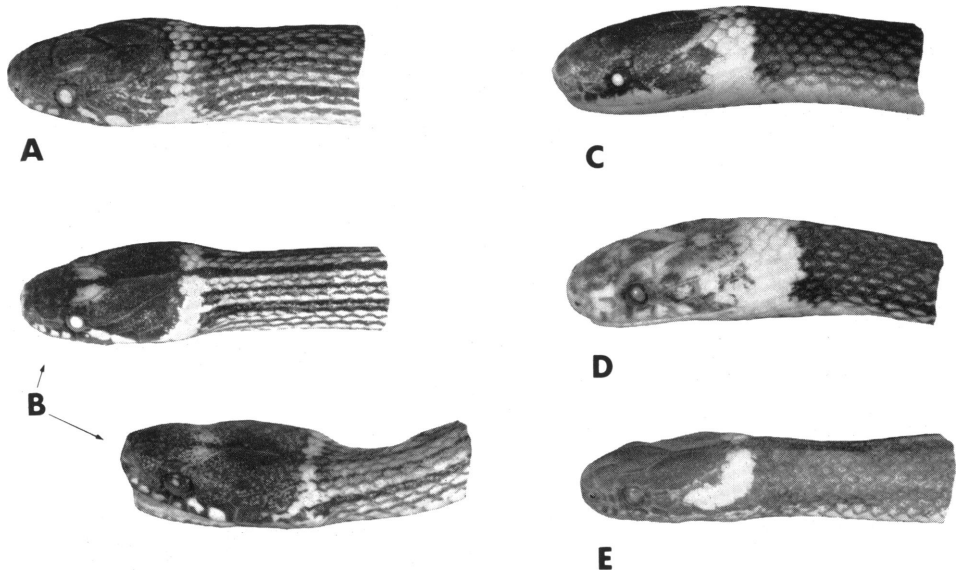


FIG. 27. Head patterns in small species of *godmani* group (*Rhadinaea pinicola* not included). A. *Rhadinaea hannsteini*, UIMNH 46128, Guatemala. B. *R. kinkelini*—upper, KU 63866, El Salvador; lower, FMNH 34739, Honduras. C. *R. posadasi*, CAS 66962 (paratype), Guatemala. D. *R. pilonaorum*, FMNH 64951, El Salvador. E. *R. schistosa*, FMNH 100297, Veracruz.

referred to the synonymy of *R. kinkelini* (*q.v.*) in the present monograph]. They are relatively small snakes, but they have the right habitus, there is a ∩-shaped dark marking on the rostral, the supralabials have dark borders enclosing pale centers, there is a tendency in some specimens for a pale postocular bar, and *kinkelini* has a pair of pale frontal blotches that are separated by a median dark streak. All of these markings are characteristic and widespread in the *godmani* group; *hannsteini* lacks the conspicuous frontal blotches, but a marked resemblance of hemipenes indicates that it is closely related to *kinkelini*.

One other pair of species has been referred to *Trimetopon* in northern Central America, namely "*T.*" *pilonaorum* and "*T.*" *posadasi*. These also are here placed in the *godmani* group of *Rhadinaea*, although on less satisfactory grounds than in the case of *hannsteini* and *veraepacis* (=*kinkelini*). *Rhadinaea pilonaorum* is quite unusual in having a basically white head and in being very slender for its length, but in most structural features it is close to *R. posadasi*. The latter has a ∩-shaped dark marking on the rostral plate, a brown head, and a pale collar, and so is not too far removed from the usual condition in the *godmani* group. Both species share with *Rhadinella* (=*Rhadinaea*, see above) *schistosa* a dorsal color pattern that is not found elsewhere in *Rhadinaea*: The dorsum is basically dark, with a tendency for a pale streak in the center of each dorsal scale. But *schistosa* has different proportions, more maxillary teeth, and, most importantly, a different hemipenis than found in *pilonaorum* and *posadasi*, and so the unusual pattern similarity is probably indicative only of rather distant relationship at best. Were there sufficient correspondences I would recommend maintaining the name *Rhadinella* for all three of these poorly known little snakes, but, for the moment at least, I believe that their relationships can best be expressed by considering them as members of the *godmani* group, with which they agree in type of maxillary dentition and several aspects of hemipenes, scutellation, and head coloration. Therefore, all species occurring in northern Central America and formerly referred to *Trimetopon* are considered by me to be members of the *godmani* group of *Rhadinaea*. This is hardly a major innovation, for Stuart (1949, p. 166) noted that *Trimetopon* (*sensu lato*) cannot be differentiated from *Rhadinaea*, and he later (1963) constructed a single key for the Guatemalan species of

Rhadinaea and "*Trimetopon.*" Comparison with *Trimetopon* (*sensu stricto*) will be made elsewhere (Myers, MS).

Note: Any *godmani*-group specimen not agreeing with one of the following species descriptions should be compared with data given below for the nominal *Erythrolamprus mentalis*, type locality "Guatemala" (Werner, 1909, p. 238). Bailey's (1939, p. 5; also see 1940, p. 17) reasons for believing that *E. mentalis* might prove to be a *Rhadinaea* seem reasonable, and I further suggest that it is most likely a member of the *godmani* group—a speculation based on geography as well as on aspects of scutellation. But this assumes that the type specimen represented a species having ungrooved maxillary teeth and smooth dorsal scales that do not normally undergo posterior reduction in number (characters not mentioned by Werner), and I therefore follow Peters and Orejas-Miranda (1970, p. 328) in assigning *Erythrolamprus mentalis* to *incertae sedis*. The holotype was destroyed in World War II according to Peters and Orejas-Miranda (*loc. cit.*), and also according to Jánis A. Roze, who kindly searched for the specimen in the Hamburg Museum in 1964. The scutellation and proportions of *E. mentalis* suggest that it might be close to *Rhadinaea kinkelini*, but the reported presence of a broad dorsal stripe does not fit. The following pertinent data are extracted from the original description of *mentalis* (Werner, *loc. cit.*): Male, 17 dorsal scale rows, 143 ventrals, divided anal, 64 pairs of subcaudals, one preocular, two postoculars, 1+2 temporals, eight supralabials (fourth and fifth in eye), 305 mm. total length, 80 mm. tail length [26.2 percent of total], head dark brown, supralabials yellow with dark sutures, black-edged dark stripe on median five scale rows [no mention of a narrow vertebral line], blackish brown lateral stripe on rows 4 and 5, three dark lines along edges of lower scale rows, yellow ventral surfaces.

Rhadinaea godmani (Günther)

Figures 26E, 28E–J, 30B, 49C; map 10

Dromicus Godmanni GÜNTHER, 1865, p. 94 (misspelling for *godmani*).

Rhadinaea Godmanii COPE, 1875a, p. 139 (here considered an unjustified emendation, hence a junior objective synonym of the correctly emended name); 1887, p. 80 ("misspelled" *godmani*); 1900, p. 755.

Henicognathus Godmanii (Cope, 1875a, *sensu* Günther, 1865): BOCOURT, 1886 (1870–1909), pp. 631–633, pl. 40, figs. 5, 5a–d (details of scutellation and color pattern of head and neck of Guatemalan specimen).

Rhadinaea godmani (Günther): BOULENGER, 1894b, pp. 179, 180 (accepted correction of original spelling, after Günther, 1893 [1885–1902], p. 110, see below under *Coronella godmani*). WERNER, 1929, p. 119. DUNN, 1932, p. 2. STUART AND BAILEY, 1941, pp. 6–8, fig. 1 (relationships and diagrammatic representation of body pattern, which is erroneously drawn *fide* Stuart, 1951, p. 64). UZZELL AND STARRETT, 1958, pp. 340, 341 (*R. g. zilchi* probably should not be recognized). STUART, 1963, pp. 112, 113.

Coronella godmani (Günther): GÜNTHER, 1893 (1885–1902), pp. 110, 111, pl. 39, figs. B (color pattern of whole body and of dorsum of head and neck; specific epithet an accepted correction [justified emendation] of original spelling).

Liophis godmani (Günther): AMARAL, 1929b, p. 172.

Rhadinaea zilchi MERTENS, 1952a, pp. 92, 93 (holotype: SMF 43175 [not seen], from shore of Laguna de las Ninfas=Laguna de Apaneca, Volcán de la Lagunita, 1630 meters elevation, Departamento Sonsonate, El Salvador; Adolf Zilch collector). New synonymy.

Rhadinaea godmani zilchi Mertens: MERTENS, 1952,c pp. 70, 71, pl. 6, fig. 23 (photograph of holotype from life). PETERS AND OREJAS-MIRANDA, 1970, p. 265.

Rhadinaea altamontana TAYLOR, 1954, pp. 740–743, fig. 16a–c (scutellation of head of holotype, KU 30962, from edge of National Forest Preserve, Pan-American Highway, Talamanca Range, 7000–8000 feet elevation, Costa Rica; Edward H. Taylor and Jack Rearck, collectors). PETERS AND OREJAS-MIRANDA, 1970, p. 264. New synonymy.

Rhadinaea binfordi ROSSMAN, 1965, pp. 4–7, fig. 2 (photograph of lateral aspect of head and neck of holotype, LSU 7565, from cloud forest, 4900 feet elevation, 12 air miles north-northeast of Zanatepec, Oaxaca, Mexico; L. C. Binford collector). New synonymy.

Rhadinaea godmani godmani (Günther): PETERS AND OREJAS-MIRANDA, 1970, p. 265.

DESIGNATION OF LECTOTYPE: There are several syntypes (BMNH 1946.1.9.14–1946.1.9.17), but only one of these was described by Günther. This is BMNH 1946.1.9.17, which is here designated lectotype. My counts of 176 ventrals (including the two preventrals) and 87 subcaudals differ by only one subcaudal from Günther's counts, and the measurements I obtained of 453 mm. total length, 128 mm. tail length are very close to Günther's figures of 18 inches (457 mm.) total, 5 inches (127 mm.)

tail length. The specimen is an adult male in fair condition; the color pattern is very close to the illustration (fig. 28F) of the midbody pattern of UMMZ 100516 (a topotype), except that the lines between rows 7–8 and 8–9 are darker on the lectotype.

The type specimens were obtained by Osbert Salvin and Frederick Ducane Godman, at Dueñas, [Departamento de Sacatepéquez], Guatemala.

DIAGNOSIS: *Rhadinaea godmani* is almost always distinguishable from all of its congeners by the presence of 21–21–21 dorsal scales, a higher number than found elsewhere in the genus. The species is likely to be confused in this regard only with the geographically adjacent (possibly sympatric in Chiapas) *R. hempsteadae*; some specimens of *hempsteadae* have 19–21–19 scale rows instead of the usual 19–19–19 rows, and one specimen of *godmani* has 19–21–17 rows. Color patterns and other features are not identical, but there is sufficient variational overlap between *godmani* and *hempsteadae* so that specimens with aberrant scale counts are best assigned on the basis of geographic range if possible.

The body pattern of most Costa Rican specimens of *godmani* is virtually identical with that of individuals from possibly sympatric populations of *R. serperaster*, which is most easily differentiated from southern *godmani* in seemingly constant differences in number of dorsal scales (19–19–19 in *serperaster*).

DISTRIBUTION: Highlands from southern Mexico to extreme western Panama, with a distributional gap in Honduras and Nicaragua.[1] In the north, *Rhadinaea godmani* occurs mainly in the Sierra Madre del Sur from eastern Oaxaca through Guatemala and into western El Salvador, with outlying populations on the Meseta Central de Chiapas and the Sierra de Chuacús of Central Guatemala. In the south, the species occurs in central Costa Rica in the Cordillera Central, and in the Cordillera de Talamanca to western Panama.

Habitats in the north are pine-oak forest and cloud forest at about 1500–2650 meters elevation; in the south this snake occurs in humid, broadleaf forests and *cafetals* in regions having a winter dry season, at about 1200–2200 meters.

DESCRIPTION (48 SPECIMENS): The largest specimen is a male 568 mm. total length, 133 mm. tail length; the next largest specimen is a female 544 mm. total, 136 mm. tail length. The tail is 23.4–32.0 percent of total length in males and 22.6–30.8 percent in females. The dorsal scales are in 21–21–21 rows with few exceptions: A specimen (KU 75747) from western Panama has 21–21–19 rows because of fusion of rows 3 and 4 at the level of ventrals 158 (for left side) and 149 (right side). Two other Panamanian specimens each have 21–21–20 rows because of loss of the paravertebral row on the left side at ventral 147 (ANSP 22575) or because of fusion of the left paravertebral row with row 9 at ventral 149 (ANSP 22915). A Mexican specimen (UMMZ 95155) has a standard formula of 19–21–17 rows, because of the following changes:

$$21\,\frac{3+4\,(15)}{3+4\,(15)}\;19\,\frac{\div 3\,(29)}{\div 3\,(24)}\;21\,\frac{-\mathrm{P}\,(132)}{-\mathrm{P}\,(132)}\;19\,\frac{3+4\,(139)}{3+4\,(139)}\;17\;(=186)$$

This is not a complete scale reduction formula, because there are some additional, non-paired changes involving the same rows indicated above, but these are reversed within short distances and would only cloud the basic pattern shown above; but the irregular changes do serve to underline the aberrant nature of the specimen.

Anal ridges are present or absent on adult males and are present on a few females. There are 160–186 ventrals (160–177, males; 168–186, females) and 71–95 subcaudals (78–95, males; 71–81, females). There are usually eight (rarely seven) supralabials, and nine (occasionally eight or 10) infralabials. There is one (in few cases two) preocular, no subpreocular, and two (in few cases one) postoculars. The basic temporal formula is 1+2, with some deviations (one or both sides) such as, 1+1, $1+^{2}_{1}$, $1+^{1}_{2}$, 1+1+2, and 1+2+3.

[1]Note added in proof: Because of unsuitable habitat, especially in the structural depression across southern Nicaragua, there doubtless is a large break in the range of *Rhadinaea godmani*. However, the apparent gap (map 10) has been narrowed by Wilson and Meyer's (1972) recent report of two specimens from montane pine forest (1450, 1740 m.) in south-central Honduras. The specimens, both males, were each said to have 19–21–21 scale rows and 92 subcaudals; the ventral counts, 156 and 159, lower the range (160–186) given herein. I interpret the color description (ventral hue omitted) of a living specimen as indicating the presence in Honduras of the bold "*zilchi*" pattern of wide, black primary stripes (see fig. 28G), heretofore known only from El Salvador. I personally concur with Wilson and Meyer's treatment of *R. godmani* as a monotypic species, but, contrariwise, the Honduran specimens might actually strengthen the argument of anyone wanting to give subspecific recognition to *zilchi*.

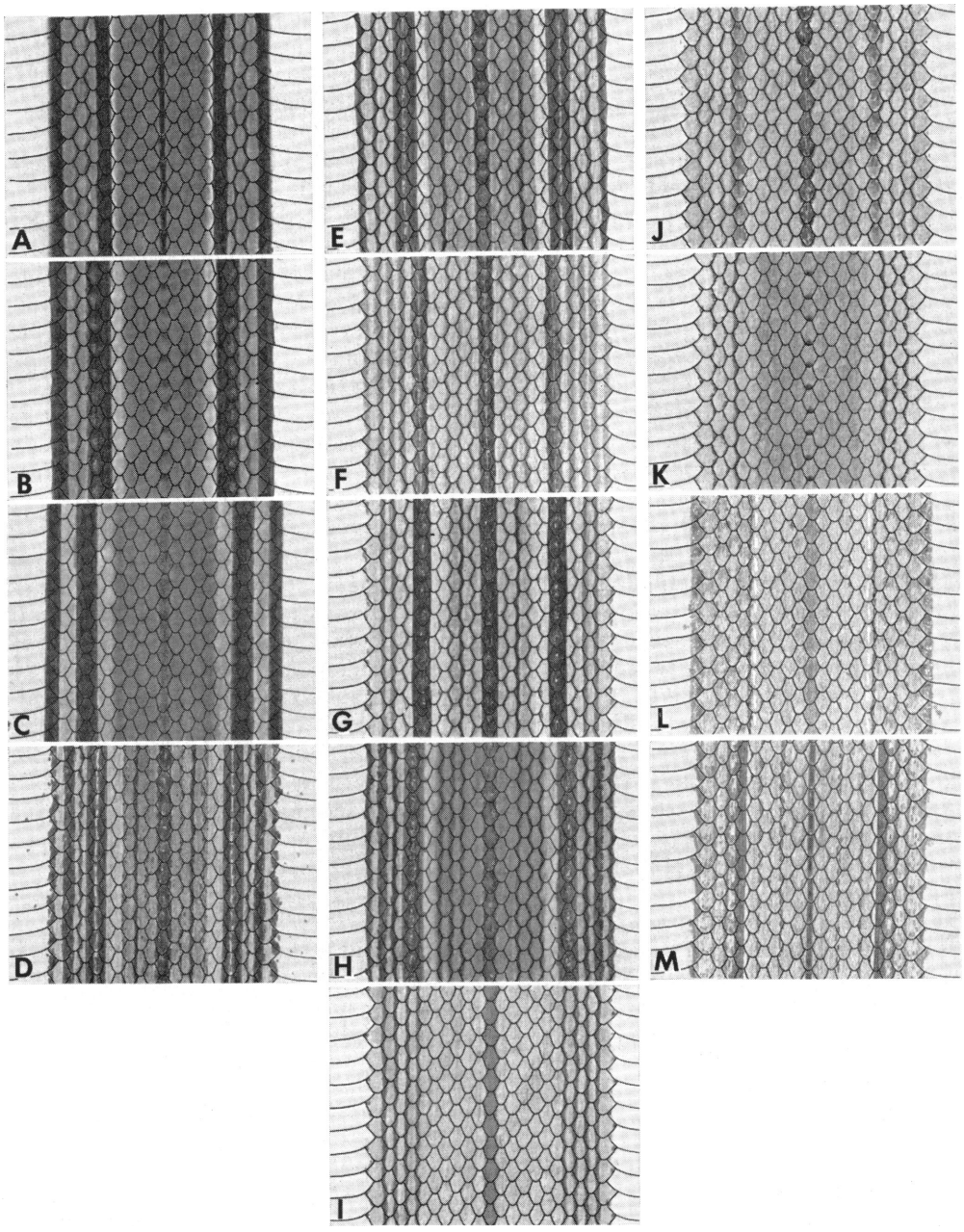


FIG. 28. Midbody patterns of large species of the *godmani* group. A, B. *Rhadinaea lachrymans* (17 scale rows), CAS 67016, 67017, respectively, from the same locality in Guatemala. C. *R. montecristi* (19 scale rows), KU 63875, El Salvador. D. *R. serperaster* (19 scale rows), EHT 4076, Costa Rica. E–J. All *R. godmani* (21 scale rows), as follows: E. UMMZ 95156, Chiapas; F. UMMZ 100516, Guatemala; G. UMMZ 117291, El Salvador; H. KU 75748, Costa Rica; I. KU 30962 (holotype of *R. altamontana*), Costa Rica; J. FMNH 20263, Guatemala. K–M. All *R. hempsteadae* (19 scale rows), as follows: K. JFC 66-60, Chiapas; L. UMMZ 89080 (holotype), Guatemala; M. UMMZ 89078 (holotype of *R. stadelmani*), Guatemala.

There is great variation, mainly geographic, in color pattern (fig. 28E–J). The body is pale to medium brown, with darker brown or blackish lines and narrow stripes; the ground color of the median seven or nine scale rows is often darker than that of the sides. There is a dark vertebral line that may overlap onto the paravertebral rows, and there is usually a dark lateral line or stripe, the width of one or two scale rows, that involves at least part of row 5. Other narrower lines may appear above and/or below the aforesaid lateral marking that involves row 5, by intensification of dark pigment on the adjacent borders of pairs of scale rows.

Snakes from Mexico and Costa Rica–Panama have very similar patterns, with several dark lines on the lower sides, including a line on the lower edge of row 1 and adjacent ventral tips, and a variable number (one to three) of dorsolateral lines. Most important is the similarity in the lateral stripe, which extends from the lower part of row 5 down onto row 3, with a tendency for a thin, pale streak along the middle of row 4. The secondary striping is generally much weaker in specimens from Guatemala, and the primary lateral marking is narrower and higher, not extending below the middle of row 4 and often almost confined to row 5. In specimens from El Salvador, the vertebral and lateral stripes are relatively broad and very dark and conspicuous, and the lateral marking is high as in Guatemala, being centered on row 5 and not extending below the upper part of row 4; secondary striping is relatively weak as in Guatemala. A few specimens from Guatemala (FMNH 20263) and Costa Rica (KU 30962, holotype of *R. altamontana*) are unusually light-colored and have weak and reduced striping (figs. 28I, J). Aside from such pale specimens, intraregional variation seems relatively slight. In the southern populations for example, the principal variations are in the intensity of the secondary lines and in the width of the lateral stripe, the upper edge of which varies from the lower half to lower three-fourths of row 5 and the lower edge of which occasionally extends down to the bottom of row 3.

There is in many cases a narrow (one-scale row), pale tan collar immediately behind the head; the collar is usually interrupted by the dark vertebral line and, in some specimens, also by one or more lateral lines, resulting in isolated pale spots around the neck. The top of the head is dark brown, with or without a pair of pale parietal dots, pale frontal blotches, or pale speckling (fig. 26E). The rostral plate is pale, with a ∩-shaped dark mark. The anterior supralabials are white, or dark with a longitudinal white stripe, or dark with an isolated white spot on each plate. Usually there is a blackish-bordered, postocular white bar, which slants obliquely across labials 6 and 7, from the lower rear edge of the eye to the mouth. Some specimens from central Guatemala (UMMZ 96647–96650) and Costa Rica (USC 2983, two hatchlings) show stages in the loss of the lower dark border of the postocular stripe, which then is confluent with the white area of the anterior supralabials. The last supralabial, the eighth, is mostly dark. The underside of the head is white, except for some slight pigmentation on the tip of the chin and adjacent infralabials. There may be a ventrolateral dark line across the tips of the ventrals, but otherwise the venter is white, sometimes with scattered dark punctations and/or a median dark streak or row of dots under the tail. The color in life is discussed later, in a separate section.

There are 16 to 20 maxillary teeth (see Geographic Variation) that increase in size from front to rear, with the last three to five being noticeably heavier and somewhat enlarged over the others. The last three teeth, or in some cases the last two or four, lie posterior to the front edge of the ectopterygoid process. A tiny gap, no greater than the length of an adjacent socket, is in some cases present in front of, behind, or on both sides of the third tooth from the rear. The ultimate tooth is in line with the others, not offset.

The hemipenis varies from about seven to 13 subcaudals long, and the origin of the retractor muscle varies from subcaudals 29 to 47 (see Geographic Variation). The hemipenis is slightly bilobated, but this is not, or only barely, evident when the organ is everted; the length of the short lobes of the retracted hemipenis is one-half to nearly a full subcaudal, and the two slips of retractor muscle are about as long. The capitulum is about two-fifths to nearly one-third the length of the hemipenis on its sulcate side. The sulcus spermaticus forks below the edge of the capitulum and the branches extend to the end of the retracted organ and about two-thirds of the way up the capitulum of the everted organ. The calyces are spinulate around the base of the

capitulum and papillate above; the calyces on the lower part of the asulcate fold are relatively large and bear enlarged, slightly recurved spinules. The wall of the asulcate side of the inverted capitulum forms a poorly defined fold that is weakly doubled; the doubled appearance is mainly caused by the basalmost calyx, which is larger than the others but which is not conspicuous on available everted hemipenes. The cluster of elongated spinules on the asulcate fold is continuous with a short row of small spines that lie basad of the edge of the capitulum; this row of little spines causes a break down the top of a naked space on the asulcate side of the hemipenis. There are two nude pockets, especially conspicuous on the everted hemipenis, on each side of the asulcate cluster of spinules; the largest pocket is a space set off by spines immediately below the edge of the capitulum, and the other pocket is an enlarged calyx that lies on the lower part of the capitulum. There is an ornamentation of small to medium, slightly recurved spines on each side of the aforesaid naked area; there are in excess of 50 such spines, which are largest toward the asulcate side. About 40–70 percent of the organ, the basal part, is adorned only with inconspicuous spinules. There is a long, naked basal pocket on the dorsal wall, from the base nearly to the spinose section of the retracted organ; the pocket remains conspicuous on one side of the everted organ. The preceding description is based mainly on everted hemipenes of KU 75748 (illustrated) and USC 2983, and the left retracted organ of UIMNH 56142. Other hemipenes examined at various times, but in less detail, are tabulated under Geographic Variation.

Color in Life: Color notes on living *Rhadinaea godmani* are available only for some specimens from the southern part of the range. A male (KU 75748) from western Panama had the head and dorsal ground color dull brown, whereas the ground color was pale tan on the sides of the body, except on the first scale row which was pale yellow between the dark lines. The supralabials were basically white, with a pink suffusion, except that the lower edges of labials 5 and 6 were pale yellow. The underside of the head was pale yellow and the rest of the venter was a uniform bright yellow. The iris was tan, with brown mottling and with a narrow ring of reddish brown around the pupil. A Costa Rican specimen (USC 2983, the adult female in this series) was noted by me to have a black tongue, with the distal half of the tips being white. The venter of this individual was gold colored, uniformly so when the specimen was first received in my laboratory, but irregular patches turned white for a period of several weeks before it died; by the time of death, the golden color had disappeared from about one-third of the total subcaudal surface and from about one-sixth of the belly. Two additional male specimens from Costa Rica did not have such bright venters as judged from the following notes: One individual had a cream venter, and was dull brown above and dull yellowish tan between the dark lines on the sides (W. E. Duellman, field notes for KU 63865). Another specimen, the holotype of *R. altamontana*, had a yellowish cream venter and yellowish cream and cream labial markings; the head was blackish above and the body ground color was brownish, except for "a more or less continuous cream stripe on outer scale row." (Taylor, 1954, p. 742).

The notes above show that adults of this species may have either bright yellow or whitish (cream) ventral surfaces. Those individuals with yellow venters possibly obtain the bright coloration through ontogenetic change. A male and a female hatchling with nearly white venters came from eggs laid by a snake having a gold-colored ventral surface (USC 2983, see above); the undersides of the heads of the hatchlings were white, turning a very pale greenish yellow posteriorly, with a tinge of orange along the ventrolateral edges. The coloration of these young snakes was otherwise not strikingly different from that of the mother. The juveniles had the body brown dorsally and orangish tan laterally, with black striping. Four spots (the broken collar) on the neck were pale orange. The head was black, with inconspicuous tan speckling; the paired parietal dots were tan and inconspicuous in one individual, and slightly larger and white in the other. The snout was orangish tan, turning black on the lower half of the rostral plate. Conspicuous white spots tended to form a horizontal stripe on the supralabials. The iris was light brown; the tongue was black, with the distal thirds of the tips being white.

Geographic Variation: The most striking variation is in color pattern, as indicated in the foregoing description. Specimens from the extremes of the range (i.e., southern Mexico and Costa Rica–Panama) have virtually identical patterns, whereas specimens from intervening

areas are generally paler, with fewer or less conspicuous dark lines or stripes. Salvadoran specimens, however, have three bold primary stripes that are much darker and more conspicuous than in other populations, but the rest of the pattern is relatively weak. The primary lateral line or stripe is positioned higher in specimens from Guatemala and El Salvador than in the more northern and the more southern populations.

One of the palest of all specimens of *godmani* is KU 30962 (the holotype of *R. altamontana*), from the Cordillera de Talamanca in south-central Costa Rica. This specimen was collected at a locality that is intermediate between known Panamanian localities and the other Costa Rican stations, but the body pattern (fig. 28I) is quite different from that of other southern specimens. The specimen is unique in lacking a bona fide lateral stripe, but in other aspects of pattern it somewhat resembles an unusually pale Guatemalan specimen (fig. 28J). The specimen was obtained by Taylor and Reark at a higher elevation (7000–8000 feet [2134–2439 meters]) than any other snake found by Taylor in Costa Rica (Taylor, 1954, p. 742). There is no way to know at present whether the specimen is representative of a high-altitude population of *godmani* or if it is an individual variant, but a typically patterned specimen of *godmani* (USC 2629) is available from 2208 meters elevation near Empalme, on the Inter-American Highway, which is at least in the same general region in which Taylor's specimen was obtained (see Taylor, 1954, p. 676, locality No. 36).

There seems to be little difference between northern (Mexico to El Salvador) and southern (Costa Rica, Panama) populations in number of ventral and subcaudal plates, and this is rather surprising considering the distance involved:

Northern Population
Ventrals: 169.1±0.94, 160–177 (20 males); 177.1, 168–186 (7 females)
Subcaudals: 88.6±0.92, 79–95 (19 males); 75.6, 71–81 (7 females)
Southern Population
Ventrals: 171.2±0.81, 169–175 (11 males); 176.0, 170–180 (6 females)
Subcaudals: 83.0±1.26, 78–91 (9 males); 75.8, 73–94 (4 females)

There is a tendency for northern specimens to have fewer maxillary teeth than southern specimens:

		Number of Teeth					
Population	N	16	17	18	19	20	Mean
Northern	13	1	6	3	3	0	17.6
Southern	11	0	0	1	4	6	19.4

There is significant variation in the length of the hemipenis and retractor muscle. Specimens from southern Mexico and central Guatemala have long slender organs, and the retractor muscles originate well back in the tail, whereas specimens from lower Central America have relatively short hemipenes and retractors. A few specimens from El Salvador have hemipenes about as long as specimens from the southern population, but the length of the retractor muscle is intermediate between Mexican-Guatemalan and Costa Rican-Panamanian snakes. The length of the hemipenis seems determined by the size of the basal, aspinose section. Data shown below were obtained from specimens at various times; closer comparison might reveal a few other differences in the copulatory organs of specimens from different populations. Length of the hemipenis is expressed by the subcaudal that lies below the distal end of the organ; length of the retractor

Specimen	Hemipenis Length	Retractor Length	Remarks
UIMNH 56142, Oaxaca	13	40	Left organ, retracted
UMMZ 95156, Chiapas	13	47	Left organ, retracted
UMMZ 96648, Guatemala	12	40	Right, retracted
UMMZ 117290, El Salvador	7	34	Both organs everted
UMMZ 117291, El Salvador	9	32	Left, retracted
KU 30962, Costa Rica	8	29	Left, retracted
USC 2629, Costa Rica	7	—	Left, everted
USC 2983, Costa Rica	8	—	Left, everted
KU 75748, Panama	9	29	Left, retracted
KU 75748, Panama	7	29	Right, everted

muscle is indicated by the subcaudal at the level of the origin of the muscle.

There are a few other features of these snakes that seem subject to interpopulational variation: Specimens from Costa Rica and Panama have a relatively smaller eye or else a relatively longer muzzle than northern snakes. The eye of southern specimens will usually go slightly more than twice into the distance from the anterior edge of the eye to the tip of the snout, in few cases less than twice. In northern specimens, the eye usually goes one and three-fourths to slightly less than two times into the length of the snout, in few cases as little as one and a half times or more than two times.

Six of 18 specimens from Costa Rica–Panama have a deviation from the normal count of 1+2 temporals, on one or both sides of the head. My records show no deviations in 28 specimens from the northern part of the range, although possibly I might not have bothered to note a few minor divisions (vertical) of the top or bottom plate in the second row. Variation in the number of infralabials, on the other hand, is more common in the north, where 10 of 27 specimens (37.0 percent) deviated from the usual count of 9/9. Only three of 18 southern specimens (16.7 percent) deviated from the normal.

REMARKS: I am greatly extending the concept of the species *Rhadinaea godmani*, which until now has been thought of as essentially a Guatemalan snake, with an outlying, slightly differentiated population (*R. g. zilchi* Mertens) in western El Salvador. Uzzell and Starrett (1958) suggested that the characteristics of "*zilchi*" were probably too slight to warrant taxonomic recognition; I agree, and I formally place the name in synonymy, although this action should not obscure the fact that Salvadoran *godmani* have unusually dark and bold primary stripes. Two other names are also here conceived as synonyms of *godmani*, namely *R. binfordi* Rossman, from Mexico, and *R. altamontana* Taylor, from Costa Rica. It was the remarkable resemblance between specimens from Mexican and Costa Rican-Panamanian populations of 21 scale-row snakes that first caused me to consider that *R. godmani* might be an unexpectedly wide-ranging snake.

I directly compared the holotype of *R. binfordi* (Oaxaca) with the lectotype of *R. godmani* and found essential differences only in color pattern of the body; the dissimilarities are of the magnitude of the differences between the midbody illustrations of UMMZ 95156 (fig. 28E, *binfordi*-type pattern) and UMMZ 100516 (fig. 28F, topotype of *godmani*), except that the latter specimen has less conspicuous dark lines between rows 7–8 and 8–9 than does the lectotype specimen. The lectotype of *godmani* has a proportionally wider head than the smaller type of *binfordi*, but this seems to be a result of ontogenetic change plus the fact that the lips of the lectotype have been loosened from both maxillae and are unnaturally spread.

The Mexican specimens seem to differ from the similarly colored southern snakes (Costa Rica–Panama) chiefly in length of the hemipenis and in the presence of a few more maxillary teeth, but in these characteristics the Mexican specimens are like the differently patterned Guatemalan snakes. The body pattern of the Salvadoran specimens, although divergent, is most similar to that of Guatemalan snakes, but the hemipenis is the same size as in southern specimens and the retractor muscle seems to be of intermediate length.

The holotype of *R. altamontana* is much paler and has fewer linear markings than any other southern specimen of 21 scale-row *Rhadinaea*, but there seem to be no other differences of note. Inasmuch as occasional Guatemalan specimens are also unusually pale, I do not presently attach particular significance to the *altamontana* type of pattern, whether it be an aberration or representative of an isolated population. In event of the latter possibility, the population would probably be of very limited distribution, as the type locality of *altamontana* lies between populations of snakes of virtually identical appearance.

In view of preceding comments, I see no reason to believe that there is more than one species of *Rhadinaea* characterized by 21 rows of dorsal scales. There are sufficient locality records to show that *R. godmani* is confined to montane habitats and that the distribution must be disjunct, with a particularly wide gap in the region of the Nicaraguan Depression. That a single species of montane snake should be distributed from eastern Oaxaca to western Panama is indeed improbable, but *R. godmani* is not unique, as *Bothrops godmani* has a virtually identical distribution. The similarity in the names of these two snakes that share the same unlikely distribution is extraordinary; the types of both species, incidentally, were obtained by the same collectors

in the same country, and Günther is the author of both names.

Rhadinaea godmani has been found in cloud forest in Oaxaca (Rossman, 1965) and El Salvador (Uzzell and Starrett, 1958), and in pine-oak forest in Guatemala (Slevin, 1939; Stuart, 1951, p. 62). Stuart (*op. cit.*) doubted that it invades the higher pine-cypress zone and thought that a mutilated tail had been carried from lower elevations, probably on the hoof of a mule. The elevation at which the tail was found (about 3000 meters) is about 350 meters higher than the known maximum. Mertens (1952c) reported specimens being found near lakes in volcanic craters in El Salvador. Taylor (1954, p. 742) found a Costa Rican specimen in a swampy area in a high elevation oak forest. Most of the aforesaid authors have stated that their specimens were found under logs or boards. William E. Duellman and I found one under a log in a *cafetal* in Panama, near the edge of a forest. The principal habitat of the species in Costa Rica and Panama seems to be montane seasonal forests that are generally humid, although affected by a winter dry season.

Rhadinaea godmani has been reported as occurring sympatrically with two other snakes of the same species group—*R. lachrymans* in Guatemala (Slevin, 1939) and *R. montecristi* at Hacienda Monte Cristo, El Salvador (Uzzell and Starrett, 1958). A third species of the *godmani* group, *R. kinkelini*, also occurs in the cloud forest at Hacienda Monte Cristo. Of most interest, however, is the macrosympatry (if not actual microsympatry), with two other species that seem especially close to *R. godmani*, namely *R. hempsteadae* in Chiapas, Mexico, and *R. serperaster* in Costa Rica.

Two pale and weakly patterned specimens of *R. hempsteadae* (JFC 66–60, fig. 31; UAZ 26581) are known from an area about 14 kilometers southeast of San Cristóbal de las Casas at approximately 2375 meters of elevation; one strongly patterned specimen (TNHC 29667) of *R. godmani* ("*binfordi*" pattern) is available from about 19 kilometers northwest of Comitán at approximately 1825 meters. These are the only specimens of either species that I have seen from the Meseta Central of Chiapas; the localities are situated along Mexican Highway 190 and are no more than 25 kilometers apart (straight line). The UAZ specimen of *hempsteadae* has 19–21–19 rows of scales (normally 19–19–19) and this might be taken as indication of genetic interchange with *godmani*. Two other specimens of *hempsteadae* with 21 midbody scale rows are known from Guatemala in the Montañas de Cuilco (UMMZ 127272) and the Sierra de los Cuchumatanes (UMMZ 120014); these two specimens are not representative of their populations and conceivably owe their unusual scale counts to the introgression of genes from *godmani*. A northern specimen of *godmani* (UMMZ 95155) has the unusual scale formula of 19–21–17, which might be supposed to be the result of gene flow from *hempsteadae*; however, the specimen is from the Sierra Madre del Sur of Chiapas, mountains in which *hempsteadae* is unknown. In spite of the usual difference in number of scale rows, and the slight difference in color patterns, *R. hempsteadae* and *R. godmani* are closely related, as attested not only by the unusual scale formulae of some individuals but also by the similarities in hemipenes, maxillary dentition, and numbers of ventrals and subcaudals. Although these snakes possibly hybridize, and might conceivably even be conspecific, their exact relationship and possible hybridization must remain an open question until the acquisition of additional material from critical areas. The region between San Cristóbal and Comitán is of special interest because of the presence of both forms; this region is also accessible on a good highway, and the extensive forest has been subjected to relatively little clearing, which suggests that gene flow may be not unnaturally impeded.

The range of *R. godmani* overlaps with that of *R. serperaster* in the mountains of central Costa Rica. Both species occur in the Cordillera Central and the northern end of the Cordillera de Talamanca, with *serperaster* evidently endemic to this region. Both species have yet to be found at the same locality, and possible habitat differences, if any, are unknown. Similarity between these two species is great, and southern specimens of *godmani* have been misidentified as *serperaster* in the literature (Dunn, 1947; Stuart and Bailey, 1941, p. 7). The color patterns of *serperaster* and southern *godmani* are almost identical, except that *serperaster* has somewhat more vivid striping on the body, and the head pattern, especially on the supralabials, seems less variable than in *godmani*. *Rhadinaea serperaster* has fewer scale rows (19 versus 21). If these were the only differences, I would be inclined to

consider *serperaster* as a form of *godmani*; the difference in number of scale rows would not seem particularly significant, as a few Panamanian specimens of *godmani* show a posterior reduction to 19 rows. But there are a few other distinctions, and the total of all differences suggest that two species are involved. *Rhadinaea serperaster* has 16 or 17 maxillary teeth (N=6), contrasted with 18–20 in southern specimens of *godmani* (N=11). *Rhadinaea serperaster* averages fewer ventrals and subcaudals and there is but slight overlap in the ranges of these plates (table 11). The hemipenis provides perhaps the best proof that we are dealing with two species. The hemipenis of *godmani* has a few enlarged calyces on the asulcate side of the capitulum, and a short, asulcate row of small spines in the otherwise nude area below the capitulum; *R. serperaster* lacks these features. The asulcate fold, on the capitulum of the retracted organ, is weakly doubled in *godmani* (because of the enlarged calyces), but it is thicker and single in *serperaster*. *Rhadinaea godmani* lacks any markedly enlarged spines, but *serperaster* has several moderately enlarged spines along the bottom of the spinose zone.

Two juvenile specimens (USC 2983A, 2983B) of *R. godmani* were hatched from eggs laid by a Costa Rican specimen (now USC 2983, one of a pair) that was lent to me by Norman Scott. Data from the hatchlings are not included in the foregoing species account, except under Color in Life, because of obvious aberrances, which probably are the result of unnatural temperatures to which the developing embryos were exposed in my laboratory. One hatchling, a female, has about 135 ventrals and 50 subcaudals, far less than counted on any wild-caught specimen (table 11); a number of the subcaudals are fused into single plates and there also are asymmetrical numbers of postoculars and temporals. The other hatchling, a male, also has low numbers of ventrals (163) and subcaudals (70). Both individuals have some divided ventrals and half-ventrals.

Miller (1968, pp. 429, 451, 453) included *Rhadinaea godmani*, under the name *Liophis*, in a study of the cochlear duct of snakes.

The species was named by Günther in honor of Frederick Ducane Godman, who was one of the collectors of the type specimens and a principal force behind the 63 quarto volumes of the "Biologia Centrali-Americana." I have shown in the synonymy the several variations in the spelling of the specific epithet, which originally was printed with a double *n* and later corrected to *godmani* by Günther in 1893. The first correct spelling actually seems to have been used by Cope in 1887, but evidently this was a *lapsus* for Cope's (1875a, 1900) own emendation of the name to "*godmanii*." I accept "*godmani*" as the correct spelling because there is only one *n* in Godman's name, and only one *i* in the original spelling; this also agrees with the usage of recent authors.

Rhadinaea hannsteini (Stuart), new combination

Figures 27A, 29D, 30D, E; map 11

Trimetopon hannsteini STUART, 1949, pp. 165–168; 1963, p. 122. PETERS AND OREJAS-MIRANDA, 1970, p. 308.

HOLOTYPE: UMMZ 98756, an adult male in good condition, from Finca La Paz, 1450 meters elevation, 18 kilometers (airline) due north of Coatepeque, Departamento de San Marcos, Guatemala, caught by L. C. Stuart on May 14, 1947.

DIAGNOSIS: *Rhadinaea hannsteini* is a small brownish snake with a pale, broken neck-ring, a dark vertebral line, and several additional lines or stripes on each side. It has 17 scale rows and thus differs from related species characterized by 19 or 21 rows, and the several well-defined dark lines distinguish it from several small species that have a pale collar but no dark lateral lines. *Rhadinaea hannsteini* can be distinguished from the remaining members of the *godmani* group (*R. kinkelini*, *R. lachrymans*, *R. pinicola*) in having only one postocular, rather than two, and in details of color pattern. The species is most likely to be confused with *R. kinkelini* (*q.v.*) and, although the number of postoculars separates all specimens examined, close attention should be given to the illustrations of heads and body patterns; in addition to the slight differences in body striping, it will be noted that *hannsteini* lacks large pale areas on the frontal plate, whereas such markings are characteristic of *kinkelini* and some other members of the *godmani* group.

DISTRIBUTION: The Pacific versant of the Sierra Madre of southwestern Guatemala and immediately adjacent Chiapas, Mexico, at known elevations of 1050–1450 meters. The only reported habitat is the ground litter in coffee plantations.

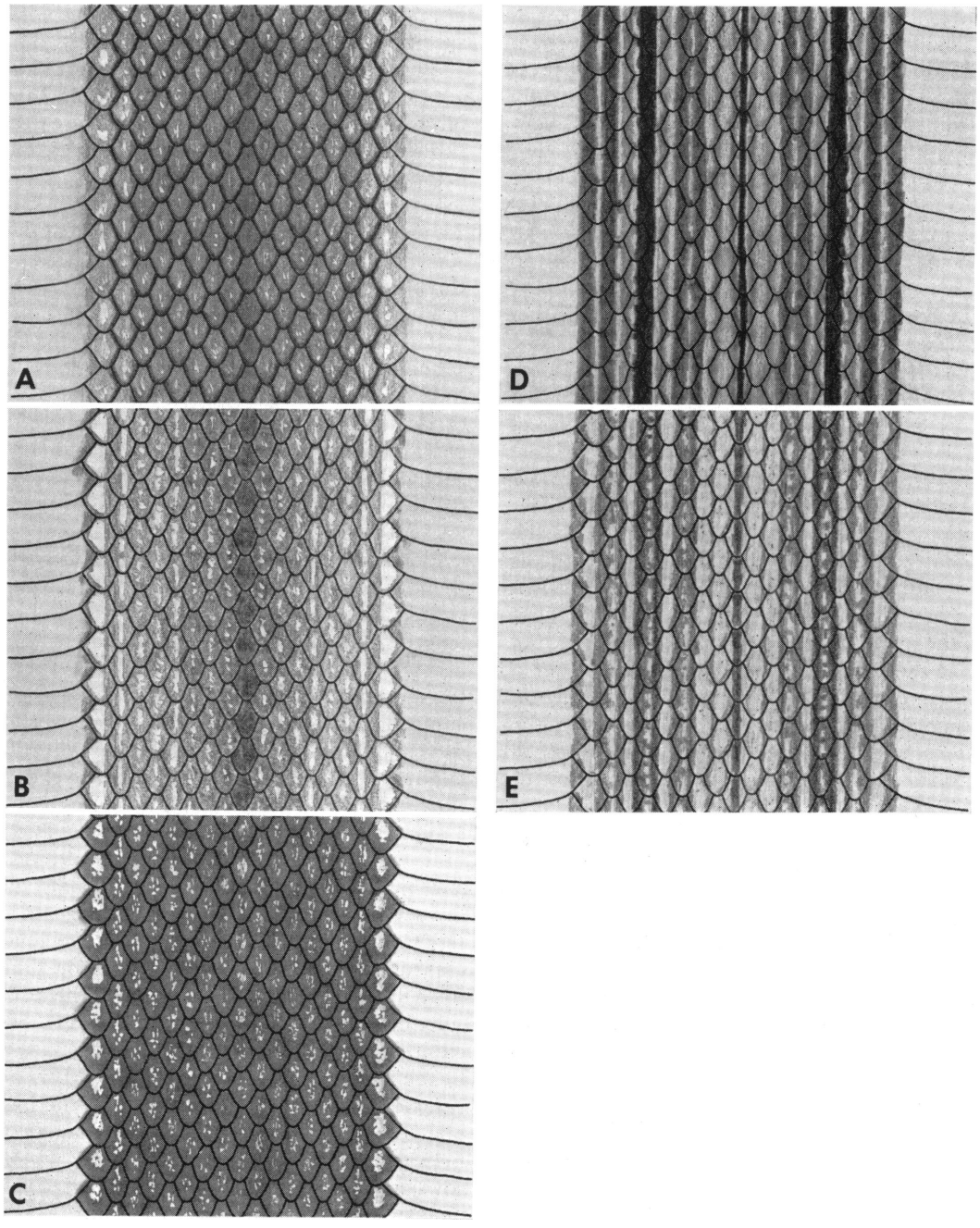


FIG. 29. Midbody patterns of small species of the *godmani* group (*Rhadinaea pinicola* not included). A. *Rhadinaea posadasi*, CAS 66962 (paratype), Guatemala. B. *R. pilonaorum*, UMMZ 102635 (holotype), Guatemala. C. *R. schistosa*, USNM 109914 (paratype), Veracruz. D. *R. hannsteini*, UMMZ 98753 (paratype), Guatemala. E. *R. kinkelini*, UMMZ 89077 (holotype of *R. veraepacis*), Guatemala.

DESCRIPTION (21 SPECIMENS): The two largest specimens are males, with total lengths of 325 and 320 mm. and respective tail lengths of 96 and 91 mm.; several females exceed 300 mm. total length, the largest one being 312 mm. total, 81 mm. tail length. The tail is 26.7–29.6 percent

of total length in males and 24.6–26.4 percent in females. The dorsal scales are in 17–17–17 rows. Anal ridges are lacking on the females but present on all males, including a small specimen only 195 mm. total length. There are 140–152 ventrals (140–147, males; 145–152, females) and 62–75 subcaudals (67–75, males; 62–68, females). There are eight supralabials (8/7 in one specimen), eight infralabials, one preocular, one postocular, and 1+2 temporals; there is no subpreocular.

The body is yellowish brown or brown, with a complex pattern of darker brown lines. The primary (i.e., darkest) markings are a narrow line on the middle of the vertebral row and a narrow lateral stripe on the adjacent halves of rows 3 and 4. There are secondary (i.e., lighter) lateral brown lines on the lower part of row 1 and adjacent ventral edges, on the adjacent parts of rows 1 and 2, and sometimes on the adjacent parts of rows 2 and 3 (usually this is only a faint streak). There is a secondary brown stripe or pair of lines on the middorsal region, from the upper part of row 5 to the lower part of row 7; this marking would be called either a stripe or a pair of close lines, depending on whether or not a series of pale dashes, on the middle of row 6, are confluent; the lower part of the dorsolateral stripe is occasionally absent or faint, leaving only the line on the adjacent parts of rows 6 and 7. The tail is striped for most of its length, by nearly contiguous ventrolateral and lateral lines and by the narrow vertebral line.

Immediately behind the head is a pale yellowish neck-ring, about two scales wide, that is interrupted by the vertebral line and, occasionally, by one or more lateral lines. The top and upper sides of the head are dark brown, with an inconspicuous sprinkling of tiny yellowish markings that sometimes include a pair of parietal dots. The margin of the rostral plate tends to be pale, leaving a central ∩-shaped dark mark. The supralabials are dark brown with a yellowish or whitish spot on each of the first four or five; the sixth and seventh supralabials have oblique yellowish or whitish markings that tend to form a broken postocular line from the eye to the corner of the mouth. The underside of the head is pale with dark brown smudging, especially on the mental and anterior labials. Occasional specimens have a few dark specks on the yellowish white ventrals and subcaudals, but usually the venter is unmarked save for the ventrolateral brown line. The color in life has not been specifically noted.

There are 15 to 17 maxillary teeth that increase in size posteriorly. The last several are enlarged but not abruptly so; there are usually three teeth posterior to the front edge of the ectopterygoid process, but there are only two teeth posterior in a specimen having a total of 15 teeth. A tiny gap, less than the length of a single socket, may occur before or behind the third tooth from the rear. The ultimate tooth is in line with the others, not offset.

The retracted hemipenis extends to the end of subcaudal 5 and is slightly bilobate from the base or the middle of subcaudal 5; the two slips of retractor muscle merge at the end of subcaudal 6 and the muscle originates at the level of subcaudal 23 or 24. The one available everted organ extended to the sixth subcaudal; the lobes are not completely expanded, and so it is not evident whether the bilobation is noticeable in the completely everted organ. The capitulum comprises between one-third and one-half of the length of the hemipenis on its sulcate side. The calyces are spinulate on the asulcate fold (retracted condition) and on the free edge of the capitulum and are papillate elsewhere. The sulcus spermaticus forks near the edge of the capitulum and the branches extend to the tip of the retracted hemipenis but little more than halfway up the head of the everted organ. The wall of the capitulum forms a single fold on the asulcate side of the uneverted hemipenis. There are several dozen small spines and several relatively large spines, slightly hooked, below the capitulum, with the largest spines originating near the base of the spinose area on the asulcate side of the organ. The asulcate edge of the capitulum overhangs a shallow nude space that, in the retracted organ only, is divided by a low ridge of tissue that extends either to the base of one of the large spines or into a nude strip between two parallel rows of spines. Each of the rows consists of about eight medium-sized spines, which gradually increase in size toward the base, then a large spine and, at the base of the row, another medium-sized spine. The nude space between the two rows of spines becomes a conspicuously broader, flat place when the organ is everted, and the arrangement of the spines is more evident (compare fig. 30D with 30E). The basal third of the hemipenis lacks ornamentation save for inconspicuous spinules. There is a

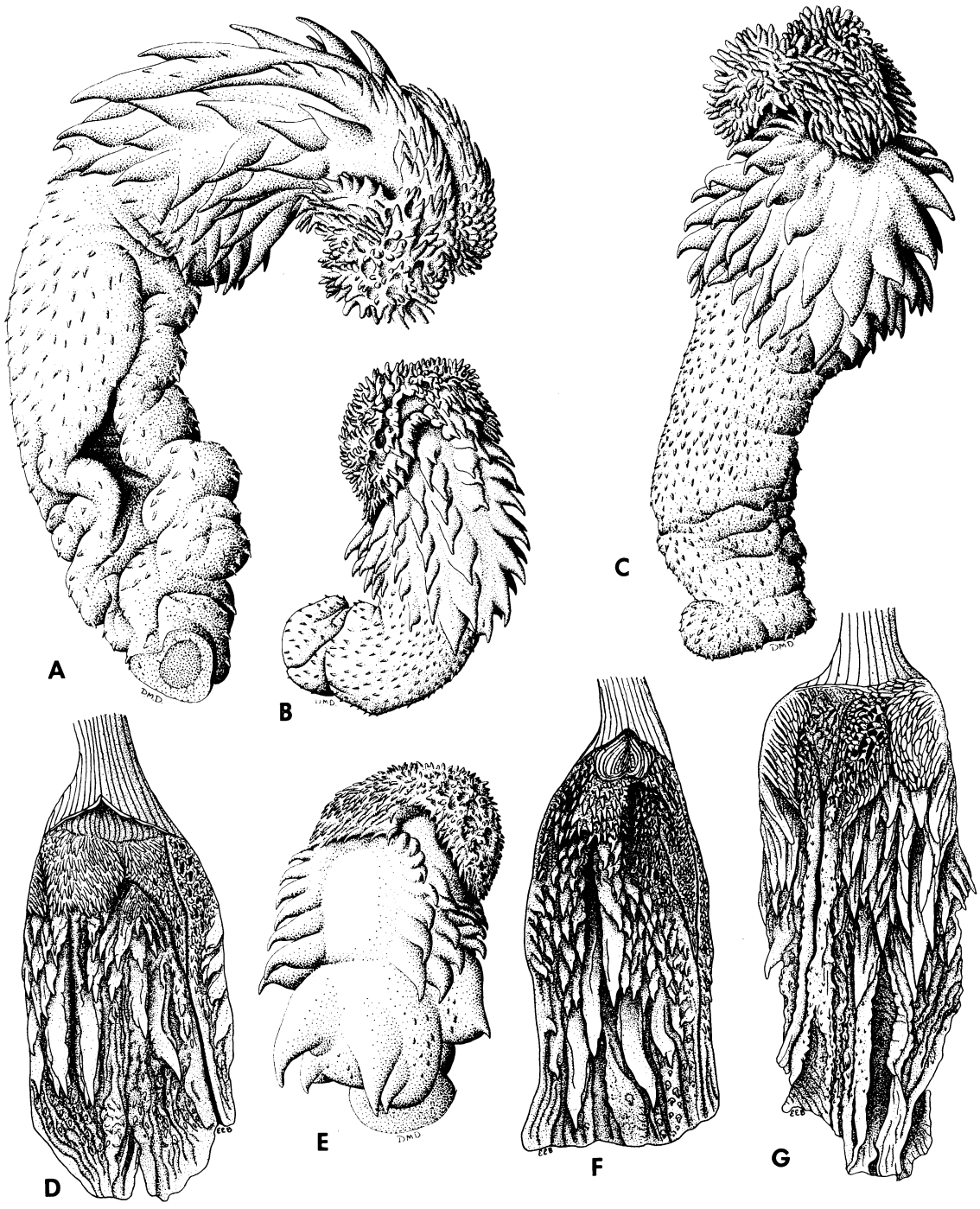


FIG. 30. Hemipenes of the *godmani* group. A. *Rhadinaea montecristi*, KU 63870, right organ. ×10. B. *R. godmani*, KU 75748, right organ. ×6. C. *R. lachrymans*, UMMZ 107325, right organ. ×9. D, E. *R. hannsteini*, right retracted organ of UMMZ 98753, ×11, and right everted organ of MCZ 53778, ×10. F. *R. pilonaorum*, FMNH 64951, right organ. ×11. G. *R. schistosa*, FMNH 100298, left organ. ×12.

basal naked pocket on the dorsal wall of the retracted hemipenis, but it is not evident on the everted hemipenis. The preceding description is based on retracted hemipenes from UMMZ 98753 (right organ illustrated), 106700, 106701, and on the everted right organ of MCZ 53778 (illustrated).

REMARKS: Stuart found the type specimens while raking in mulch on the ground of a coffee *finca*. He named the species in honor of his host, Walter Hannstein.

Rhadinaea hempsteadae Stuart and Bailey

Figures 2A, 26D, 28K–M, 31; map 10

Rhadinaea hempsteadae STUART AND BAILEY, 1941, pp. 2–4. STUART, 1963, p. 113. PETERS AND OREJAS-MIRANDA, 1970, p. 265.

Rhadinaea stadelmani STUART AND BAILEY, 1941, pp. 4–6 (holotype: UMMZ 89078, from Todos Santos, 8000 feet elevation, Departamento Huehuetenango, Guatemala; Raymond Stadelman collector). STUART, 1963, p. 113. PETERS AND OREJAS-MIRANDA, 1970, p. 268. New synonymy.

HOLOTYPE: UMMZ 89080, an adult male from the cloud forest zone at approximately 5700 feet [1738 meters] elevation, above Finca Chichén, Departamento Alta Verapaz, Guatemala; caught by L. C. Stuart on May 26, 1940. Finca Chichén is in the pine zone about 10 kilometers (airline) south and slightly east of Cobán (*fide* Stuart and Bailey, 1941, p. 2).

DIAGNOSIS: *Rhadinaea hempsteadae* normally has 19–19–19 rows of scales, which distinguishes it from all other species of *Rhadinaea* except the geographically separated *R. montecristi* and *R. serperaster*, which are less variable in pattern than *hempsteadae* and which seem invariably to be much more boldly striped (see fig. 28).

Some specimens of *R. hempsteadae* have 21 rows of scales at midbody and might be confused with *R. godmani*, which usually has 21 rows throughout. Such specimens are best assigned on the basis of locality if possible, although *hempsteadae* and *godmani* may be sympatric on the Meseta Central of Chiapas. It seems possible that at least limited gene exchange might occur between these species. One aspect of color pattern—a line of pale dashes on the side of the body—has not been observed in *R. godmani*, but these markings also are evidently absent in some populations of *hempsteadae*.

DISTRIBUTION: Oak-pine and cloud forests from western Chiapas, Mexico to central Guatemala, mostly north of the subhumid corridor (see below), at known elevations of 1200–2600 meters. The highlands occupied are, from west to east, the Meseta Central de Chiapas, the Montañas de Cuilco, the Sierra de los Cuchumatanes, and the mountains of the Alta Verapaz. Of the foregoing, only the Montañas de Cuilco lie south of the subhumid corridor (described by Stuart, 1954c) that occupies a series of tectonic depressions from the Valley of Chiapas (Río Grijalva) through the Negro and upper Montagua valleys of central and eastern (Caribbean) Guatemala.

DESCRIPTION (15 SPECIMENS): The largest individual is a female 593 mm. total length, 162 mm. tail length; the largest male is 490 mm. total, 156 mm. tail length. The tail is 30.6–32.8 percent of total length in males and 24.3–29.4 percent in females. The dorsal scales are usually in 19–19–19 rows, but in two specimens (UAZ 26581 and UMMZ 127272) the formula is 19–21–19; I recorded a count of ?–21–20 in a damaged juvenile (UMMZ 120014). Scale row increment from 19 to 21 rows involves a division of row 3 (forming a new fourth row), and reduction from 21 to 19 rows occurs by the reverse fusion of rows 3 and 4. In UMMZ 127272 for example, row 3 divides at the level of ventrals 42/52 and the reverse fusion occurs at ventrals 77/87. The situation is more irregular in UAZ 26581, as follows:

$$19 \frac{\div 3\,(33)}{\div 3\,(33)}\ 21\ \frac{3+4\,(96)}{3+4\,(119)}\ 19\ \underline{\div 3(127)}\ 20\ \underline{3+4\,(128)}\ 19\ (=168)$$

In addition, the above specimen has many divisions of the paravertebral rows, but in each case reverse fusion occurs within a distance of only one to three ventrals and new rows of normal-sized scales are not formed. Enumeration of the paravertebral changes would have little purpose; suffice it to state that such changes are staggered along both sides of the body and that a scale count made at the place of such a change, near midbody, will give a maximum count of 22 rows.

Anal ridges are absent. There are 162–189 ventrals (162–174, males; 168–189, females) and 74–94 subcaudals (89–94, males; 74–82, females). There are eight supralabials, and also eight infralabials (8/9, 9/10, two specimens). There is one preocular, no subpreocular, two postoculars, and 1+2 temporals.

The ground color of preserved material varies from light, rich brown to dark grayish brown, and the pattern is likewise variable. All specimens examined have a blackish vertebral line, although this is very faint on a few individuals and, on one (JFC 66–60; figs. 28K, 31) the line is continuous only on the neck and is posteriorly reduced to a series of dots on the apexes of the vertebral scales; the dark line may be narrow and confined to the middle of the vertebral row or wider and overlapped onto the edges of the paravertebral rows. A dorsolateral dark line is present or absent, between rows 6 and 7 or on row 7; one individual (UMMZ 89079) has an additional, darker line between rows 7 and 8. Most specimens (12 of 15) have a dark lateral line that usually occupies the lower three-quarters of row 4 and which often overlaps onto the top of row 3. The lateral dark line usually is bordered along its upper edge by a series of whitish dashes on the top of row 4, and in most cases there is an additional row of dashes, staggered with the others, along the bottom edge of row 5; in a few cases only the upper row of dashes is present, or the dashes may be confluent and form a vague line. A specimen (UMMZ 127272) with 19–21–19 scale rows has the lateral dark line on row 5 at midbody, where the double row of staggered dashes is on rows 5 and 6. A few specimens with 19 rows of scales throughout have the lateral dark line on the lower part of row 5 and a single series of pale dashes along the middle of the same row. The sides of the body below the lateral line may be either perceptibly lighter or darker than the ground color of the dorsum. UMMZ 89081 has a pale dot on the base of each scale in row 2. The linear markings become vague on the tail and disappear well before the tip.

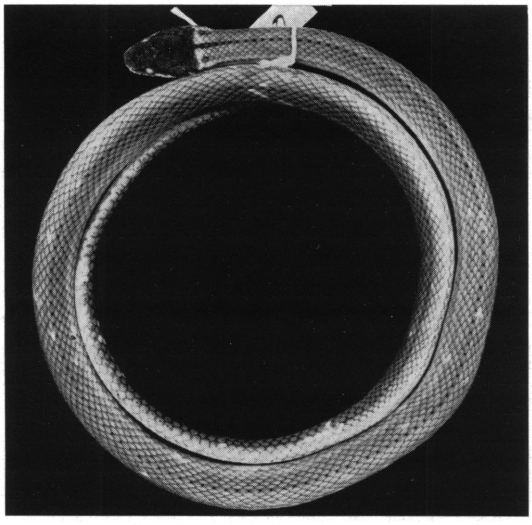


FIG. 31. *Rhadinaea hempsteadae*, JFC 66-60, a specimen from Chiapas. Relationship of this species to *R. godmani* needs further investigation.

Three of the 15 specimens (JFC 66–60, UAZ 26581, UMMZ uncatalogued specimen [field no. LCS 182]) lack dorsolateral and lateral dark lines and pale dashes, and have the vertebral dark line very faint and even broken. Although there is some vague dark edging on the lower scale rows, these specimens seem nearly unicolor in general aspect; they are females, but the male holotype is similar, except for a faint dark line and row of pale dashes on row 5, and such lack of pattern seems geographically rather than sexually correlated.

The top of the head is little darker than the body in some specimens, whereas in others the head is conspicuously blackish brown from the edge of the rostral back to the first or second scale on the neck. Several individuals have a pair of variably sized, poorly defined, yellowish brown nape spots, one on each side of the vertebral dark line, just behind the dark head. There is a small white spot, or else a short white bar that is confluent with the pale throat, just behind the angle of the jaws. A pair of pale parietal dots is present or absent. In several specimens, approximately the posterior third of the frontal plate is pale yellowish brown, except for a blackish median strip. The edges of the rostral plate are pale, thus enclosing a ∩-shaped dark marking. The dark coloring of the head encroaches onto the tops and along the sutures of the anterior supralabials; as these plates are often edged with black along the lower edges, the white ground color may be reduced to a spot on each supralabial in front of the eye. The posterior labials are dark or mostly so, except for a usually conspicuous oblique, white line across labials 6 and 7, from the lower edge of the eye to the corner of the mouth; there is no apparent postocular line on UMMZ 89081 because the lower dark edge is lacking. The underside of the head is white except for some small spots or dark smudging along the edges of the mouth, especially on the mental and anterior infralabials. The

ventral surfaces are white or pale yellowish, in a few cases with some scattered and inconspicuous dark specks. The ventrals and subcaudals are weakly to strongly tipped with brown coloring from the sides of the body; a few individuals (UMMZ 127273, 127275) have these plates edged with very dark pigment, which thus appears as a distinct ventrolateral line.

On the basis of preserved material alone, it is evident that there is considerable variation in the dorsal hue. This is borne out by color descriptions of two specimens from life: The holotype was reddish brown dorsally; the labial spots and postocular line were bright yellow and the ventral surfaces were lemon yellow (Stuart and Bailey, 1941). Charles J. Cole (field notes for UAZ 26581) noted that a Chiapas specimen had a brown head that was sharply demarcated from the olive-brown body. The supralabials and underside of the head were light yellow; the venter was yellow, being brightest on the proximal half of the tail. There was a light tan smudge on the posterolateral corners of most ventrals. The iris was brown with light flecks, except for an orangish gold patch dorsally.

There are 17 to 19 maxillary teeth, the anterior of which are subequal and the last several of which are enlarged and heavier. The last three teeth lie posterior to the front edge of the ectopterygoid process. A small gap, no greater than the length of an adjacent socket, is sometimes present before and/or behind the third tooth from the rear. The ultimate tooth is in line with the others, not offset.

The hemipenis is long and slender and has a slight bilobation that is probably discernible even when the organ is everted. One retracted *in situ* hemipenis extended to the end of subcaudal 13 and was bifurcated from the end of subcaudal 12; the two slips of retractor muscle merged at the middle of subcaudal 15 and the muscle originated at subcaudal 45; the other retractor muscle of the same specimen originated at subcaudal 48. The retractor muscles of a specimen with partly everted hemipenes originated at subcaudals 46. The capitulum comprises about one-third of the length of the organ on its sulcate side. The lobes of the capitulum are roughly one-seventh the length of the retracted hemipenis. The sulcus spermaticus forks below the basal edge of the capitulum and the branches extend virtually to the tips of the lobes. The calyces are spinulate around the base of the capitulum and papillate above; the calyces on the asulcate fold are larger than the others and bear elongated, slightly recurved spinules. The wall of the capitulum forms a single, poorly defined fold on the asulcate side, except that the basalmost calyx is much larger than all the others and causes the fold to seem doubled at the base. The very large basal calyx possibly forms a conspicuous nude pocket when the hemipenis is everted, and there is a similar but somewhat smaller pocket on each side and slightly distad of the large one. The large calyx and its fringe of elongated spinules form a conspicuous overhang, which is divided underneath by a thin partition of tissue that is continuous with a short, partly double row of several small spines that lie basad of the edge of the capitulum. This row of small spines causes a short break in the top of a relatively large naked area on the asulcate side of the hemipenis. There is an ornamentation of small to medium, slightly recurved spines on each side of and below the naked area; there are in excess of 50 such spines, which are largest toward the asulcate side. More than half of the organ, the basal part, is adorned only with inconspicuous spinules. There is a long, basal naked pocket on the dorsal wall for about half of the length of the retracted organ; the pocket forms a rather broad, conspicuous groove on one side of the everted organ. The preceding description is based on the left retracted hemipenis of UMMZ 127274 and on the basal halves of the partially everted organs of UMMZ 127272.

Geographic Variation: The holotype and paratype of *Rhadinaea hempsteadae*, both from the same area in central Guatemala, are the only specimens that have the lateral dark line (which is faint on the holotype) on row 5 rather than on row 4, not counting a specimen on which the line is raised because of an increase in scale rows (from 19 to 21) at midbody.

The three specimens that have nearly unicolored bodies (see Description) come from opposite ends of the known range—from Chiapas (JFC 66–60, UAZ 26581) and from Finca Volcán, Alta Verapaz (UMMZ uncatalogued specimen); the holotype also has little pattern and is from near the eastern end of the known range, although the topotypic paratype has distinct lines. The remaining specimens, including all of those with dorsolateral dark lines, have relatively strong patterns and are from the Montañas de Cuilco and the Sierra de

los Cuchumatanes, in Departamento Huehuetenango.

Also, specimens from opposite ends of the known range seem to have lower numbers of ventrals, although data are scant. The male types of *hempsteadae* from near the eastern end of the range (in Alta Verapaz) have 162 and 165 ventrals, whereas three males from the Montañas de Cuilco have 169–174 ventrals. Two females from the western end of the range (Chiapas) have 168 and 169 ventrals, whereas six females from the Montañas de Cuilco and the Sierra de los Cuchumatanes have 177–189 ventrals. Elevation does not seem to be much of a factor as the Chiapas specimens are from one of the highest localities and the Alta Verapaz specimens are from among the lowest localities.

REMARKS: My preconceived notion of the distribution of *Rhadinaea hempsteadae* was altered by a series of specimens (UMMZ 127271–127276) obtained by L. C. Stuart in the Montañas de Cuilco, where I would have expected *Rhadinaea godmani* instead. These mountains near the Mexican border lie south of the Río Selegua, which is one of the narrowest parts in the subhumid corridor that cuts through Chiapas and central Guatemala (Stuart, 1954c). L. C. Stuart informed me (*in litt.*) that, "the fauna of the Montañas de Cuilco shows a number of relationships to that of the wet Caribbean slopes of the Mesa Central of Chiapas."

Two names have been proposed for this species, by the same authors in the same paper (Stuart and Bailey, 1941). As first reviser I choose *Rhadinaea hempsteadae* as the valid name, primarily because its holotype is an adult male, whereas the name *Rhadinaea stadelmani* is based on a juvenile female. Supposed diagnostic characters (Stuart and Bailey, 1941; Stuart, 1963, p. 112) are now thought to be based on geographic variation in color pattern and on geographic variation and sexual dimorphism in numbers of ventrals and subcaudals (the types of *hempsteadae* are males and those of *stadelmani* are females). L. C. Stuart (*in litt.*) concurs with this conclusion, at which we arrived independently.

The species is known from pine forest and cloud forest in Guatemala, where specimens were found under a log in a cleared *milpa* and under wood chips in a forest (Stuart and Bailey, 1941, pp. 4, 6). A specimen from Chiapas was found in a damp situation under a pine log in pine-oak forest (Charles J. Cole, field notes for UAZ 26581). The only other Chiapan specimen (JFC 66–60) is from the same forest, which was characterized by the collector (Dennis E. Breedlove, *fide* Joseph R. Copp *in litt.*) as a very open forest on gentle slope, at about 7800 feet [2378 meters] of elevation, with the following vegetation: *Pinus ayacahuite*, *P. michoacana*, *P. montezumae*, *P. oaxacana*, and *P. pseudostrobus*; *Quercus corrugata*, *Q. crassifolia*, *Q. mexicana*, and *Q. rugosa*; *Buddleia skutchii*, and *Arbutus xalapensis*.

The holotype contained an arboreal salamander (*Bolitoglossa helmrichi*), which led Stuart and Bailey (1941, p. 4) to suggest that *Rhadinaea hempsteadae* may climb to some extent at night. Stuart (1948, p. 73) later stated that *hempsteadae* appears to be secretive and terrestrial and that the salamander record was difficult to explain, but even arboreal salamanders must come to the ground once in a while.

The specific epithet was a dedication to Mrs. R. W. Hempstead, of Cobán, Guatemala, in recognition of courtesies rendered to L. C. Stuart in the course of his investigations on the fauna of Alta Verapaz.

Some additional comments on *Rhadinaea hempsteadae* are to be found in the Remarks section under *R. godmani*.

Rhadinaea kinkelini Boettger

Figures 27B, 29E; map 11

Rhadinaea kinkelini BOETTGER, 1898, p. 68. WERNER, 1929, p. 118. DUNN, 1932, p. 2. PETERS AND OREJAS-MIRANDA, 1970, p. 266.

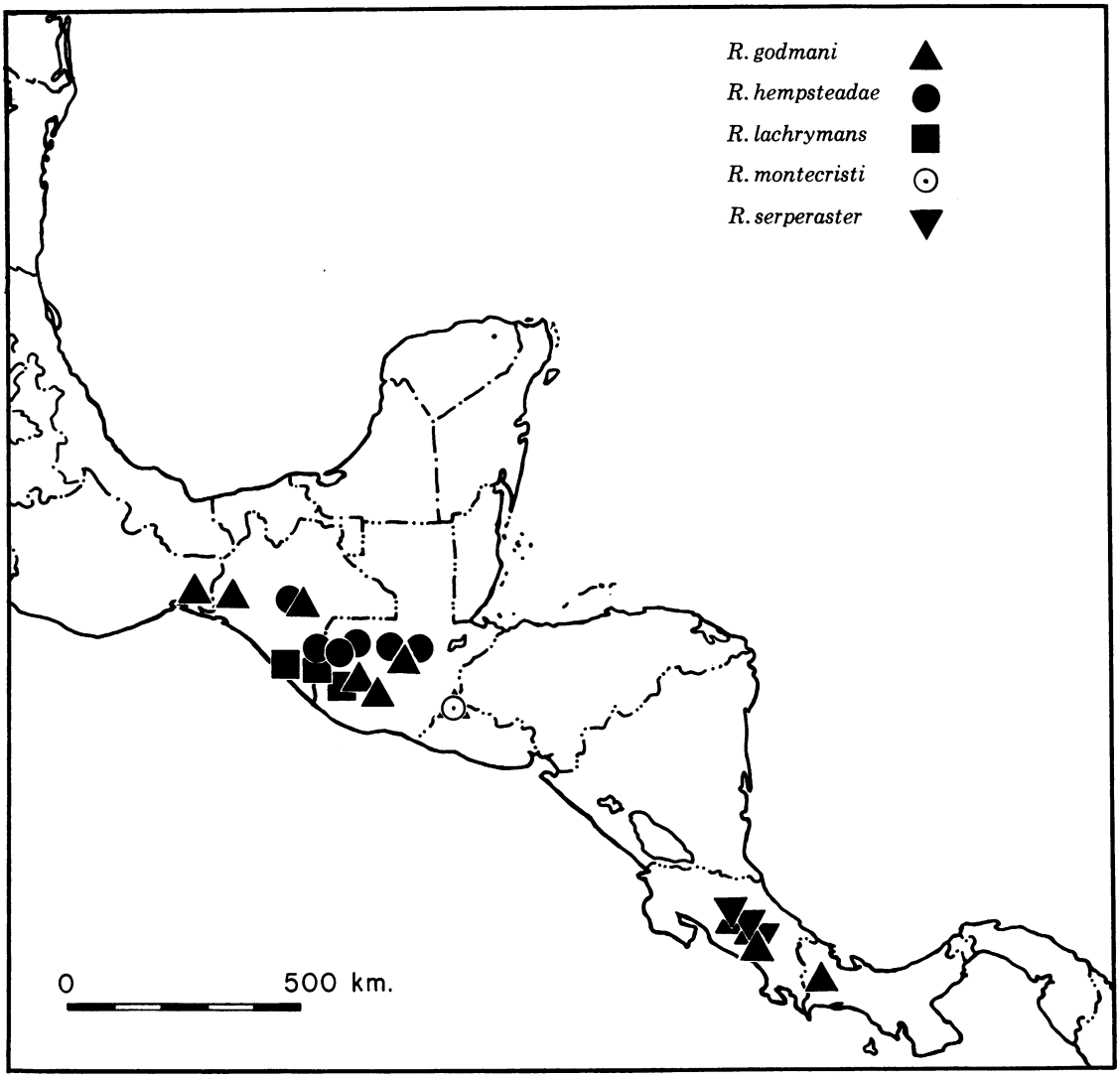
Liophis kinkelini (Boettger): AMARAL, 1929b, p. 172.

Rhadinaea veraepacis STUART AND BAILEY, 1941, pp. 10, 11 (holotype: UMMZ 89077, from pine zone at 5100 feet elevation, Finca Chichén, Dept. Alta Verapaz, Guatemala; L. C. Stuart collector). New synonymy.

Trimetopon veraepacis (Stuart and Bailey): STUART, 1949, p. 167; 1963, p. 122. PETERS AND OREJAS-MIRANDA, 1970, p. 309.

HOLOTYPE: SMF 8178, 1a (not seen), from Matagalpa, Nicaragua, obtained by Adolf Kinkelin in 1897.

DIAGNOSIS: *Rhadinaea kinkelini* is a small brownish snake with a pale, broken neck-ring, a dark vertebral line, and several additional lines or stripes on each side. *Rhadinaea kinkelini* differs from *R. hannsteini*, a close relative, in having two (not one) postoculars, in having much of the frontal plate paler than the rest of the head, and

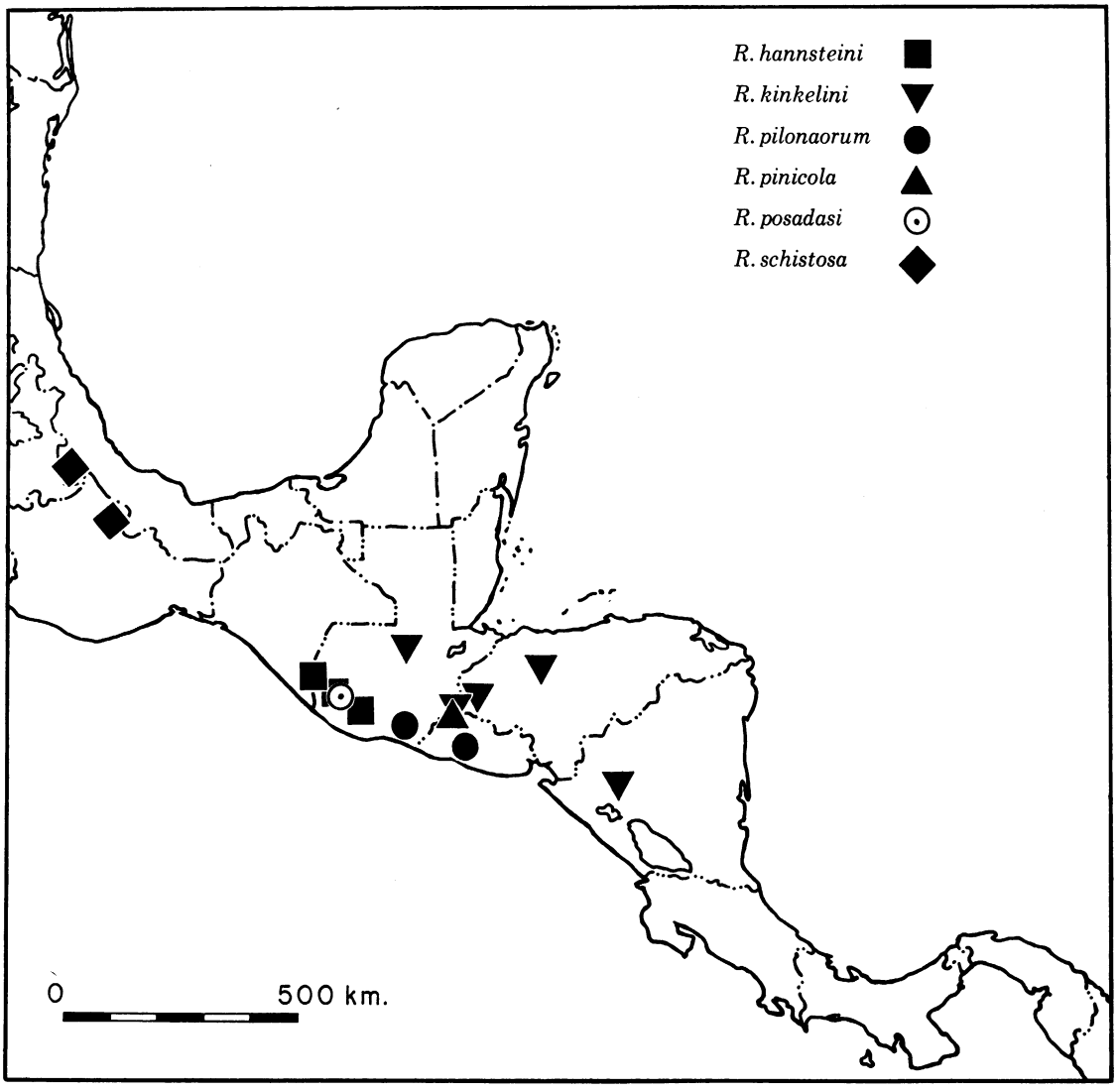


MAP 10. Locality records for large species of the *godmani* group.

in details of the body pattern (figs. 27, 29). *Rhadinaea kinkelini* is distinguishable from all other members of the *godmani* group except *R. pinicola* by the same criteria given for *R. hannsteini* (*q.v.*); *R. pinicola* has similar scutellation but a different pattern, including a pale line or series of dashes on the fifth scale row.

DISTRIBUTION: The pine-oak zone and cloud forest, in the mountain complexes from central Guatemala (Alta Verapaz) through Honduras and northwestern El Salvador to northern Nicaragua. Specimens have been taken at 2200 meters elevation in El Salvador and at about 1550 meters in Guatemala.

DESCRIPTION (FIVE SPECIMENS): The largest specimen examined is a male 350 mm. total length, 103 mm. tail length; a female is 255 mm. total, 66 mm. tail length. These specimens are probably adults because of the well-developed hemipenes of the male and the presence of anal ridges on both the male and female. The tail is 29.4–32.4 percent of total length in males and 25.9 percent in a female. The dorsal scales are in 17–17–17 rows; anal ridges are present on three



MAP 11. Locality records for small species of the *godmani* group.

males and one female. There are 136–163 ventrals (136–148, males; 161, 163, females) and 73–83 subcaudals (81–83, males; 73, female). There are eight supralabials and eight infralabials, except for KU 63866 which has only six infralabials as a result of fusion of plates 3–5. There is one preocular, no subpreocular, two postoculars, and 1+2 temporals (1+1+2 on one side of one specimen).

The body is pale brown or tan with a complex pattern of darker brown lines and stripes. The primary (i.e., darkest) markings are a median line that is either confined to the middle of the vertebral row or overlapped slightly onto the paravertebral rows, and a lateral stripe on row 4 and adjacent edges of rows 3 and 5. The primary lateral stripe tends to be broken by a central series of pale dashes on row 4. There is at least a tendency (in the few specimens seen) for secondary brown lines on the adjacent edges of the ventrals and row 1, and on the adjacent edges of rows 1–2, 2–3, 5–6, 6–7, and 7–8. Certain neighboring lines—those on rows 1–2 and 2–3, and especially those on rows 5–6 and 6–7—may

show a tendency toward fusion into broader stripes. The line on rows 7–8 is virtually absent on some specimens, whereas the line on rows 6–7 may be nearly as dark as the primary markings. The line on rows 1–2 may also be nearly as dark as the primary lateral stripe.

Immediately behind the head is a pale yellowish or whitish neck-ring, about two scales wide, that is interrupted by the vertebral line. The top and upper sides of the head are mostly dark brown, with an inconspicuous sprinkling of tiny yellowish markings; but the posterior three-quarters of the frontal plate are conspicuously pale yellowish or whitish and bisected by an anterior extension of the dark vertebral line. The extreme tip of the snout is pale, with a ∩-shaped dark brown marking on the rostral plate. The supralabials are dark brown, with a pale yellowish or whitish spot on each of the first seven; in some specimens, the pale markings on labials 6 and 7 are fused to form an oblique postocular line from the eye to the corner of the mouth. The whitish ventral surfaces are unmarked, except for brown spots or smudges on the mental and infralabials and the dark tips of the ventral and subcaudal plates.

Color notes on a Honduran specimen (LSU 23828) obtained by John R. Meyer and Larry D. Wilson reveal that there is more than one ground color in the interspaces between the dark lines on the body: The ground color of the lower sides (rows 1–3) was yellowish cream, row 5 was tan, and the dorsum between the sixth row on each side was brown. The neck-ring was tan; the supralabial spots, the chin, and the posterior ventral surface were cream, whereas the anterior surface of the venter was creamy yellow. Data from L. D. Wilson, *in litt.* (since published by Meyer and Wilson, "1971" [1972]).

There are 16 teeth on a maxilla from each of four specimens. The teeth increase in size posteriorly and the last several are noticeably enlarged, but not abruptly so. The last three teeth are posterior to the front edge of the ectopterygoid process. The last two teeth are close-set but there is no real diastema, although there is a slight gap (less than the length of a single socket) both before and behind the third tooth from the rear. The ultimate tooth is in line with the others, not offset.

The retracted hemipenis extends to subcaudal 8 (FMNH 34739) or 10 (UMMZ 89077) and the everted organ to subcaudal 6; the retractor muscle originates at the level of subcaudal 23 or 25. The hemipenis is slightly bilobate, but the short division may be difficult to detect until the overlying mesentery is teased away. The capitulum comprises between one-third and one-half of the hemipenis on its sulcate side. The calyces are spinulate on the asulcate fold (retracted condition) and on the free edge of the capitulum, and papillate elsewhere. The sulcus spermaticus forks near the edge of the capitulum and the branches extend to the tip of the retracted organ, but only about halfway up the capitulum when the organ is everted. The wall of the capitulum forms a double fold on the asulcate side of the uneverted hemipenis. There are nearly 50 small spines and several relatively large spines, slightly hooked, below the capitulum, with the largest spines originating near the base of the spinose area on the asulcate side. The asulcate side of the capitulum overhangs a shallow nude space that, in the retracted organ only, is divided by a low ridge of tissue that extends part way down into a nude strip between two parallel rows of spines. Each of these rows consists of about six medium-sized spines, which gradually increase in size toward the base of the organ, then two large spines, the basalmost of which is slightly smaller than the upper one. The nude space between the two rows of spines becomes a conspicuously broader, flat place when the organ is everted, and the arrangement of the spines is more evident. (Reference can be made to the illustrations of the very similar hemipenis of *Rhadinaea hannsteini* [fig. 30D, E], which differs only slightly in the arrangement and number of small spines on the side of the organ and in having an undivided asulcate fold when the organ is retracted.) The basal third of the hemipenis lacks ornamentation except for inconspicuous spinules. There is a basal naked pocket on the dorsal wall of the retracted hemipenis, but it is not evident on the everted organ. The preceding description is based on the right everted hemipenis of LSU 23828 and the left retracted organ of FMNH 34739, and on less complete notes on a retracted organ from a juvenile specimen, UMMZ 89077.

REMARKS: *Rhadinaea kinkelini* is here envisaged as a species that occupies a rather large but probably interrupted range in the Central American highlands, north of the Nicaraguan Depression. Unfortunately I have been unable

to examine the holotype, which is from northern Nicaragua, but Boettger's description reasonably fits several specimens of small snakes, including the holotype of *R. veraepacis* Stuart and Bailey, from northern Central America. Jánis Roze compared my midbody drawing of the holotype of *veraepacis* (fig. 29E) with the holotype of *kinkelini* in the Senckenberg Museum, and reported that the patterns are very similar but not quite equal. Roze's sketch of the pattern of *kinkelini* shows that the line at the top of row 1 is about as dark as the primary stripe that is centered on row 4, and that the latter marking is uniformly dark. The intensity of the lateral markings is somewhat variable in the northern specimens, all of which, however, have a series of pale dashes breaking the primary stripe on row 4. Nevertheless, my sample is small and I am inclined to think of the presence or absence of the pale dashes as a character that is probably subject to intraspecific variation. Boettger does not mention the posterior part of the frontal plate as being unusually pale, but an outline sketch of the head by Roze shows a large, median pale area that is bisected by an anterior extension of the dark vertebral line; this marking is conspicuous on the northern specimens. Boettger's mention of two closely spaced "weisse Fleckchen" on the parietals presumably refers to a pair of parietal dots (not the frontal blotches), the presence or absence of which is a variable feature in *Rhadinaea*. The name *Rhadinaea veraepacis* is here placed in synonymy with the same "hesitation" used by Stuart and Bailey in proposing the name. The alternative would be to consider *veraepacis* and *kinkelini* as distinct albeit related species that cannot be satisfactorily diagnosed with available data.

One specimen, the holotype of *R. veraepacis*, was found "ensnared in a spider-web in the hacienda at Finca Chichén, which lies in the heart of the pine zone of the Alta Verapaz" (Stuart and Bailey, 1941, p. 11). A Honduran specimen (LSU 23828) is from a region having "vestiges of cloud forest . . . [and] came from underneath a log in a pasture at the edge of the forest" (Larry D. Wilson, *in litt.*). Two specimens (KU 63866, 63867) from El Salvador were obtained by William E. Duellman at Hacienda Monte Cristo, 2200 meters, a locality described by Uzzell and Starrett (1958, p. 339) as virgin cloud forest except where cleared for pasture. The type locality of *R. kinkelini* is given as Matagalpa, Nicaragua, but I suspect that the specimen actually came from humid montane forest above the town. Matagalpa is nestled in the foothills of the Cordillera Dariense, at 720 meters according to my altimeter, and the environment is relatively xeric compared with the forest above. The species was named for the collector, Adolf Kinkelin, a pharmacist from Nürnberg.

Rhadinaea lachrymans (Cope)

Figures 1A, 26A, 28A, B, 30C; map 10

Lygophis lachrymans Cope, "1869" [1870?], p. 154.
Rhadinaea lachrymans (Cope): Cope, 1875a, p. 140; 1887, p. 80; 1900, pp. 758, 759. Boulenger, 1894b, p. 174. Werner, 1929, p. 119. Dunn, 1932, p. 2. Bailey, 1940, pp. 6, 7, pl. 1, fig. 4 (midbody pattern of FMNH 20337). Smith and Taylor, 1945, p. 118. Alvarez del Toro, 1960, p. 202 (listed only, and misspelled "*lachrymosa*"). Stuart, 1963, p. 113. Peters and Orejas-Miranda, 1970, p. 266.
Dromicus lachrymans (Cope): Günther, 1894 (1885–1902), p. 114.
Liophis lachrymans (Cope): Amaral, 1929b, p. 172.

Holotype: ANSP 5539, an adult female in fair condition; F. Sumichrast collector. I agree with Bailey (1940, pp. 6, 7) that, "The type locality given by Cope (1900: 759) as Orizaba, on the basis of Sumichrast's memory, is doubtless erroneous. The type probably came from Chiapas." The holotype has 172 ventrals, two preventrals, and 77 subcaudals.

Diagnosis: *Rhadinaea lachrymans* is easily distinguished from other members of the *godmani* group in having 17 rows of scales in combination with heavy lateral and ventrolateral stripes (see fig. 28A, B).

Rhadinaea montecristi has a very similar pattern but 19 rows of scales. *Rhadinaea lachrymans* frequently has a dark vertebral line, and some individuals have additional dark lines between certain scale rows. It is conceivable that such specimens, at least if juvenile, might be confused with the diminutive *R. hannsteini* or *R. kinkelini*. However, the patterns are by no means identical and comparison of the midbody illustrations will allow proper identification. In addition, *R. hannsteini* has only a single postocular.

Distribution: The Pacific versant of the Sierra Madre of western Guatemala and Chiapas, Mexico, in the pine-oak zone at known elevations of 1050–2637 meters.

Description (37 specimens): The largest

female is 493 mm. total length, 117 mm. tail length; the largest male is 454 mm. total, 133 mm. tail length. The tail is 26.5–30.7 percent of total length in males and 23.3–28.4 percent in females. The dorsal scales are in 17–17–17 rows; anal ridges are absent. There are 154–183 ventrals (154–170, males; 160–183, females), and 61–89 subcaudals (75–89, males; 61–77, females). There are eight supralabials and eight or nine (or occasionally 10 on one side) infralabials. There is one preocular, no subpreocular, two postoculars (2/3 in one specimen), and 1+2 temporals (1+1+2 in one specimen).

The middorsum of the body (the median five or seven scale rows) is medium or dark brown. There is a blackish vertebral line or row of dots on the bases of the vertebral scales. Some specimens have a narrow blackish line on the adjacent edges of rows 6 and 7 or on the outer edge of row 7; this line occurs independently of whether the median seven or only the median five rows of scales are dark brown, although in the latter case the dark middorsum is confined by the dark line on each side. In some cases there are also vague dark lines between rows 5 and 6, and 7 and 8. The ground color of the sides is paler brown and there are two conspicuous, blackish brown stripes: A lateral stripe, which is variable in width, may extend from the middle of row 2 onto the lower three-fourths of row 4, or it may be as narrow as the upper part of row 3 and the adjacent half of row 4. The lateral stripe, when it is broad, is occasionally broken by a pale line on the middle of row 3, or it may be eroded by encroachment of pale areas from below; the upper edge of the lateral stripe is occasionally emphasized by a series of pale dashes on row 4. The other conspicuous blackish brown stripe is ventrolateral in position; it crosses the tips of the ventral plates and often extends onto the lower part of row 1. Sometimes there is a vague dark line between rows 1 and 2, and, if the lateral stripe is narrow, there may be a similar line between rows 2 and 3.

There are usually four poorly defined, pale spots immediately behind the dark head—one spot on each side of the vertebral dark line and another on each side of the neck. Occasionally, the spots are fused on each side, forming a narrow neck-ring that is broken by the vertebral dark line; a whitish bar that extends a short distance dorsad from the throat, just behind the mouth, may also become part of the neck-ring. The top of the head is dark brown, sometimes unicolor, but usually the posterior one-third to three-fourths of the frontal plate bears a pale yellowish or whitish area that is divided by a dark median streak (an anterior extension of the vertebral dark line). The rostral plate is pale, and usually has a ∩-shaped dark marking. The anterior supralabials may be mostly white, with some dark dots or a horizontal dark line, or they may be blackish with a white spot on each. The posterior supralabials are dark, except for an oblique whitish postocular stripe that has blackish edges and extends across the sixth and seventh labials, from the eye to the corner of the mouth. The underside of the head is whitish, either immaculate or with inconspicuous dark dots on the infralabials, especially the anterior ones. The venter is whitish and unmarked, except for the ventrolateral stripe and, occasionally, a line of dark dots or a dark zigzag line under the middle of the tail. The color in life has not been reported.

There are 18 to 21 maxillary teeth, which are subequal except for the last several which are enlarged and heavier. The last three teeth lie posterior to the front edge of the ectopterygoid process. A tiny gap, no greater than the length of an adjacent socket, is in some cases present either before or behind the third tooth from the rear. The ultimate tooth is in line with the others, not offset.

The hemipenis is long and slender and has a slight bilobation that is discernible even when the organ is everted. One everted hemipenis extended *in situ* to the level of subcaudal 13 and the retractor muscle originated at subcaudal 39. The capitulum comprises about a third of the length of the organ on its sulcate side. The lobes of the capitulum comprise less than a tenth the length of the retracted organ. The calyces are spinulate around the base of the capitulum and papillate above; the calyces on the asulcate fold bear elongated, slightly recurved spinules that form a conspicuous cluster even when the organ is everted. The sulcus spermaticus forks just below the edge of the capitulum and a branch extends virtually to the tip of each lobe, regardless of whether the organ is retracted or everted. The asulcate wall of the capitulum forms a weak fold that is doubled in the middle; the cluster of elongated spinules on the base of the fold project down from the capitulum in a conspicuous overhang. There is a relatively large nude space

below this overhang, in the midst of a densely spinose area. There are approximately 50 medium-sized, slightly recurved spines, which are replaced by tiny spines on each side of the sulcus. The basal one-half or five-eighths of the hemipenis is adorned only with minute spinules. There is a basal naked pocket on the dorsal wall for nearly half the length of the retracted hemipenis; this "pocket" is a shallow groove on the everted organ and is conspicuous as much for its lack of spinules as for its depth. The preceding description is based on the retracted hemipenes of UIMNH 54847 and the right everted organ of UMMZ 107325 (illustrated).

GEOGRAPHIC VARIATION: The lateral dark stripe, and probably the ventrolateral stripe as well, tend to be wider in specimens from Guatemala than in specimens from Chiapas. In those from Chiapas the lateral stripe usually covers the upper part of row 3 and the lower half or three-quarters of row 4. In specimens from Guatemala this stripe usually extends from the middle or top of row 2 to the lower half or three-quarters of row 4. These differences are not absolute. For example, one specimen (CAS 67016) in a series of four, from Tecpán, Guatemala, has a narrow stripe (upper half of row 3 and adjacent three-quarters of row 4) like specimens from Chiapas. Vague dark lines between certain rows of scales (see Description) appear on more specimens from Chiapas than on ones from Guatemala.

REMARKS: Slevin (1939, pp. 395, 401) found four specimens under old boards and pieces of bark, in a region of oak, pine, and alder, with some open ridge country; this was at about 8650 feet [2637 meters], which is the highest reported elevation for the species. Slevin's (*op. cit.*, p. 401) snakes evidently were found in the same spot as several specimens of *Rhadinaea godmani*, an interesting case of sympatry in members of the same species group. In Chiapas, specimens have been found under and in rotten logs (Smith, 1943) and under a log at the edge of a corn field (Landy et al., 1966). No author has seen fit to mention the color of living specimens, so I presume that the ventral surfaces are probably uninteresting white or pale yellow in life.

The specific epithet is an alternative spelling of the Latin *lacrimans*, meaning "tearful," probably an allusion to the pale marking at the lower, rear edge of the eye (fig. 26A).

Rhadinaea montecristi Mertens

Figures 26B, 28C, 30A; map 10

Rhadinaea montecristi MERTENS, 1952b, pp. 136, 137; 1952c, pp. 71, 72, pl. 15, fig. 84 (photograph of anterior part of holotype, in lateral aspect). PETERS AND OREJAS-MIRANDA, 1970, p. 267.

HOLOTYPE: SMF 43188 (not seen), a male from Hacienda Monte Cristo, 2200 meters elevation, mountains of Metapán, Departamento Santa Ana, El Salvador; Adolf Zilch collector, August 26 or 27, 1951. The type locality is close to the Salvadoran border, a short distance southeast of the border junction with Honduras and Guatemala (Mertens, 1952c, map).

DIAGNOSIS: *Rhadinaea montecristi* differs from all of its congeners save *R. hempsteadae* and *R. serperaster* in having 19 scale rows. It differs from these two species in having very heavy lateral and ventrolateral stripes (see fig. 28C). The color pattern of the body is virtually identical with some specimens of *R. lachrymans*, which differs in having 17 scale rows and pale blotches on the rear of the frontal.

DISTRIBUTION: Known only from the type locality, at 2200 meters elevation in cloud forest in the extreme northwestern corner of El Salvador.

DESCRIPTION (32 SPECIMENS): The largest female is 555 mm. total length, 141 mm. tail length; the largest male is 447 mm. total, 134 mm. tail length. The tail is 28.3–31.2 percent of total length in males, 24.9–27.6 percent in females. The dorsal scales are in 19–19–19 rows. Anal ridges are present on adult males and frequently on females also. There are 158–176 ventrals (158–165, males; 164–176, females) and 71–87 subcaudals (79–87, males; 71–79, females). There are eight supralabials and also eight or occasionally nine infralabials (10/9 in one specimen). There is one or occasionally 2/1 preoculars, no subpreoculars, two or occasionally 2/1 or 1/2 postoculars, and 1+2 temporals.

The middorsum of the body (the median seven, nine, or 11 scale rows) is medium brown. There is usually a weak, blackish vertebral line. The ground color of the sides is whitish and there are two conspicuous, blackish stripes: A lateral stripe is positioned on row 3 and usually the adjacent halves of rows 2 and 4, but some individuals have this stripe shifted up on row 4,

or down on row 2, or even expanded in both directions. A narrower but nonetheless prominent ventrolateral stripe includes the ventral tips and the lower part of row 1. The ventrolateral stripe terminates at the cloaca but the lateral stripe extends to the end of the tail.

There is no obvious, pale collar or pale nape spots. A whitish bar or thin line extends a short distance anterodorsad from the throat, immediately behind the mouth, or this marking may be indicated only by a small, isolated white spot at the rear of the mouth. The top of the head is brown like the dorsum of the body, without pale blotches on the rear of the frontal but with a pair of pale parietal dots. The rostral plate has pale edges and a central ∩-shaped black marking. The anterior supralabials are mostly white, except for a black line that crosses the first several plates close to the mouth and, in some specimens, a dorsal black border that extends along the labials under the eye. An oblique, white postocular line or stripe extends across the sixth and seventh labials from the eye to the corner of the mouth; this marking owes its existence to conspicuous black borders, the lower of which tends to be the widest; the upper black border expands near the mouth and darkens most of the last supralabial and, in some specimens, is continuous with the lateral body stripe. The underside of the head is whitish. The infralabials have a variable amount of black dots and flecks, which tend to lie close to the lip and which are most concentrated anteriorly. The belly and subcaudal surfaces are immaculate white in some individuals, but usually there are a few scattered black dots, which in some cases tend to form a median line under the tail. On a few individuals with conspicuously dotted venters there is a tendency for the dots to form two parallel rows anteriorly.

Color transparencies taken by William E. Duellman indicate that, in life, the labials, postocular stripe, and lateral ground color between the black stripes are whitish (same as in preservative). The underside of the head is white and the rest of the ventral surfaces are bright yellow.

There are 19 to 23 maxillary teeth, which are subequal except for the last several which are enlarged and heavier. The last three teeth lie posterior to the front edge of the ectopterygoid process. A tiny gap, no larger than the length of an adjacent socket, often sets off the last two or the last three teeth, or sometimes there is a tiny gap both before and after the third tooth from the rear. The ultimate tooth is in line with the others or very nearly so and is not conspicuously offset.

The hemipenis is moderately long and slender and has a slight bilobation that is discernible even when the organ is everted. A retracted *in situ* hemipenis extended to the middle of subcaudal 11 and was bifurcated from the end of subcaudal 10; the two slips of retractor muscle merged at the end of subcaudal 11 and the muscle originated at subcaudal 38. The capitulum comprises less than one-third the length of the organ on its sulcate side. The lobes of the capitulum comprise about one-third its length in the retracted organ. The calyces are spinulate around the base of the capitulum and papillate above; the calyces on the asulcate fold bear elongated, slightly recurved spinules that form a conspicuous cluster even when the organ is everted. The sulcus spermaticus forks below the lower edge of the capitulum and a branch extends virtually to the tip of each lobe, regardless of whether the organ is retracted or everted. The asulcate wall of the capitulum forms a fold that is doubled in the middle section; the cluster of elongated spinules on the base of the fold project down from the capitulum in a conspicuous overhang that is firmly attached on its underside. Below this is a short row of several tiny spines that causes a short break in the top of a relatively large naked area on the asulcate side of the hemipenis. There is an ornamentation of small to medium-sized, slightly recurved spines on each side of and below the naked area; there are in excess of 50 such spines, which are largest toward the asulcate side. About half of the organ, the basal part, is ornamented only with minute spinules. There is a conspicuous basal naked pocket on the dorsal wall of the basal half of the retracted hemipenis, and the pocket remains conspicuous when the organ is everted. The preceding description is based on the left retracted hemipenis of KU 62113 and on the right everted organ of KU 63870 (illustrated).

REMARKS: *Rhadinaea montecristi* was described by Mertens on the basis of two specimens, which were thought to show closest affinity with *R. hempsteadae*, which agrees with *montecristi* in having 19 rows of scales. A large series of topotypes amply confirms the validity of *montecristi*, the types of which I have not seen, but, as noted by Uzzell and Starrett (1958), the color pattern

suggests that the species may be closest to *R. lachrymans* with 17 scale rows. Hemipenial structure bears out this relationship: The hemipenes of *lachrymans* and *montecristi* are quite similar, differing in details of length and in whether or not there is a short row of tiny spines in the naked space below the asulcate side of the capitulum. The hemipenis of *hempsteadae* is somewhat similar but differs importantly in the presence of several greatly enlarged calyces on the asulcate side of the capitulum.

The specific epithet is based on the name of the type locality, Hacienda Monte Cristo, which was described by Uzzell and Starrett (1958) as virgin cloud forest except where cleared for pasture.

Rhadinaea pilonaorum (Stuart), new combination

Figures 27D, 29B, 30F; map 11

Trimetopon posadasi (not of Slevin): MERTENS, 1952c, p. 76. RAND, 1957, p. 531. (Both references are based on FMNH 64951.)

Trimetopon piloñaorum STUART, 1954a, pp. 176, 177.

Trimetopon pilonaorum Stuart: STUART, 1963, p. 122. PETERS AND OREJAS-MIRANDA, 1970, p. 309 (tilde deleted, in accordance with International Commission . . ., 1964, art. 32c).

HOLOTYPE: UMMZ 102635, a female in good condition except that the lower jaws are mangled, from Finca La Gloria, about 950 meters elevation, approximately 12 kilometers (airline) northeast of Chiquimulilla, Departamento de Santa Rosa, Guatemala. Obtained by Antonio Piloña from an unnamed collector, about July 25, 1949.

DIAGNOSIS: This is a small, very slender, long-tailed *Rhadinaea*; there is an indication of a dark line on the vertebral scales, but the other dorsal scales have pale streaks on their centers. The body coloration is similar to that of *R. posadasi* and the shorter tailed *R. schistosa*. *Rhadinaea pilonaorum* is easily distinguished from the aforesaid species, and from all other of its congeners, in having a brown-mottled white head. No other species of *Rhadinaea* has a basically white head, although a dark body and white head is characteristic of occasional species of small snakes in other genera (including *Enulius*, *Geophis*, *Tantilla*, and *Trimetopon*).

DISTRIBUTION: Known only from the Pacific versant of southeastern Guatemala and western El Salvador, at 670–950 meters of elevation.

DESCRIPTION (THREE SPECIMENS): The only specimen with a complete tail is the female holotype, which is 300 mm. total length (310 mm. when measured by Stuart) and which has a tail that comprises 100 mm. (30.3 percent) of the total. Another female is 300+ mm. total length (217 mm. snout to vent), and the only male is 255+ mm. (213 mm. snout to vent). I would judge that these specimens are adults, although the holotype seemed "half-grown" to Stuart. The male has ossified spines on its hemipenes; the male, and the female holotype, both possess anal ridges, another indication of sexual maturity. The dorsal scales are in 17–17–17 rows. There are 151–164 ventrals (151, male; 159, 164, females) and 100 subcaudals (one female). The male has seven supralabials and the females have eight; the male has eight infralabials and one female has 8/7 (number of infralabials cannot be determined from the mangled jaws of the holotype). All three specimens have one preocular and one postocular, and there is no subpreocular. Temporal counts are $1+2/1+2$, $1+2/1+\frac{1}{2}$, and $1+1/1+\frac{1}{2}$.

The body is dark brown and, except for a dark line the width of the vertebrals, all the scales have a central whitish streak. The white markings are largest and most conspicuous on the lower sides, especially in the first scale row where the markings are largest and may even be nearly confluent with the pale venter. The tail is patterned like the body. The top and sides of the head, including the supralabials, are basically white and are about half covered with light brown mottling. The neck is white (not mottled) for about two to three scales behind the head, which gives the appearance of a pale collar; the collar is broken by the brown vertebral line in the Guatemalan specimens. The infralabials may be slightly touched with brown, as are the lateral edges of the ventrals and subcaudals, but otherwise the white ventral surfaces are immaculate. The color in life is not known.

Two specimens each have 11 maxillary teeth, increasing in size posteriorly, with the ninth lying level with the edge of the ectopterygoid process. The seventh to ninth interdental spaces are larger than the others but are still less than the length of a single tooth socket, and a real diastema is not present. The last tooth is in line with the others and is not offset. The holotype has 10 maxillary teeth, without a diastema, according to the original description.

The retracted hemipenis extends to the base of subcaudal 7 and is slightly bilobed from the end of subcaudal 6. The two short slips of retractor muscle merge near the end of subcaudal 7 and the muscle originates at subcaudal 22. The hemipenis is only weakly capitate, and the capitulum comprises nearly half the length of the organ on its sulcate side. The calyces are papillate except on the asulcate fold, where they are spinulate. The sulcus spermaticus forks at the edge of the capitulum and a branch extends almost to the tip of each lobe of the inverted organ. The wall of the capitulum forms a single fold on the asulcate side, where the edge of the capitulum overhangs a shallow space that is not divided by a partition. The hemipenis is densely spinose below the capitulum, with more than 50 small to large spines that are slightly hooked. A short, naked strip below the asulcate fold of the capitulum is bordered by some medium to large spines on each side and by a large spine below. The spines to each side become smaller toward the sulcus spermaticus. A pair of large spines, on the asulcate side, extend well onto the basal third of the organ, where there are also some inconspicuous spinules. The basal region of the retracted organ is an area of ridges of tissue, except for a basal naked pocket on the asulcate side of the basal third. The preceding description is based on the retracted right hemipenis of FMNH 64951 (illustrated).

REMARKS: *Rhadinaea pilonaorum* lacks the usual habitus of *Rhadinaea* in that specimens are exceptionally slender for their length; the coloration of the head is also very unusual for *Rhadinaea*. A specimen from El Salvador was found at night at the beginning of the rainy season, on a trail "at the bottom of a brush-grown gully running through pastureland" (Rand, 1957, p. 531, under "*Trimetopon posadasi*").

The species was named in honor of Antonio and Marta Piloña, who were L. C. Stuart's hosts at Finca La Gloria, the type locality; the holotype was given to Stuart by A. Piloña, administrator of the *finca*.

Rhadinaea pinicola Mertens

Map 11

Rhadinaea pinicola MERTENS, 1952b, pp. 135, 136; 1952c, p. 72, pl. 15, fig. 85 (photograph of preserved holotype in dorsal aspect). PETERS AND OREJAS-MIRANDA, 1970, p. 267.

HOLOTYPE: SMF 43191 (not seen), a male from pine forest above Hacienda San José, 1500 meters elevation, mountains of Metapán, Departamento Santa Ana, El Salvador; Adolph Zilch collector, June 4, 1951. The museum number was originally given as "43188" (the same number as given for the holotype of *Rhadinaea montecristi* in the same paper), but this is an error as indicated by the use of a different number in Mertens, 1952c, and by a handwritten annotation in a reprint of the original description; the date of collection is also corrected in Mertens, 1952c. The type locality is shown by Mertens (1952c, map) to be a short distance north of Metapán (probably near the road to Anguiatú).

DIAGNOSIS: The only known specimen of *Rhadinaea pinicola* (which I have not examined) is a weakly marked member of the *godmani* group, with 17 scale rows. It is evidently similar to *Rhadinaea kinkelini* (*q.v.*) in scutellation and color pattern, but lacks dorsolateral dark lines and two pale blotches on the rear of the frontal plate; it probably also differs from *kinkelini* in lacking a pale center in the middle (row 4) of the lateral stripe. It is similar to *Rhadinaea hannsteini* in lacking the frontal blotches but different in lacking the dorsolateral dark lines of *hannsteini* and in having the lateral stripe on all of row 4 and parts of each adjacent row (only on adjacent halves of rows 3 and 4 in *hannsteini*). It is similar to some weakly marked specimens of *Rhadinaea hempsteadae* (and different from most other species) in having a thin, conspicuous, pale line on the middle of row 5, but with 17 rather than 19 scale rows as in *hempsteadae*.

DISTRIBUTION: Known only from the type locality, at 1500 meters elevation in pine forest in the extreme northwestern corner of El Salvador.

DESCRIPTION (SPECIMENS NOT EXAMINED): The following pertinent data are extracted from the original description of the holotype (Mertens, 1952b) and from a poor photograph of the same specimen (Mertens, 1952c, pl. 15, fig. 85).

The specimen is a male 327 mm. total length, of which the tail comprises 102 mm. (31.2 percent). The dorsal scales are given as 19–17–17, but I suspect that the first count was made very close to the head and that the standard formula (starting a head's length behind the head) would be 17–17–17. Weak anal ridges are present. There are 150 ventrals and 77 subcaudals. There are eight supralabials and also eight

infralabials, and one preocular, two postoculars, and 1+2 temporals.

The dorsal ground color is gray-brown in preservative, with a dark vertebral line and a primary lateral stripe that covers all of row 4 and the adjacent thirds of rows 3 and 5. This stripe is bordered above by a narrow, pale line down the middle of row 5. There are several dark lines on the side of the body below the lateral dark stripe—a primary line on adjacent thirds of rows 1–2, a secondary (lighter) dark line on the edges of the ventrals and lower third of row 1, and another secondary line on adjacent thirds of rows 2–3. The dark lines and stripes do not stand out vividly in the photograph of the holotype, but the thin, pale line on row 5 is clearly discernible.

There is a large, pale spot, confluent with the throat color, on each side of the neck, with a vague, dorsal connection between the spots in the form of a rather pale zone of ground color; the photograph indicates that the dorsal connection lies immediately behind the parietals and somewhat sets off the dark head. The head is without marking above and the rostral is patternless. The first four supralabials are dark brown, each with a central white spot. The upper borders of labials 5 and 6 are pale, and an oblique white stripe crosses labials 6 and 7 from the eye to the mouth; the last supralabial is dark. The ventral surfaces are yellowish white and unmarked, except for the dark edging on the ventral tips.

There are about 13 maxillary teeth, the last two longest but not set off by a diastema.

REMARKS: I concur with Uzzell and Starrett (1958) that *Rhadinaea pinicola* probably is not so closely related to *R. lachrymans* as indicated by Mertens (1952b, 1952c). Anyway, the two specimens of "*lachrymans*" that Mertens (1952c) compared with *pinicola* are really representatives of the Guatemalan population of *R. godmani*. There may well be merit in alternative suggestions (Uzzell and Starrett, 1958; Mertens, 1952c) that the affinities of *pinicola* are with *R. kinkelini* or with the genus *Trimetopon* (*sensu lato*). *Rhadinaea kinkelini* (including its synonym *Trimetopon veraepacis*) ranges from Nicaragua to Guatemala and has similar scutellation and a similar pattern of stripes on the sides. *Rhadinaea pinicola* seems to lack two characteristics of *kinkelini*, a light center to the lateral dark stripe and a conspicuous pale blotch on each side of the posterior part of the frontal plate, but it should be noted that *R. hannsteini* also lacks the frontal blotches but nevertheless is clearly related to *kinkelini*. The general weakness of the dark lines and stripes, and the pale lateral line (possibly series of pale dashes), are reminiscent of *Rhadinaea hempsteadae* as indicated by Uzzell and Starrett, but I would not stress close relationship in that direction without knowing something about the hemipenis of *pinicola* and whether the "19" anterior scale rows extend for more than a very short distance behind the head of *pinicola*. I suspect that dissection of the male holotype would reveal that *pinicola* has the distinctive *hannsteini-kinkelini* type of hemipenis (see illustrations of hemipenes of *hannsteini*, especially the everted organ, fig. 30D, E).

The specific epithet evidently is formed of the words *pinus* (pine) plus the suffix *-cola* (from *colo*, to inhabit), in reference to the pine forest habitat.

Rhadinaea posadasi (Slevin), new combination

Figures 27C, 29A; map 11

Trimetopon posadasi SLEVIN, 1936, pp. 79–81. STUART, 1963, p. 122. PETERS AND OREJAS-MIRANDA, 1970, p. 309.

HOLOTYPE: CAS 66964, an adult male from the southern slope of Volcán Zunil, Departamento de Suchitepequez, Guatemala, caught by Joseph R. Slevin on August 8, 1924. The specimen is in good condition except that both hemipenes have been removed and somewhat mutilated. I twice obtained a total length measurement of 257 mm., in contrast to Slevin's figure of 276 mm.

DIAGNOSIS: This species is close to *Rhadinaea pilonaorum* (*q.v.*), but in *posadasi* the head is dark brown (rather than whitish with brown-mottling), the pale dashes on the body scales are less conspicuous, there are fewer ventrals, and the body is relatively less slender. The two species are readily separated by head color alone, if the small number of specimens is representative. The color pattern is close to *R. schistosa* (*q.v.*) of Mexico, but *posadasi* has a much longer tail and fewer maxillary teeth.

DISTRIBUTION: Known only from the slopes of volcanoes in the Pacific versant of the Sierra Madre of southwestern Guatemala. Specific elevations are not recorded, but one locality lies between 3800 and 6000 feet (1159–1829 meters) according to Smith (1959, p. 210).

DESCRIPTION (SEVEN SPECIMENS): The largest female is 288 mm. total length, 103 mm. tail length; the largest of two males, the holotype, is 257 mm. total, 96 mm. tail length. The holotype is probably sexually mature because it has anal ridges and ossified hemipenial spines; anal ridges are also present on females, including one as small as 192 mm. total length (64 mm., tail). The tail is 36.0 and 37.4 percent of total length in two males, and 33.3–35.8 percent in females. The dorsal scales are in 17–17–17 rows except for three specimens with the following counts: 16/15–17–17, 16/16–17–17, 17/15–17–17. There are 136–146 ventrals (136, 139, males; 143–146, females) and 86–95 subcaudals (92, 95, males; 86–93, females). There are seven supralabials, eight infralabials, one preocular, one postocular, and no subpreocular. There are 1+2 or 1+1 (one or both sides, two specimens) temporals.

The upper surfaces are dark brown, with a scarcely distinguishable darker brown line occupying the width of the vertebral row of scales; the lower two rows of scales are paler than the others. Pale speckling or streaking may be present on the centers of all scales except the vertebrals, or such markings may be confined principally to the lateral rows. The head is brown with some paler specks. The rostral is pale, with a ∩-shaped dark mark. A whitish collar, two or three scales wide, crosses the neck at the rear of the parietals and is interrupted by the vertebral dark line in most specimens; the collar tends to have on each side a narrow extension that projects forward onto the temporal region. The supralabials are whitish except for some encroachment of brown pigmentation from above. The underside of the head is whitish, with some touches of brown. The ventrals and subcaudals are lightly tipped with brown and there is a diffused brown line under the middle of the tail, but otherwise the whitish venter is unmarked.

It was my impression from preserved material that the collar and the pale scale centers might be yellowish in life. The ventral surfaces can be either yellowish or whitish in specimens from the same locality, according to the original description.

There are 11 teeth on a maxilla from each of five specimens. The teeth increase in size posteriorly and the last teeth are not abruptly enlarged. There is no diastema. The ultimate tooth is in line with the others, not offset.

The length of the hemipenis could not be determined, as both organs had previously been removed from the holotype, and the only other available male has the organs fixed in a partially everted position. The hemipenis is slightly bilobed and is distinctly capitate. The capitulum comprises about half of the length of the organ on its sulcate side. The calyces are papillate, except on the asulcate fold and on the peripheral calyces toward the asulcate side, where they are spinulate. The sulcus spermaticus forks at the edge of the capitulum and a branch extends nearly to the tip of each lobe of the retracted organ. The wall of the capitulum forms a single fold on the asulcate side, where the edge of the capitulum overhangs a rather deep, nude area that is not divided by a partition. The hemipenis is densely spinose below the capitulum, with approximately 50 small to large, slightly hooked spines. A short naked strip below the asulcate fold of the capitulum is bordered by several medium-sized spines on each side and by a large spine below. The spines on each side become smaller toward the sulcus spermaticus. There are medium to relatively large spines nearly to the base of the organ (assuming that not too much of the base was left *in situ*, by whoever removed both organs), and there is a scattering of inconspicuous spinules. There seems to be one or two basal naked pockets among the basal folds and spines, on the asulcate side, but these are not well defined and I doubt that they are retained as distinct depressions when the organ is everted.

REMARKS: The closest relative of *Rhadinaea posadasi* seems to be *R. pilonaorum*; these two species occur in the same volcanic belt but the nearest known localities are more than 100 kilometers apart. Although I think that *posadasi* and *pilonaorum* are distinct species, specimens from intervening localities will nevertheless be of much interest. A record of "*posadasi*" from El Salvador (Mertens, 1952c, p. 76; Rand, 1957) is based on a specimen of *pilonaorum*.

The species was named in honor of Juan Zenon Posadas, owner of the coffee plantation where Slevin collected the holotype and several of the paratypes.

Rhadinaea schistosa (Smith), new combination

Figures 27E, 29C, 30G; map 11

Rhadinella schistosa SMITH, 1941, pp. 7–10, fig. 1

(details of scutellation and color pattern of head of holotype). SMITH AND TAYLOR, 1945, p. 120.

HOLOTYPE: FMNH 100065 (originally E. H. Taylor-H. M. Smith no. 23580), an adult male in good condition, from Cuautlapan, Veracruz, Mexico; caught by Edward H. Taylor in August, 1940.

DIAGNOSIS: This is a diminutive, orange-bellied *Rhadinaea* that has a pale, U-shaped collar, and little or no evidence of striping on the body; there tends to be a small, pale spot on each scale in row 1, and pale dashes on the other scales of the trunk and tail, but these markings are relatively obscure on some individuals. The body pattern is similar to that of *Rhadinaea pilonaorum* and *R. posadasi* of Guatemala, but these species have much longer tails (about 30–40 percent of total length and more than 70 subcaudals, contrasted with less than 20 percent and fewer than 50 subcaudals in *schistosa*), and *pilonaorum* additionally has a distinctive whitish head.

Rhadinaea schistosa is likely to be confused with small snakes of other genera, especially *Tantilla schistosa phrenitica* Smith which occurs sympatrically and has the same coloring as *R. schistosa* (*fide* Smith, 1941, 1945). *Tantilla* is easily eliminated by the presence of only 15 rows of dorsal scales and the absence of a loreal plate. Other sympatric snakes (*fide* Smith, *loc. cit.*) that have somewhat similar patterns are distinguishable by the presence of keeled scales (*Ninia*) or by the combination of fused prefrontals and lack of a preocular (*Chersodromus*). Species of *Geophis* lack a preocular and have fewer than eight supralabials.

DISTRIBUTION: Foothills along eastern slope of Sierra Madre de Oaxaca, in Veracruz and northern Oaxaca. The type specimens were evidently collected in a banana grove (Smith, 1945).

DESCRIPTION (FIVE SPECIMENS): The holotype, the largest male examined, has a total length of 186 mm. and a tail length of 34 mm. One female is 215 mm. total, 33 mm. tail length, but Smith (1941, p. 9) gave measurements of 250 mm. total, 37.5 mm. tail length for a larger female (now UIMNH 18725) that I did not examine. These specimens are adults, as indicated by well-developed hemipenes and anal ridges in the male and eggs in the largest female (*fide* Smith, *loc. cit.*). The tail is 16.5 and 18.3 percent of the total length in two males, and 14.4 and 15.3 percent in two females. The dorsal scales are in 17–17–17 rows; anal ridges are present on the males. Ventrals number 145–154 (145–147, three males; 153, 154, females), and subcaudals are 31–42 (40, 42, males; 31, 34, females). There are eight supralabials and also eight infralabials. There is one preocular, no subpreocular, one or two postoculars, and 1+1 temporals. Two specimens have 1/1 postoculars, one has 2/1, and two have 2/2; the reduction from two postoculars to one occurs by fusion of the upper plate with the supraocular.

The body is dark brown above, with a pale dash or some speckling on each scale center. The pale centers are vivid and readily perceivable by the naked eye on some specimens, which have nearly a salt and pepper appearance; but on other individuals these markings are scarcely discernible, except on the lower scale rows, especially the first row, where the pale centers are widened to form small spots rather than dashes. The tail is patterned like the body. There is a U-shaped whitish collar, about the width of two scales, starting on the middle or posterior temporal region and curving across the nape. The collar is wholly or partly broken by a dark brown vertebral line that is visible on the neck but is only faintly or not at all discernible on the body.

The top of the head is dark brown with some pale specks. The rostral plate may be uniformly dark or it may be pale on its upper and lower margins, thus causing the hint of a ∩-shaped dark marking. The side of the head is dark brown except for a whitish line or series of spots (one on each labial) along the middle of supralabials 1–7 or 2–7. The underside of the head is whitish, with heavy brown smudging on the mental, anterior genials, and all the infralabials. The subcaudals are tipped with the brown body coloring and the ventrals slightly so, but otherwise the venter is uniformly pale yellowish.

The coloration is brighter in life or in freshly preserved specimens (*fide* Smith, 1941, p. 9): The nuchal collar and the gular region are white; the rest of the venter is orange, brightest on the posterior part of the body and fading somewhat on the tail. The light centers of the dorsal scales are "less distinct and more brownish medially, more distinct and reddish laterally."

There are 16 teeth on a maxilla from each of four specimens and 17 teeth on one other. The

last two teeth are separated from the others by a barely discernible gap in three cases, the last three teeth are set off in another, and in still another there is a tiny gap both before and after the third tooth from the rear. There are two or three teeth behind the front edge of the ectopterygoid process. The last two teeth may be markedly or only slightly larger than the third one from the rear; the ultimate tooth is in line with the others and is not offset.

The retracted hemipenis extends to the end of subcaudal 7 or the end of subcaudal 8. The organ is single, but there is a slight bifurcation of the retractor muscle, which originates at the level of subcaudal 23. The capitulum comprises about a third the length of the organ on its sulcate side. The calyces are papillate except for some peripheral ones and those on the asulcate fold which are spinulate. The sulcus spermaticus forks about one-third of its length on the capitulum and the branches extend virtually to the tip of the retracted organ. The wall of the capitulum forms a single fold on the asulcate side. The hemipenis is densely spinose below the capitulum; there are 30+ to 40+ small to large spines, which are nearly straight, with but slight recurvedness. The edge of the capitulum on the asulcate side overhangs a deep nude space, which is partly divided by a thin wall of tissue that has a simple (not fringed) free edge. The partition lies entirely under the overhang and the basal edge is continuous with a short spine that projects from under the edge of the capitulum (inverted condition). Below and to each side of this spine are two closely parallel rows of four spines each, with the basal spines being largest. The largest spine on the hemipenis is roughly a fifth of the length of the entire organ and lies between and just below the two aforesaid rows of spines. There are no spines on the basal third of the hemipenis, only inconspicuous spinules. The basal region is an area of convoluted folds of tissue, except for a basal naked pocket that extends along the dorsal wall for nearly half the length of the organ. The preceding description is based mainly on the left retracted hemipenis of FMNH 100298 (illustrated) and also on a cursory examination of the left hemipenis *in situ* of the holotype.

REMARKS: *Rhadinaea schistosa* is the smallest species in the genus and is very much like a *Tantilla* in general appearance. Smith (1941, 1945) commented on the amazing resemblance of *R. schistosa* to the sympatric *Tantilla schistosa phrenitica* and suggested (1945) that it might be a case of mimicry. This may be so, but probably not for the reason that one or both species might be slightly poisonous; the rear fangs (grooved in *Tantilla*) in snakes of these genera seem to be utilized only for the killing of prey and seldom or never for purposes of defense. Both *R. schistosa* and *T. schistosa phrenitica* were found under stones at the same place (Smith, 1941), evidently in a banana grove (Smith, 1945).

I have not examined a specimen (Univ. Colorado Mus. 39790) recently reported (Smith, 1971) from northern Oaxaca, although I have plotted the locality on map 11. The only other known specimens are the original holotype and topoparatypes, which are now distributed among several institutions. Of the latter specimens, I have not examined UIMNH 18725 nor the one deposited at Stanford University (no. 20618, *fide* Hobart M. Smith, *in litt.*).

The hyoid of *Rhadinaea schistosa* was described by Langebartel (1968, p. 30).

The specific epithet is formed of the word *schistos* (divided, cleft), probably in allusion to the broken collar.

Rhadinaea serperaster Cope

Figures 26C, 28D; map 10

Rhadinaea serperaster COPE, 1871, pp. 212, 213. STUART AND BAILEY, 1941, pp. 6–9 (part, specimens with 21 scale rows = *R. godmani*), fig. 1 (diagram of body pattern). TAYLOR, 1954, pp. 737, 738, fig. 15 (photograph of a preserved juvenile, KU 31953). PETERS AND OREJAS-MIRANDA, 1970, p. 268.

Rhadinaea serperastra COPE, 1875a, p. 140 (emendation?); 1887, p. 80; 1900, p. 755. BOULENGER, 1894b, p. 172; 1896, p. 635. WERNER, 1929, p. 117. DUNN, 1932, p. 2. TAYLOR, 1951, pp. 112, 113.

Ablabes serperaster (Cope): GÜNTHER, 1893 (1885–1902), pp. 105, 106.

Liophis serperastra (Cope): AMARAL, 1929b, p. 174.

HOLOTYPE: ANSP 3739, a juvenile male in fair condition, obtained by Van Patten "near San José, Costa Rica." There are 157 ventrals, two preventrals, and 71 subcaudals, rather than 164 ventrals and 78 subcaudals as stated by Cope. The small size of the specimen (176 mm. total, 45 mm. tail length) might well have caused Cope to err in his counts but, although I have no reason to question the identity of this specimen as the holotype, there unfortunately is nothing in the original description that positively

identifies the specimen. Not even size nor sex was mentioned in the description.

DIAGNOSIS: *Rhadinaea serperaster* differs from all other species of the genus, except the geographically distant *R. hempsteadae* and *R. montecristi*, in having 19–19–19 rows of scales. *Rhadinaea serperaster* has a complex pattern of body stripes that differs markedly from *hempsteadae* and *montecristi* (see fig. 28). However, the pattern of *serperaster* is nearly identical with that of individuals of some possibly sympatric populations of *R. godmani*, which is most easily differentiated by its greater number (21) of scale rows.

DISTRIBUTION: Mountains of central Costa Rica, in the Cordillera Central and in the northern end of the Cordillera de Talamanca, at known elevations of 1220–1450 meters.

DESCRIPTION (13 SPECIMENS): The largest specimen is a female 445 mm. total length, 110 mm. tail length; the largest male is 368 mm. total, 97 mm. tail length. The tail is 25.6–27.5 percent of the total length in males and 23.9–26.1 percent in females. The dorsal scales are in 19–19–19 rows; anal ridges are present on some males and on one female. There are 156–172 ventrals (156–159, males; 165–172, females) and 66–79 subcaudals (69–79, males; 66–71, females). There are eight supralabials and usually eight or occasionally nine infralabials. There is one preocular (1/2, 2/1, two specimens), no subpreocular, two postoculars, and 1+2 temporals.

The body pattern is a complex one of many dark brown lines and stripes on different ground colors. The middorsum (median seven scale rows) of the body is light or medium brown, whereas the lateral ground color is paler, probably tan in life. All specimens have five primary (very distinct) markings: There is a dark vertebral line that overlaps slightly or broadly onto the paravertebrals. There is, on each side, a dark line on the adjacent thirds or halves of rows 1–2. There is, on each side, a dark stripe from the upper half of row 3 to the lower part of row 5, broken by a pale, interrupted line along the middle of row 4. All specimens have at least an indication of three secondary (lighter) dark lines on each side: A line on the ventral tips and lower part of row 1 is in some cases reduced to a series of dashes. There is a line or series of dark dashes on the common border of rows 2–3. A dark line on the common border of rows 7–8 is, on some specimens, expanded to include about one-third of each of these rows. In addition to the preceding markings, some individuals have distinct lines of pigment between rows 6–7 and 8–9.

There tend to be four poorly defined, pale spots immediately behind the dark head—one spot on each side of the vertebral dark line and another on each side of the neck; these spots were not noted to fuse into a collar on any specimen examined. The top of the head is dark brown, usually with a pair of tan blotches in the middle of the head, each blotch occupying adjacent parts of the frontal, supraocular, and parietal; a pair of small parietal dots is present on a few specimens. The rostral plate is tan, with a ∩-shaped brown mark.

The supralabials are dark brown, with conspicuous white spotting in a pattern that shows little variation in the material studied: The upper part of the first labial has a spot that may overlap onto the nasal and/or be continuous with the spot on the second labial. Supralabials 2–4 have a median spot each that extends from the center of the plate forward to the anterior suture. Supralabials 5–6 have their lower borders white, and the sixth labial also has an oblique, short stripe or spot extending from the lower, rear edge of the eye; the oblique marking sometimes runs into the lower pale edge of the plate or into the marking on the next labial. The seventh labial has a spot or short vertical bar extending up from its lower edge; the bar is in some cases contiguous with the aforementioned oblique marking. The last supralabial, the eighth, is uniform dark brown or with only inconspicuous pale specks.

The infralabials are marked irregularly and sparsely with small spots of dark brown. The ventral surfaces are white except for the dark edging of ventral and subcaudal tips. Some specimens have occasional dark dots on the venter, and one (USC 1204) has a slight accumulation of pigment posteriorly on the ventral midline, especially under the tail.

The color of living specimens has not been reported. KU 103895–103897 had cream venters that tended toward pale yellow posteriorly (field notes of William E. Duellman), but these are small specimens (180–240 mm. total length) and the possibility of an ontogenetic change to a brighter color cannot be ruled out (a change from white to bright yellow occurs in the related *Rhadinaea godmani*). Other colors in life for these

specimens are as follows: The paired blotches on the middle of the head were reddish brown; the ground color of the rostral plate and the pale markings on the supralabials were pale yellow; the chin was white; the iris was reddish tan above and dark brown below, and the tongue was black with white tips.

There are 16 or 17 maxillary teeth, the last five of which are heavier and somewhat enlarged over the others. The last three teeth lie posterior to the front edge of the ectopterygoid process. A tiny gap, no greater than the length of an adjacent socket, is sometimes present in front of, behind, or on both sides of the third tooth from the rear. The ultimate tooth is in line with the others, not offset.

A retracted hemipenis extended *in situ* to the base of subcaudal 7 and was slightly bilobated from the end of subcaudal 6. The two slips of retractor muscle merged at the end of subcaudal 7, and this muscle originated at subcaudal 27. It is not known whether there is any indication of bilobation when the organ is everted. The capitulum is about two-fifths the length of the hemipenis on its sulcate side. The sulcus spermaticus forks at the edge of the capitulum and the branches extend to the end of the organ. The calyces are spinulate on the asulcate edge of the capitulum and on the asulcate fold; the other calyces are papillate. The wall of the asulcate side of the capitulum forms a thick, single fold that shows no sign of doubling and lacks any oversized calyces. The recurved spinules on the calyces of the asulcate fold are elongated and form a conspicuous cluster, which overhangs the edge of the capitulum. There is a hidden, nude space immediately below the edge of the capitulum on each side of the cluster of elongated spinules; these spaces probably appear as conspicuous pockets when the organ is everted, but there seems to be no additional pockets formed from large calyces (as in *godmani*). There is a spinose zone below the capitulum, except for a nude space on the asulcate side. The naked area is bordered by thick rows of spines, the basal few of which are larger than the others; there is no median row of small spines in the top of the naked area and no median spine(s) at the lower edge of the area. There are in excess of 50 small to somewhat large spines. The spines toward the sulcate side are small and those bordering the asulcate naked area are medium-sized; several of the basalmost spines, especially one on the dorsal wall, are conspicuously larger than the others. Between one-fourth and one-third of the organ, the basal part, is adorned only with minute spinules; there is a basal naked pocket on the dorsal wall of this section of the hemipenis, but it is not conspicuous. The preceding description is based on the left, retracted hemipenis of USC 1204, which is the only adult male that I have seen. A bit of the base was left in place when the hemipenis was removed for detailed examination, so the proportions given are approximate.

REMARKS: *Rhadinaea serperaster* greatly resembles specimens of the southern form of *R. godmani*, and a few references to *serperaster* are based entirely (Dunn, 1947) or partly (Stuart and Bailey, 1941, p. 7) on specimens of *godmani*. Comparisons and additional details are given in the Remarks section under *R. godmani*.

Three small specimens of *Rhadinaea serperaster* were found under moss on logs and in an earthen bank in a *cafetal* (William E. Duellman, field notes for KU 103895–103897).

Perhaps the specific epithet is based on the noun *serpens* or *serpis* (snake) plus the suffix *-aster* (small), but it may be that Cope had something else in mind. He seems to have consistently used the spelling "*serperastra*" after the original description, in which the spelling was "*serperaster*," but it is not evident whether this was an intended emendation or an inadvertent error. Taylor (1954, p. 737) noted the existence of the nouns *serperaster* (hanger on) and *serperastra* (knee-splints or severe officers), but I doubt that Cope's imagination was tickled by any of these meanings. In any case, the word seems to be a noun in apposition to the generic name.

THE *calligaster* GROUP

The *calligaster* "group" is comprised of but one species, from the mountains of Costa Rica to western Panama, and is defined especially by the following combination of features (see also table 3): The hemipenis is bilobed, completely without capitation, and has only soft papillae (no spinules) on the calyces. There is no subpreocular and the temporal formula is 1+1. The supralabials are boldly margined with black, and there is a midventral series of black triangles or half-moons, or a fusion of such markings to form a midventral stripe.

Rhadinaea calligaster has differentiated to such an extent that its relationships with other groups

TABLE 13

ASPECTS OF VARIATION[a] IN *Rhadinaea calligaster*, SOLE MEMBER OF THE *calligaster* GROUP

Sample	N	Ventrals		Subcaudals		Tail Length as a Percentage	
		Males	Females	Males	Females	Males	Females
Hatchlings from communal nest, W. Panama	17	142–153 (11) 148.8±0.98	151–156 (6) 154.0±0.73	51–60 (11) 54.8±0.87	46–53 (6) 49.1±1.05	20.3–23.4 (11) 21.9±0.26	18.6–20.7 (6) 19.6±0.34
All other specimens	23	141–152 (8) 146.1±1.37	145–155 (15) 149.3±0.85	58–68 (8) 62.1±1.31	46–58 (13) 52.6±0.95	24.7–28.9 (8) 26.5±0.46	20.4–25.2 (12) 22.7±0.50
Total sample	40	141–153 (19) 147.9±0.84	145–156 (21) 150.6±0.79	51–68 (19) 57.9±1.12	46–58 (19) 51.5±0.81	20.3–28.9 (19) 23.8±0.59	18.6–25.2 (19) 21.8±0.48
Maxillary teeth	19	15+2 (4), 16+2 (12), 17+2 (2), 19+2 (1)					

[a]The following statistics are given in the first part of the table: Above, range followed by number of specimens in parentheses; below, mean and standard error of the mean. In the second part of the table are shown counts of maxillary teeth followed by number of maxillae (one from each specimen) in parentheses.

are obscure, although the bilobated hemipenis, absence of a subpreocular, and, especially the occasional tendency for a pale bar from the eye to the corner of the mouth bespeak an ancestry from the *godmani* group. The characteristic midventral markings, and the dorsal green coloration of some individuals, are found elsewhere in the genus only in occasional specimens of *R. decipiens* (*q.v.*), a member of the *lateristriga* group. But, curiously, other kinds of evidence fail to suggest any special degree of relationship between the *calligaster* and *lateristriga* groups (compare data in tables 2 and 3). The occurrence of these rare (in *Rhadinaea*) characteristics in two congeners from the same region is unlikely to be fortuitous, but I do not believe that direct relationship is indicated. The completely different hemipenes, the elongated, thickened tail in the *lateristriga* group, and basic pattern differences (white versus dark lines) are too basic to ignore. The ventral markings and green coloring possibly represent independent responses to the same environmental stimuli or, possibly, even some kind of mimicry, but no satisfactory hypothesis presents itself at this time.

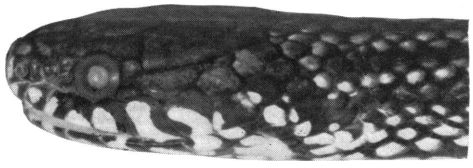


FIG. 32. Head pattern of *Rhadinaea calligaster*, KU 107816, from western Panama.

Rhadinaea calligaster (Cope)

Figures 32–35, 50; map 12

Contia calligaster COPE, 1875a, p. 146, pl. 28, fig. 12 (lateral view of cephalic scutellation). GÜNTHER, 1893 (1885–1902), p. 104.

Rhadinaea calligaster (Cope): BOULENGER, 1894b, p. 164. WERNER, 1929, p. 117. DUNN, 1932, p. 2. TAYLOR, 1951, p. 113. PETERS AND OREJAS-MIRANDA, 1970, p. 264.

Liophis calligaster (Cope): AMARAL, 1929b, p. 171.

DESIGNATION OF LECTOTYPE: The original description is based on two syntypes, USNM 30607 and 30679, collected by William M. Gabb on "Pico Blanco" (actually Cerro Utyum *fide* Savage, 1970, p. 282), 5000–7000 feet, Limón

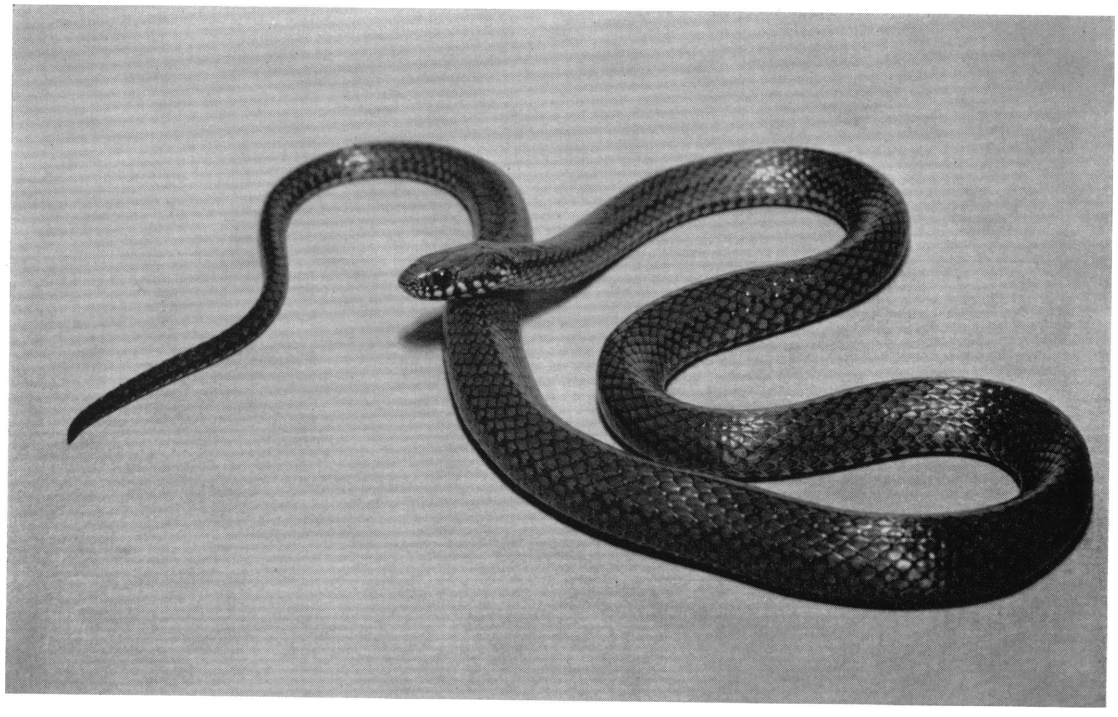


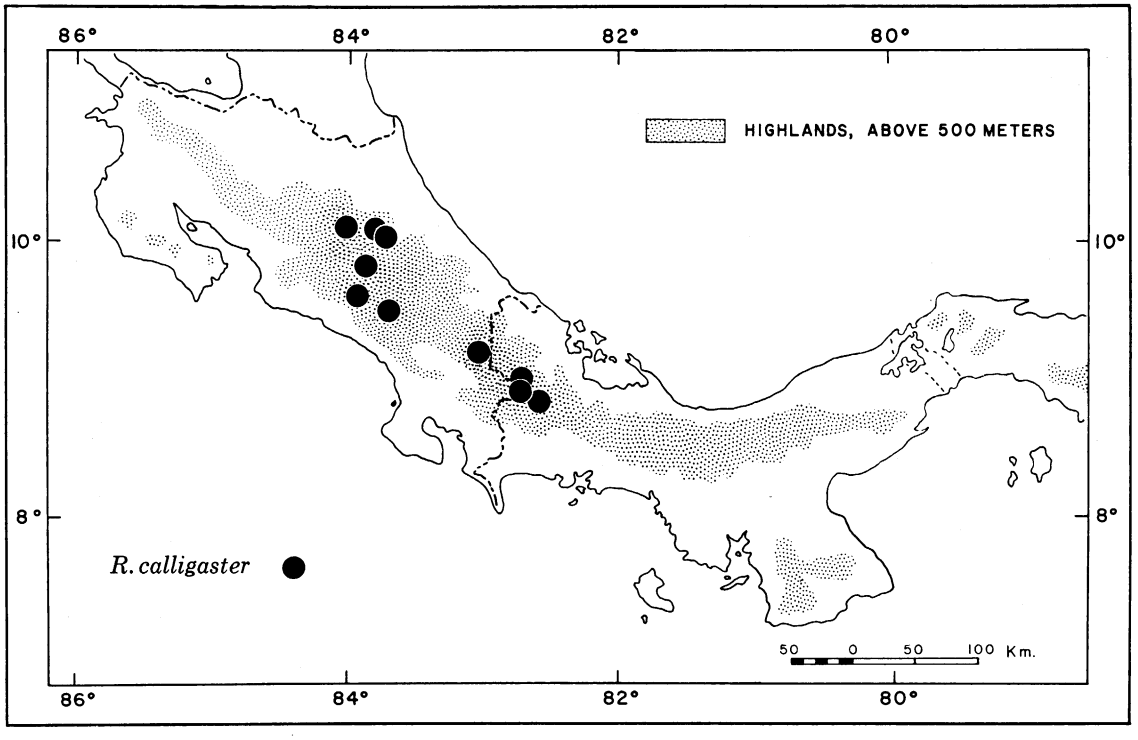
FIG. 33. *Rhadinaea calligaster*, KU 107819, from western Panama.

Province, Costa Rica. Both syntypes are in poor condition and counts of ventrals and subcaudals cannot now be made, although the heads are satisfactory and the different color patterns mentioned by Cope are evident. The larger specimen, USNM 30679, is here designated as lectotype because it is the one figured and described in most detail by Cope (1875a, p. 107, pl. 28, fig. 12, left side of head). It is recognizable not only by characteristics of pattern but also because there are only seven supralabials on the left side, with the third and fourth labials touching the eye. On the right side of the lectotype, and on both sides of the other syntype, there are eight supralabials, with the fourth and fifth bordering the eye. Cope (*loc. cit.*) stated that there are 1+1+2 temporals in the specimen that is here designated lectotype. Actually there are 1+2 (Cope's row 3 is considered as post-temporals), but the top plate in row 2 is minute on the left side of the head and this tiny scale is not shown in the original figure.

DIAGNOSIS: *Rhadinaea calligaster* differs from all of its congeners, except occasional specimens of *R. decipiens*, in having a line of black markings (from small spots to a solid stripe) down the middle of the belly. It also has conspicuously black-margined supralabials, and a variably patterned dorsum (unicolored to heavily striped), the ground color in life ranging from gray to brown to green (gray and especially green are unusual colors in the genus). Although mid-ventral black markings are occasionally seen in *R. decipiens*, this is a very different appearing snake than *calligaster*. *Rhadinaea decipiens* has a much longer tail, one or two thin white lines on each side of a basically brown or black body, and there often is a conspicuous nape collar.

DISTRIBUTION: Wet, montane forest, in the Cordillera Central of middle Costa Rica and in the Cordillera de Talamanca to extreme western Panama. The known elevational range is 1220–2439 meters.

DESCRIPTION (42 SPECIMENS): Most adults are in the 300–500 mm. range. The largest male examined is 440 mm. total length, of which 127 mm. is tail; the largest female is 513 mm. total length and 112 mm. tail length. The tail is 20.3–28.9 percent of the total length in males and 18.6–25.2 percent in females. The dorsal



MAP 12. Locality records for *Rhadinaea calligaster* in highlands of Costa Rica and Panama.

scales are in 17–17–17 rows and anal ridges are present on some adult males. Ventrals are 141–156 (141–153, males; 146–156, females) and subcaudals are 46–68 (51–68, males; 46–58, females). There are usually eight supralabials and eight infralabials or, in both cases, occasionally seven or nine. There is one preocular, no subpreocular, and two postoculars. Temporals are usually 1+1, or occasionally 1+2, or even 1+1+2 (on one side of the head of a hatchling).

There is remarkable variation of color pattern in this species. The dorsal ground color varies from light brown to dark grayish brown, and some individuals are green in life (see below). All available specimens have a middorsal blackish line or stripe, or row of small spots, confined to the center of the vertebral row or broadly overlapping onto the paravertebrals. Some individuals have virtually unicolored dorsums except for a remnant of the vertebral line on the neck. In many cases there are black lateral stripes, especially on the adjacent parts of rows 6 and 7 and/or on adjacent parts of 3 and 4; but the lateral stripes (when present) vary greatly in width and location from the above "normal" locations. In the lectotype, for example, there are lines along the lower edge of row 7 and the top edge of row 5, and the low stripe occupies all of row 3 and the adjacent halves of rows 2 and 4. The top of row 4 may have a line of pale dashes, which in some individuals sets off a dark stripe below. Some specimens, especially those of dark ground color and broad stripes, have the lower two or two and one-half scale rows conspicuously light; if the scale edges in these rows are very dark, the pale centers appear as a series of oval spots. The body markings may extend onto the tail which, however, is not vividly patterned. Some specimens have a small, indistinct light spot on either side of the vertebral line on the nape. The head is either nearly unicolor brown or else mottled dark and lighter brown, and seldom is there any indication of a pair of pale parietal dots. The supralabials are whitish and heavily margined with black; in some cases there is a black postocular stripe that slants toward the corner of the mouth and, occasionally, this marking and some lower ones tend to set off a white, oblique postocular bar. The infralabials are margined with black and the genials are spotted.

The entire ventral ground color is perhaps always pale in life, but in preserved specimens the venter may be white, pale brown, or gray (see Geographic Variation). The ventrals are tipped with black, in some cases rather broadly. All available specimens have at least some degree of midventral black markings. Often

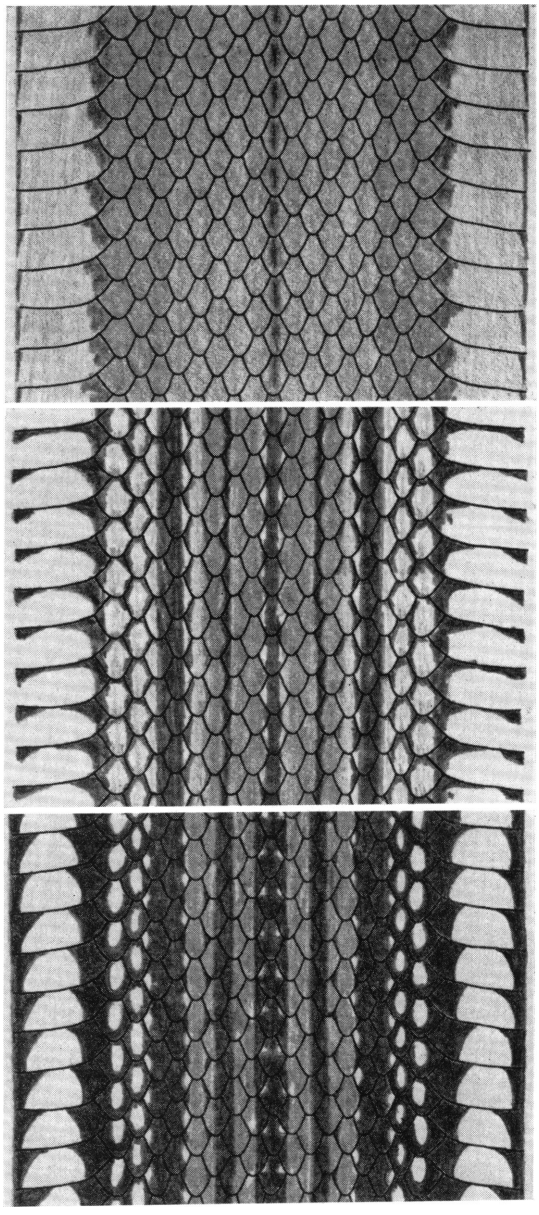


FIG. 34. Variation in midbody color pattern of *Rhadinaea calligaster* from central Costa Rica. *Top*: USC 41. *Center*: USNM 38335. *Bottom*: UMMZ 117650.

these are in the form of discrete triangles or half-moons, one at the base of each ventral plate. These markings vary greatly in size, and may even be part of a transverse streak that extends from one side of a ventral to the other side; in many cases there is fusion into either a narrow or broad midventral stripe. The subcaudals may be nearly immaculate, or have dark borders and/or a dark median line or stripe. The amount of black pigment on the venter possibly increases with age in some individuals; none of 17 juveniles from Cerro Pando, western Panama had as much black as several adults from the same locality. The coloration in life is described below, under a separate heading.

The maxillary teeth range from 15+2 to 19+2. The prediastemal teeth lie anterior to the front edge of the ectopterygoid process, except in a specimen with 19 prediastemal teeth, in which two teeth are posterior to the process. The last fang is offset laterad.

The hemipenis is slightly bilobate and is not capitate. Two retracted organs extend to the base of subcaudal 8 or the middle of 10, with the bilobation starting from the base of subcaudal 7 or the end of 9, respectively. The two slips of retractor muscle merge at the base of subcaudal 9 or 11, and this muscle originates at the level of subcaudal 30 or 21, respectively. The everted hemipenis extends to the end of subcaudal 7 or 8. Approximately the distal third of the organ is covered with large calyces that bear soft, conspicuous papillae. The calyculate area is not set off by a basal groove (i.e., is not capitate) and the papillae are not replaced by tiny spines on any of the calyces. The sulcus spermaticus forks below the calyculate area, opposite subcaudal 4 or 6 in the retracted organ, and its branches extend all the way to the tips of the short lobes, even when the hemipenis is everted. There are several dozen slightly curved, medium-sized spines below the calyculate area; the basal spine is somewhat larger than the others. The basal third of the organ is ornamented only with spinules, except on the extreme base, which is nude. The preceding description is based on retracted hemipenes of MCZ 50195 and USC 2923, and the everted organs of KU 107820 (illustrated), UMMZ 117650, and USC 3048.

Color in Life: Seventeen *R. calligaster* (KU 107822–107838) were hatched in Panama City from eggs found on Cerro Pando in western Panama, and color notes were written about 10 days after hatching. In the description following, these hatchlings are compared with seven adults (KU 107815–107821) from the same population. (Colors of the eye and tongue were determined with the aid of a dissecting microscope; the black stripes, labial and ventral markings are not mentioned, as these do not change in preservative.) The juveniles ranged from dark gray to grayish brown above, some having a tinge of tan or pale orange on the nape; of the adults, two were gray, four were dark green, and one was gray above and green on its lower sides. The juveniles had white labials and chins, and the rest of the ventral surfaces ranged in a uniform gradient from white through pale greenish yellow, without any one hue dominating the sample; the adults all had bright yellow labials and venters. In the juveniles, the iris ranged from dull grayish brown through brown to nearly black, whereas it was simply noted as brown in the adults. The tongues of the adults and several selected juveniles were black, turning white on the tips of the fork.

The descriptions above denote considerable ontogenetic variation, especially in dorsal and

Fig. 35. Hemipenis of *Rhadinaea calligaster*, KU 107820, left organ. ×9.6.

ventral colorations, and also show considerable intrapopulational variation among adults in color of the dorsum. The total range of variation is extended even farther by four specimens from Heredia and Cartago provinces, Costa Rica, on the basis of color notes made by William E. Duellman (KU 103889 and 103891), Norman Scott (USC 7055), and me (KU 103890, collected by W. E. Duellman). USC 7055 was yellow tan above and bright yellow below. KU 103891 was dull grayish green above and greenish yellow below. KU 103889 had an olive-brown dorsum with green on the anterior borders of the scales and turning dull green on the lowest scale row and ventral tips; labials, chin, and anterior two-thirds of the belly were bright yellow, but the posterior third and the subcaudal surfaces were greenish yellow; the iris was pale orange-tan and the tongue brown with black tips. KU 103890 was brownish green above, turning olive-green on the lower two scale rows; labials and chin were bright yellow but the rest of venter was bright olive-green; the iris was light brown and the tongue, including tips of the fork, was black. The foregoing three individuals in the KU series were collected within a few days of each other at the same locality and are further demonstration that there is great intrapopulational variation in adult coloration.

Geographic Variation: The color in life of *R. calligaster* is given above for samples from near the opposite ends of the range; despite considerable intrapopulational variation, some differences between the samples are evident. Adults from near the northern limits of the range, in Costa Rica, tend to have some brown in the dorsal color, whereas those from western Panama are gray or green. There is a tendency for green to appear in the ventral coloration of the Costa Rican specimens, whereas the ventral ground color of Panamanian adults is uniform bright yellow. The Panamanian specimens have white tips to the fork of the tongue, but two Costa Rican individuals have black tips. Differences in ventral coloration are even obvious in preserved specimens, after the yellow and green hues have faded. In specimens from Heredia and Cartago provinces, Costa Rica, the venter turns gray, or white with gray suffusion, or even pale brown. At least I assume that no Costa Rican specimen had a gray or brown venter in life, because the following changes were actually observed. KU 103889–103891 had ventral surfaces ranging from bright yellow to olive-green, but in preservative their venters are mostly gray; this change seems mainly associated with the greenish color, because the individual with the most yellow in life has the greatest areas of white in preservative.

In regard to the black markings on the belly and striping of the trunk, there is a gradient between strikingly different patterns, as indicated in the description and by the figure. However, geographical differences are not readily apparent, as individuals hatched from eggs found at a single nesting site (Cerro Pando, western Panama) range from virtually unmarked to heavily striped. Also, the total range in ventral pattern can be seen in selected juveniles (nearly unmarked) and adults (heavily marked) from the Cerro Pando population. Different patterns quite possibly occur in different frequencies from one population to the next, but large samples are needed for meaningful analysis.

Remarks: *Rhadinaea calligaster* was an uncommon species in museums until quite recently. This was due to its habitat rather than actual rarity, because it may be moderately common in montane rain forest (Myers, 1969c, fig. 16), few areas of which have been worked by herpetologists. It also occurs in high-elevation cloud forest of the montane thicket variety (Myers, 1969c, fig. 15). Specimens have been found abroad by day as well as under such cover as rocks, moss, and ground litter. Several adult females were found at a communal nest in a pile of decaying palm fronds, in a forest clearing in western Panama (fig. 50). The reader is referred to the remarks under *Rhadinaea decipiens*, for details of a curious parallelism in the coloration of certain individuals of *calligaster* and the distantly related *decipiens*.

Wettstein's (1934) specimen of "*Liophis* (=*Rhadinaea*) *pulveriventris*" from Volcán Irazú, Costa Rica, quite certainly is a misidentified *R. calligaster*, which the detailed description fits in every respect.

The specific epithet is a combination of the prefix *calli-* (beautiful) plus the noun *gaster* (belly), in reference to the bright, black-marked venter.

The *vermiculaticeps* Group

Three species are included in the *vermiculaticeps* group: *Rhadinaea pulveriventris*, *R. sargenti*, and

TABLE 14
ASPECTS OF INTERSPECIFIC VARIATION[a] IN THE *vermiculaticeps* GROUP

Species	N	Ventrals		Subcaudals		Tail Length as a Percentage	
		Males	Females	Males	Females	Males	Females
pulveriventris	12	119–124 (5) 121.6	124–134 (6) 128.8	71–80 (5) 74.8	63–70 (7) 66.4	28.9–31.5 (5) 30.1	25.9–29.5 (6) 27.4
sargenti	5	117–121 (4) 118.9	122 —	73, 74 73.5	67 —	33.8, 34.9 34.4	31.9 —
vermiculaticeps	5	117–119 (4) 118.0	121 —	76–82 (3) 78.7	63 —	33.7, 35.0 34.4	30.5 —
Combined ranges	22	117–124	121–134	71–82	63–70	28.9–35.0	25.9–31.9

[a]The following statistics are given: Above, range followed by number of specimens in parentheses (if more than two); below, mean.

R. vermiculaticeps. They inhabit wet montane and hill forest from northern Costa Rica to central Panama. The group is defined especially by the following combination of characters (see also table 3): The hemipenis (unknown in *pulveriventris*) has virtually straight spines, a basal naked pocket, and only soft papillae (no spinules) on the calyces. Scutellation is generalized; a subpreocular is present or absent. A broad middorsal dark stripe, or at least the hint of one in some individuals, in many cases encloses a paler vertebral line. The dark stripe diverges on the nape and, in two species, takes part in formation of a conspicuous, dark-edged, pale reticulum atop the head.

The species *R. sargenti* and *R. vermiculaticeps* are closely related and conceivably might even be conspecific, although the differences are ample to keep them separated at this time. They seem to be geographically separated by the structural depression across central Panama (region of the Panama Canal). *Rhadinaea pulveriventris* of Costa Rica lacks the conspicuous reticulum on the head, and its relationships were unsuspected until I noticed that some individuals have a median break in the short black stripe on the dorsum of the neck. It was then easy to visualize how loss of the dorsal head reticulation, and tendency for loss of the vertebral pale line, would result in the characteristically patterned head and neck of *pulveriventris*. I predict that the hemipenis of this species will prove similar to the virtually identical organs of *sargenti* and *vermiculaticeps*.

TABLE 15
NUMBER OF MAXILLARY TEETH IN THE *vermiculaticeps* GROUP

Species	N[a]	No. of Teeth			Range
		17+2	18+2	19+2	
pulveriventris	3	—	2	1	18+2–19+2
sargenti	1	—	—	1	19+2
vermiculaticeps	5	1	—	4	17+2–19+2

[a]A single maxilla from each specimen.

Rhadinaea pulveriventris Boulenger

Figures 36C, 37C, 38; map 13

Rhadinaea pulveriventris BOULENGER, 1896, pp. 635, 636. WERNER, 1929, p. 118. DUNN, 1932, p. 2. TAYLOR, 1951, p. 116. PETERS AND OREJAS-MIRANDA, 1970, p. 268.

Liophis pulveriventris (Boulenger): AMARAL, 1929b, p. 174.

HOLOTYPE: BMNH 1946.1.9.6 (not seen), formerly BMNH 95.7.13.15 (A. F. Stimson, *in litt.*), a female obtained by Underwood at Azahar de Cartago, [Cartago Province?], Costa Rica.

DIAGNOSIS: A median black streak extends forward a short distance on the neck and expands and bifurcates at the nape. Such a marking is found in no other species of *Rhadinaea*. A black stripe on the side of the head extends posteriorly as a diffused or narrow line along the side of the body. There is little or no indication of a vertebral stripe along most of the body,

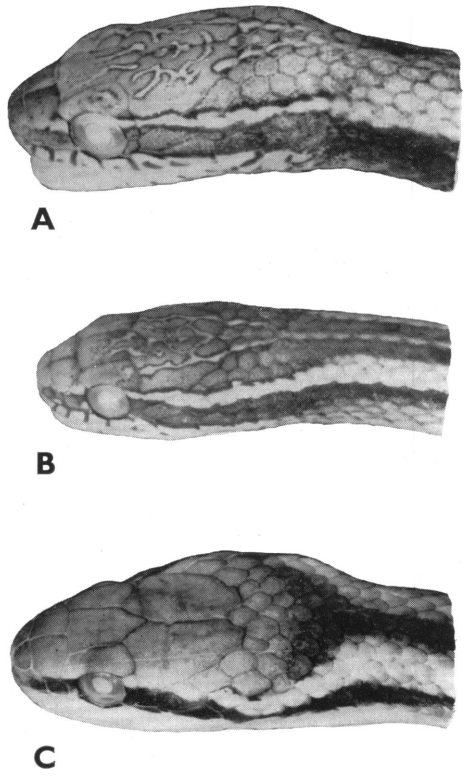


FIG. 36. Head patterns in the *vermiculaticeps* group. A. *Rhadinaea sargenti*, GML (no number), Panama. B. *R. vermiculaticeps*, FMNH 47464, Panama. C. *R. pulveriventris*, KU 112459, Panama.

which is nearly uniformly brown. Some individuals have dark-speckled venters.

DISTRIBUTION: Central Costa Rica, in the Cordillera Central, and in the Cordillera de Talamanca to extreme western Panama. Known elevations are 1372–1600 meters and the habitat, at least in Panama, is lower montane rain forest.

DESCRIPTION (12 SPECIMENS): The largest individual is a female 502 mm. total length, of which 148 mm. is tail; an adult male is not available. The tail is 28.9–31.5 percent of total length in juvenile males and 25.9–29.5 percent in females. The dorsal scales are in 17–17–17 rows, and weak anal ridges are present on one adult female. Ventrals are 119–134 (119–124, males; 124–134, females), and subcaudals are 63–80 (71–80, males; 63–70, females). There are eight supralabials and a variable number of infralabials, usually 10 but ranging from eight to 11. There is one preocular, no subpreocular,

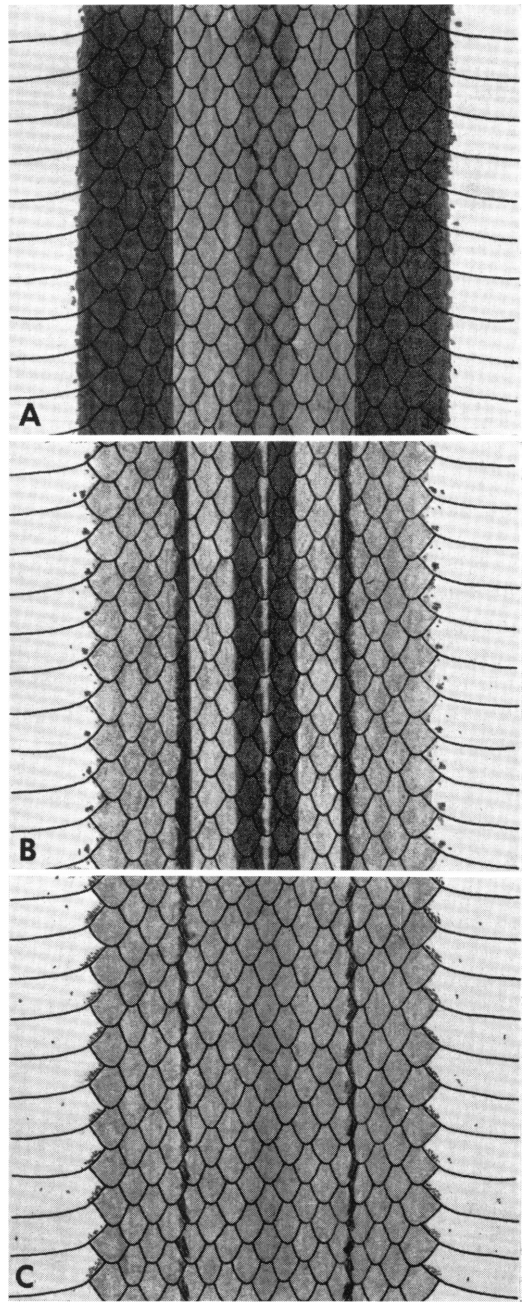


FIG. 37. Midbody color patterns in the *vermiculaticeps* group. A. *Rhadinaea sargenti*, GML specimen, Panama. B. *R. vermiculaticeps*, FMNH 109721, Panama. C. *R. pulveriventris*, MCZ 15261, Costa Rica.

two postoculars, and 1+2 temporals (1+1+2 in two individuals).

The body is nearly uniform brown for most of

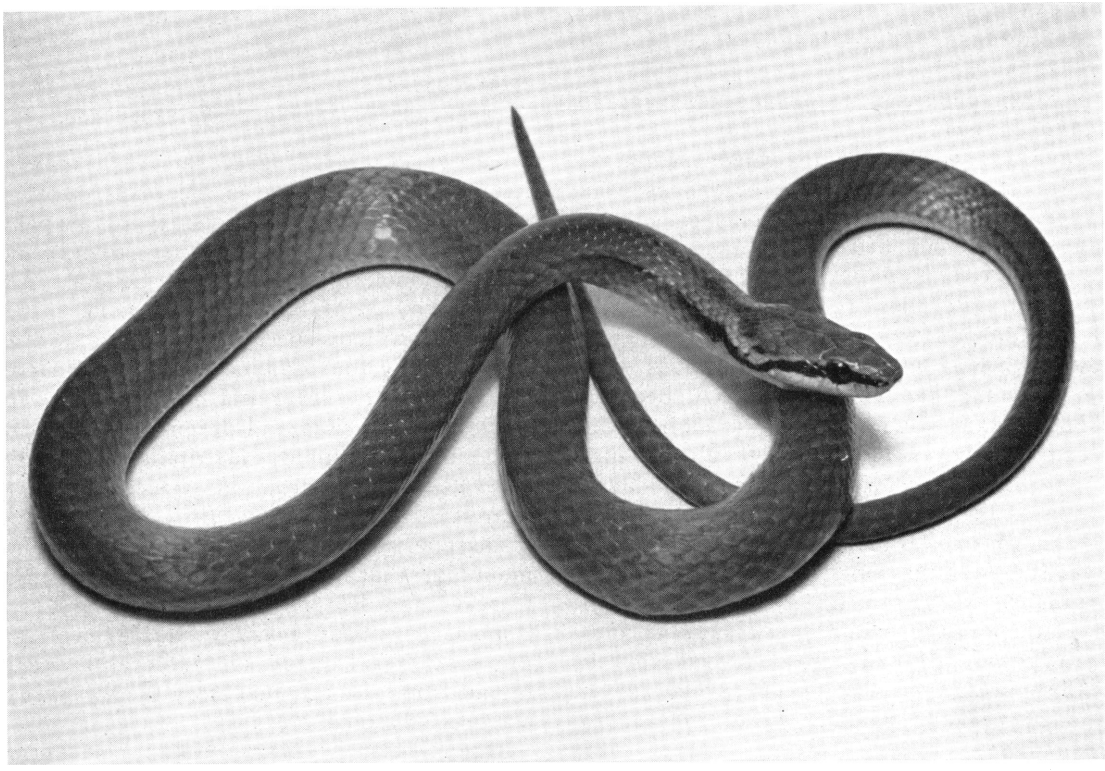


FIG. 38. *Rhadinaea pulveriventris*, KU 112459, from western Panama.

its length. A short, median black streak extends anteriorly on the neck and widens and bifurcates at the nape, producing on each side a short branch, the lower edge of which may continue as a thin line to the posterodorsal edge of the eye. The black streak on the neck is three rows of scales wide, but the middle (vertebral) row is in some cases brown like most of the body. The black streak fades behind the neck, although on some specimens it re-forms as a dark vertebral line on the end of the body and base of the tail. A black line across the rostral widens to form a black stripe that extends through the eye and crosses the corner of the mouth. This stripe then slants up to the neck and extends along the side of the body as either a black line on the adjacent edges of rows 4 and 5 or as a diffused line covering row 4 (and also the top of row 3 in one specimen). A conspicuously pale brown or whitish stripe extends from the upper rear edge of the eye to the side of the neck, between the dorsal and lateral black stripes.

The top of the head is uniform brown like the ground color of the body. The lateral black stripe edges the tops of the anterior supralabials and crosses the last two; otherwise the supralabials are white, being either immaculate or with a few black dots. Ventral surfaces are whitish, varying from immaculate to being heavily dotted with black; some individuals have slight concentrations of blackish pigment on the tips of the ventrals and subcaudals.

A specimen (KU 112459) from Panama had the following coloration in life: Body golden brown with yellowish tinge on lowest two scale rows. Supralabials pinkish white. Underside of head and throat white, turning slightly yellowish on the ventral surfaces posteriorly. Iris deep reddish brown, turning pale reddish tan on extreme upper part. Tongue reddish brown with black tips. I neglected to note the color of the postocular light stripe, but color transparencies show it to be pale brown, almost whitish.

There are 18+2, 18+2, and 19+2 teeth on a maxilla from each of three adults. The ultimate prediastemal tooth is anterior to the front edge

of the ectopterygoid process in two specimens and posterior in a third. The last fang is offset laterad.

The hemipenis has not been studied, as no adult males were available.

REMARKS: Nearly the entire range of variation can be seen in a lot of nine hatchlings from Volcán Poas, Costa Rica. The eggs (two clutches) were hatched in Michigan, and the artificial environment may have been the cause of certain scale aberrations. One of the juveniles has the prefrontals fused along the posterior halves, whereas another has an azygous scale below the first temporal on the left, between labials 6 and 7. The only specimen not from the volcanic region of central Costa Rica is one that I found in extreme western Panama in lower montane rain forest (Myers, 1969c, fig. 17), a little known habitat that probably is continuous along the Atlantic slopes of the Cordillera de Talamanca. My specimen was stretched motionless on the forest floor in a sunny period at midday and evidently had been disturbed while it was foraging. It was very docile, twining about one's fingers and making little attempt to escape.

Taylor (1951) accepted a record (Wettstein, 1934) of this species from Volcán Irazú, Costa Rica, but translation of Wettstein's detailed description provides sufficient proof that it is based on a specimen of *Rhadinaea calligaster*. The specimen falls within the range of variation of *calligaster* in all details, especially in the presence of black-edged labials and transverse black streaks across the belly.

The specific epithet is formed from the genitive of *pulvis* (dust) plus *ventris* (belly) in obvious allusion to the dark speckling on the belly of the holotype. The dark specks are absent on some specimens. I have not seen the holotype, and Boulenger does not mention the black nape marking that is a conspicuous feature of specimens that I examined. However, A. F. Stimson (*in litt.*) kindly provided the following information about the holotype: "The ground colour on the neck between the light stripes is dark brown forming a median dark stripe 4 scales wide which bifurcates anteriorly. The dorsal ground colour on the body is pale brown, minutely speckled with darker. These speckles are a little more numerous on the vertebrals and paravertebrals thus producing an obscure vertebral stripe which becomes very indistinct anteriorly."

Rhadinaea sargenti Dunn and Bailey

Figures 36A, 37A; map 13

Rhadinaea sargenti DUNN AND BAILEY, 1939, pp. 10, 11. PETERS AND OREJAS-MIRANDA, 1970, p. 268.

HOLOTYPE: MCZ 42788, an adult male in fair condition, from the Pequení-Esperanza ridge near the head of the [Río] Pequení, 1800 feet [549 meters], [Panama Province, not Canal Zone], Panama. The specimen was obtained by W. M. Sargent about 1936.

DIAGNOSIS: This species differs from all of its congeners by the combined features of a pale reticulum on the head and blackish sides. The uniformly dark sides and the presence of weak, rather than bold, middorsal striping distinguishes *Rhadinaea sargenti* from *R. vermiculaticeps*, its nearest relative.

DISTRIBUTION: Known only from the low mountains that form the watersheds of the Río Chagres and Río Pequení, east of the Canal Zone in central Panama. The known elevational range is 305–771 meters, and all localities are in humid tropical forest that is on the wet side of evergreen seasonal forest.

DESCRIPTION (FIVE SPECIMENS): The largest female is 310 mm. total length, of which 99 mm. is tail; the largest male (the holotype) is 307 mm. total, 107 mm. tail length. The large female is an adult as proved by the presence of large oviductal eggs, and the holotype is sexually mature as indicated by the condition of the ducti deferentia, which are enlarged and convoluted. The tail is 33.8 and 34.9 percent of total length in two males and 31.9 percent in a female. The dorsal scales are in 17–17–17 rows; anal ridges are present on one of the male paratypes. Ventrals are 117–122 (117–121, males; 122, female) and subcaudals are 67–74 (73, 74, males; 67, female). There are eight supralabials and 10 infralabials (9/10 in one). There is one preocular, two postoculars, and 1+2 temporals. One individual has a subpreocular between the upper edges of supralabials 3 and 4.

The tips of the ventrals and the lower three and one-half scale rows are black or blackish brown. The dorsum is brown. Either the median three scale rows, or only the paravertebrals and adjacent edges of the vertebral row, are somewhat darkened and have a grayish aspect, turning to a more definite median gray line atop the tail. The top of the head is brown, with a black-edged, whitish reticulum from the level of the

eyes back. The reticulum tends to merge to a single line on the nape. A narrow, black-edged whitish stripe extends from the canthus rostralis through the top of the eye and passes on to the side of the neck, where it blends into the dorsal brown coloring above the black side. A dark brown stripe passes along the side of the head and into the dark side of the body. A few specimens (especially MCZ 42764) have a tendency for a black-edged white line extending from the lower edge of the eye to the lower side of the neck, immediately below the dark head stripe. The supralabials have black sutures and black spots. The ventral surfaces are white, with irregular black punctation that in some specimens becomes heavy under the tail. The venter is red in life, judged from recently preserved specimens (Dunn and Bailey, 1939; personal observ.).

I examined a single maxilla that has 19+2 teeth. The ultimate prediastemal socket is anterior to the front edge of the ectopterygoid process; the last fang is offset laterad.

The retracted hemipenis extends to the level of subcaudal 8 or 9, and the retractor muscle originates at subcaudal 23 or 24. The capitulum comprises less than half the length of the hemipenis on its sulcate side. The calyces bear soft papillae only. The sulcus spermaticus forks barely above the edge of the capitulum and the branches extend to the end of the uneverted organ; the inner walls of the sulcus are slightly convoluted (at least in the Gorgas Memorial Laboratory specimen). The wall of the capitulum makes a single large fold on the asulcate side. Below this, the edge of the capitulum overhangs a rather large nude area, which is partitioned by a wall of thin tissue fringed with slender papillae on the free edge. Below this overhang there are two close rows of four spines each, with a median spine between the bases of the two rows. The top of one of the rows is continuous with the basal edge of the thin wall of tissue under the edge of the capitulum, but otherwise the rows are equivalent. These spines are long and virtually straight, and the basal ones are largest, being about one-third the length of the entire organ. To either side of the large spines are several dozen medium and small, slightly recurved spines. The basal fourth (at least) of the organ is free of ornamentation except for minute spinules. The base is an area of thick, convoluted folds of tissue except for a nearly smooth basal naked pocket on the dorsal wall. The preceding description is based on the uneverted hemipenes of MCZ 42764 and especially an unnumbered specimen of the Gorgas Memorial Laboratory. The hemipenis is quite similar to the illustration for *R. vermiculaticeps*. The convoluted walls of the sulcus spermaticus might mean that the organ was not completely retracted, rather than indicating a specific difference. A smaller part of the base seems to be free of spines in *sargenti* as contrasted with *vermiculaticeps*, but the specimens are not at hand and I cannot check this.

REMARKS: There are some minor mistakes concerning scale counts in the brief, original description, but these are not worth elaborating. A single "type" is designated at the start of the description, and so the word "cotypes" on a following page has no validity. The four numbered specimens (MCZ) listed in the original description may be regarded as paratypes; the two unnumbered heads probably were returned to the Gorgas Memorial Laboratory.

The species was named for W. M. Sargent, head of a surveying party that obtained five of the six specimens available to Dunn and Bailey. The workmen called this snake "*vibora candela*" according to Dunn and Bailey. This is a general sort of name used for some other red or partly red snakes (e.g., *Pseudoboa neuwiedii*) in Panama, and does not imply that *Rhadinaea sargenti* is common or widespread enough to have its own vernacular name.

Rhadinaea vermiculaticeps (Cope)

Figures 2B, 36B, 37B, 39; map 13

Taeniophis vermiculaticeps COPE, 1860a, pp. 249, 250; 1861, p. 74.

[*Rhadinaea*] *vermiculaticeps* (Cope): COPE, 1863, p. 101.

Rhadinaea vermiculaticeps (Cope): COPE, 1887, p. 80. BOULENGER, 1894b, p. 177. WERNER, 1929, p. 119. DUNN, 1932, p. 1. TAYLOR, 1951, pp. 116, 117 (part, MCZ 42764 is a paratype of *R. sargenti*).

Coronella vermiculaticeps (Cope): GÜNTHER, 1893 (1885–1902), p. 111.

Liophis vermiculaticeps (Cope): AMARAL, 1929b, p. 175 (misspelled "*vermimaculaticeps*").

DESIGNATION OF LECTOTYPE: The name *Taeniophis vermiculaticeps* was based on three specimens in the Academy of Natural Sciences of Philadelphia. Two specimens were said to have been discovered by R. W. Mitchell in "Veragua, New Grenada," and the third was listed as

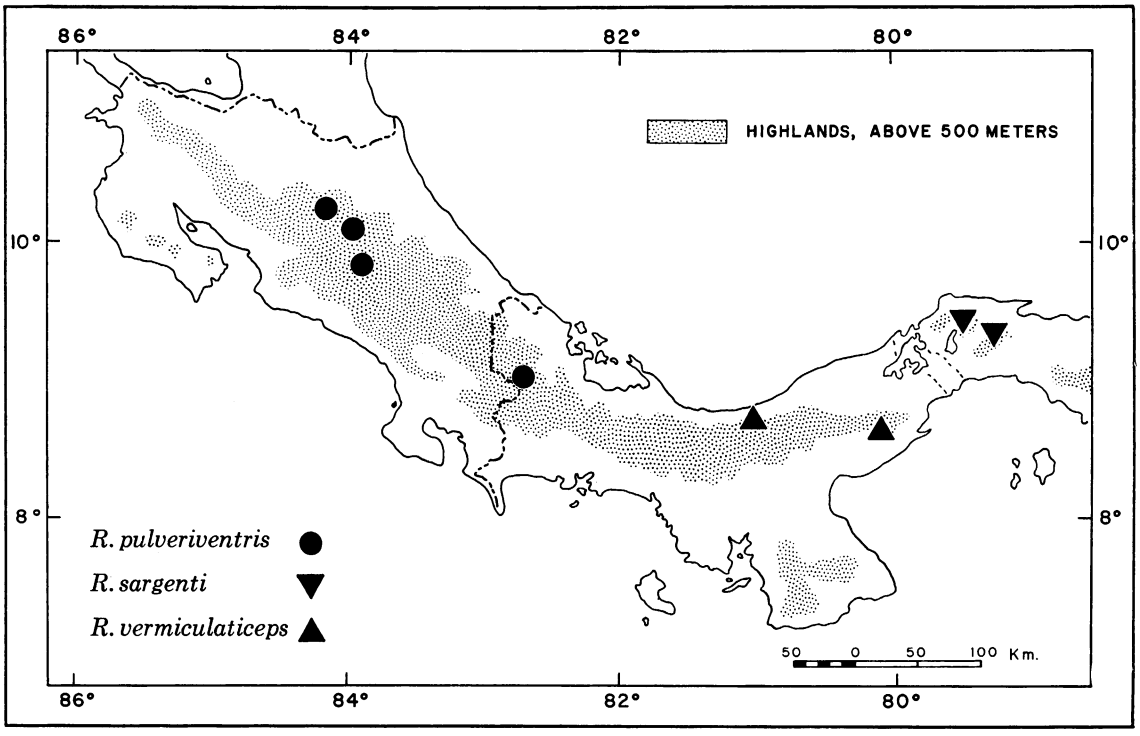
"native country unknown" (Cope, 1860a, p. 250). The two Mitchell specimens evidently are ANSP 3534 and 3535, now labeled "Panama: Cocuyas [*sic*] de Veraguas," and the third is ANSP 3741. All three are males.

ANSP 3535 is here designated lectotype because it is somewhat the best preserved of the syntypes and because it seems to be the one that Cope used for data on scutellation. The lectotype has the fourth and fifth supralabials entering the eye (on each side) as stated by Cope. This applies also to ANSP 3741 but not to ANSP 3534, which has the third to fifth labials entering the eye on each side. The lectotype has 9/10 infralabials (plates 3 and 4 are fused on the left side). Cope gave 10 infralabials, which could apply to ANSP 3534 (10/10) but not to ANSP 3741, which has 9/9. Not one of the specimens agrees precisely with the 117 ventrals and 79 subcaudals cited by Cope. ANSP 3534 has 117 ventrals but only 76 subcaudals, whereas ANSP 3741 has 118 ventrals and 82 subcaudals. The lectotype is perhaps closest, with 118 ventrals and 78 subcaudals. Cope stated that the anal plate is single but all three syntypes have it divided. Cocuyos de Veraguas, Veraguas Province, Panama, is here accepted as the probable type locality (see Remarks).

DIAGNOSIS: Specimens of *Rhadinaea vermiculaticeps* are easily recognized by the combination of a pale reticulum on the head and a broad (three scale rows) middorsal black stripe that is broken along the middle by a pale line. The related *R. sargenti* may have a weak indication of the dorsal stripe but the sides and ventral tips are uniformly dark, whereas *vermiculaticeps* has lighter sides with a dark line and the ends of the ventrals have dark dots.

DISTRIBUTION: West-central Panama, probably in humid forest of moderate elevation. The only definite elevation is 2750 feet (838 meters) for a specimen (FMNH 109721) from El Valle, Coclé Province. The species is sometimes listed from "Costa Rica" (but see Remarks).

DESCRIPTION (FIVE SPECIMENS): The largest individual is a female 374 mm. total length, of which the tail is 106 mm. The male lectotype is 340 mm. total, 119 mm. tail length. These are considered adults because they are larger than sexually mature specimens of the very similar



MAP 13. Locality records for species of the *vermiculaticeps* group in highlands of Costa Rica and Panama.

R. sargenti (*q.v.*) and because the hemipenis of the lectotype is well developed. The tail is 33.7 and 35.0 percent of total length in two males and 30.5 percent in a female. The dorsal scales are in 17–17–17 rows; a few weak anal ridges are present on two males. Ventrals are 117–121 (117–119, males; 121, female) and subcaudals are 63–82 (76–82, males; 63, female). There are eight supralabials (9/8 in one) and 10 infralabials (9/9, 9/10, in two specimens). There is one preocular, two postoculars, and 1+2 temporals. Two specimens from El Valle are the only ones in which a subpreocular is present, between the upper edges of the third and fourth labials on one or both sides. One of the syntypes (ANSP 3741) has the left loreal fused with the nasal plate.

The ground color of the body is light brown. A brown stripe passes along the side of the head and onto the neck, where it is narrowed to a blackish line that extends the length of the body on adjacent parts of scale rows 4 and 5. This line tends to be somewhat blurred along its lower edge. A broad, blackish middorsal stripe on the median three scale rows is broken along the middle by a whitish line, which either covers all of the vertebral row or only its midline. (Because of the pale line, the middorsal pattern could as well be described as a pair of dark paravertebral stripes.) The lateral and dorsal stripes extend nearly to the end of the tail; the pale vertebral line disappears gradually on the tail. The top of the head is brown, with a conspicuous black-edged, whitish reticulum from the eyes back. The posterior parts of this reticulum merge on the nape, thus forming the pale vertebral line that extends to the tail. A narrow, black-edged whitish stripe extends from the canthus rostralis (where it is faint) through the top of the eye and passes to the neck, where it blends into the brown of the body. The supralabials and infralabials are dotted with black and also may tend to have black sutures. The venter is white. There is a conspicuous dark dot near the rear margin of each ventral tip, changing to a dark line along the ends of the subcaudals. Two specimens from El Valle have an additional amount of dark speckling along the sides of the belly and over the subcaudal surfaces.

A maxilla was examined from each of five specimens. There are 17+2 (one specimen) or 19+2 teeth. The ultimate prediastemal socket is posterior to the front edge of the ectopterygoid process; the last fang is offset laterad.

The retracted hemipenis extends to the level of subcaudal 8 or 9, and the retractor muscle originates at subcaudal 21 or 23. The capitulum comprises less than half the length of the hemipenis on its sulcate side. The calyces bear soft papillae only. The sulcus spermaticus forks barely above the edge of the capitulum and the branches extend to the end of the uneverted organ; the inner walls of the sulcus are smooth and straight, without convolutions. The wall of the capitulum makes a single large fold on the asulcate side; the papillae are somewhat larger and thinner on this fold than elsewhere. Below the fold, the capitulum overhangs a rather large

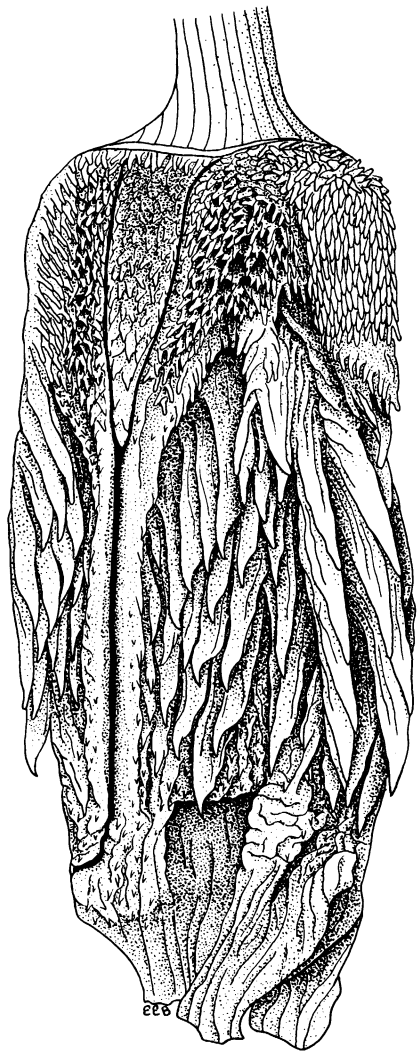


FIG. 39. Hemipenis of *Rhadinaea vermiculaticeps*, FMNH 47464, left organ. × 12.

nude area, which is partitioned by a wall of thin tissue that is fringed with slender papillae on the free edge. Below this overhang there are two close rows of four spines each, with a median spine at the base of the two rows. The top of one of the rows is continuous with the basal edge of the thin wall of tissue under the edge of the capitulum, but otherwise the rows are equivalent. These spines are long and virtually straight, and the basal ones are largest, being about one-third the length of the entire organ. To either side of the large spines are several dozen medium and small, slightly recurved spines. There are no spines on the basal third of the organ, only minute spinules. The base is an area of thick, convoluted folds of tissue, except for a nearly smooth basal naked pocket on the dorsal wall. The preceding description is based on the retracted hemipenes of ANSP 3535 (lectotype) and especially FMNH 47474 (illustrated).

REMARKS: "Costa Rica" usually is listed as part of the range of this species, on the authority of Cope (1887, p. 80; not 1863, p. 101 as stated by Taylor, 1951). It would be no surprise to find *Rhadinaea vermiculaticeps* in Costa Rica, especially on the Atlantic slopes of the Cordillera de Talamanca, but the species should not be included in the fauna of that country until a specific record becomes available.

Cocuyos de Veraguas, the probable type locality, is occasionally misspelled "Cucuyas" or "Cucullo." In western Panama, the name *cocuyo* is applied to elaterid beetles having luminescent ocelli, and perhaps also to fireflies. The locality itself is a gold mine near the Río Concepción on the Atlantic side of Veraguas Province; Alexander Wetmore (*in litt.*) placed the locality near latitude 8°45′N, longitude 81°W. I collected near the mouth of the Río Concepción for several days in late October, 1966, and was told by local residents that the mine was about a one-day walk from the mouth of the river. Unfortunately I was unable to make the trip, as the sudden onset of seasonally strong winds (about November to April along this coast) forced us to put to sea while the mouth of the river could still be navigated. The mine had been closed for several decades at that time, but there was local expectation that it might soon be reopened.

The specific epithet is formed from the adjective *vermiculatus* (wormy) plus the New Latin noun *ceps* (head), in obvious reference to the vermiculated color pattern of the head.

THE *lateristriga* GROUP

Seven or possibly eight species are included in the *lateristriga* group: *Rhadinaea decipiens*, *R. dumerilii*, *R. fulviceps*, *R. guentheri*, *R. lateristriga*, *R. multilineata*, *R. pachyura*, and a *species inquirenda*. They are snakes both of the highlands and of humid, forested lowlands, and occur in lower Central America, in the northern Andes to Peru, and in the coastal cordillera of Venezuela. The group is defined especially by the following combination of characters (see also table 3): The hemipenis and retractor muscle are undivided, and there is a small naked pocket in the asulcate edge of the capitulum (the pocket is formed either from an enlarged calyx or between two fusions of the edge of the capitulum with the underlying stalk). There is a subpreocular, a tendency toward 1+1 temporals, usually no anal ridges, and a high number of subcaudals (more than 80). The tail is very long (usually more than 35 percent of total length) and disproportionately thick (fig. 5) for much of its length. The brown or black body tends to have one or two white lateral lines or to be unicolor; there is a tendency for pale ocelli or a ring on the neck, or for the head to be a paler color than the body.

The *lateristriga* assemblage is one of the most distinctive and easily recognized groups of *Rhadinaea*, but its species have been among the most difficult to define and diagnose, and I should not be surprised if new material necessitates revision of some of the species concepts. The specimen treated as "*species inquirenda*" is the only specimen of *Rhadinaea* that I have been unable to identify. Possibly it represents an undescribed species, but this is by no means certain.

Rhadinaea decipiens (Günther)

Figures 40A, 41D, E, 42F, 43, 49D; map 14

Ablabes decipiens GÜNTHER, 1893 (1885–1902), p. 105, pl. 37 (color pattern, and details of cephalic scutellation).

Urotheca lateristriga (not of Berthold): BOULENGER, 1894b, pp. 181, 182 (part); 1896, p. 636 (?part; specimens not seen).

Rhadinaea albiceps AMARAL, 1924, p. 200 (holotype: USNM 22446, "probably from Ecuador," obtained by Mark B. Kerr in 1890s). New synonymy.

Liophis albiceps (Amaral): AMARAL, 1925, p. 7; 1929b, p. 170. PETERS, 1960, p. 527. PETERS AND OREJAS-MIRANDA, 1970, p. 176.

TABLE 16

ASPECTS OF INTERSPECIFIC VARIATION[a] IN THE *lateristriga* GROUP

Species	N	Ventrals		Subcaudals		Tail Length as a Percentage	
		Males	Females	Males	Females	Males	Females
decipiens	13	132–137 (5) 134.4	122–140 (8) 134.8±1.55	121 —	90–114 (5) 104.2	46.9 —	35.2–46.3 (5) 41.2
dumerilii	4	128, 129 128.5	137, 139 138.0	— —	117 —	— —	37.5 —
fulviceps	18	138–142 (8) 139.8±1.58	136–143 (9) 138.6±1.39	112–122 (7) 115.4	98–109 (6) 102.3	41.9–44.6 (7) 43.3	39.3–43.5 (4) 41.1
guentheri	11	135–164 (7) 141.7	147–176 (4) 160.5	98, 110 104.0	82, 98 90.0	38.5, 42.7 40.6	27.5, 36.3 31.9
lateristriga	12	144–162 (4) 153.5	153–167 (8) 159.9	87, 92 89.5	82, 87 84.5	32.0, 32.3 32.2	32.3, 33.3 32.8
multilineata	16	133–146 (6) 140.0	142–151 (10) 147.2±1.28	99–103 (4) 102.0	84–100 (6) 90.7	36.8–42.9 (4) 40.1	34.7–37.3 (5) 36.1
pachyura	7	130–134 (3) 131.7	132–138 (4) 134.3	124 —	104 —	40.9 —	— —
species inquirenda	1	132 —	— —	119 (+ ?) —	— —	41.1 —	— —
Combined ranges	82	128–164	122–176	87–124	82–117	32.0–46.9	27.5–46.3

[a]The following statistics are given if the sample is sufficiently large: Above, range followed by number of specimens in parentheses (if more than two); below, mean and standard error of the mean.

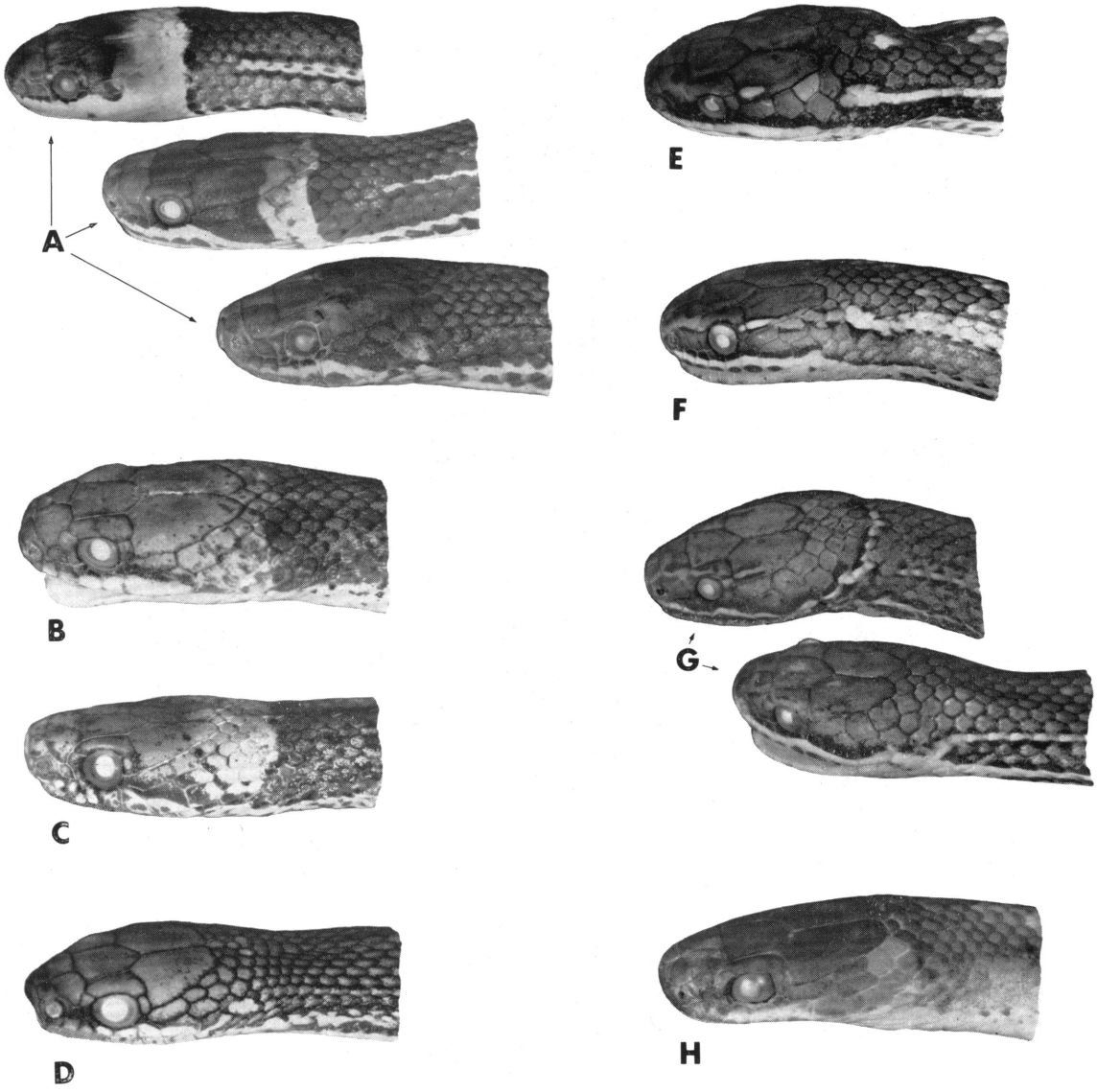


FIG. 40. Head patterns in the *lateristriga* group. A. *Rhadinaea decipiens*—top, KU 84677, Costa Rica; middle, KU 35637, Costa Rica; bottom, KU 112440, Panama. B. *R. pachyura*, USC 2933, Costa Rica. C. *R. fulviceps*, KU 112455, Panama. D. *R. dumerilii*, AMNH 103823, Colombia. E. *R. guentheri*, LSU 8761, Costa Rica. F. *R. multilineata*, AMNH 98284, Venezuela. G. *R. lateristriga*, Ecuador—upper, ANSP 3348; lower, UIMNH 55724. H. *Species inquirenda*, USC 1036, Costa Rica.

Rhadinaea pachyura decipiens (Günther): DUNN, 1938, p. 198; 1942b, pp. 4, 5. TAYLOR, 1951, pp. 118, 119.
Rhadinaea decipiens decipiens (Günther): TAYLOR, 1954, pp. 679, 740. SMITH AND GRANT, 1958a, p. 212. PETERS AND OREJAS-MIRANDA, 1970, p. 264.

SYNTYPES: Three specimens in the British Museum of Natural History, obtained by Rogers at [Volcán?] Irazú, [Cartago or San José Province], Costa Rica. Only one of these three specimens is a male (A. F. Stimson, *in litt.*), rather than two as indicated by Boulenger (1894b, p. 182). I have seen only the male (BMNH 1946.1.3.96), which is in poor condition; it has decayed at the head and at

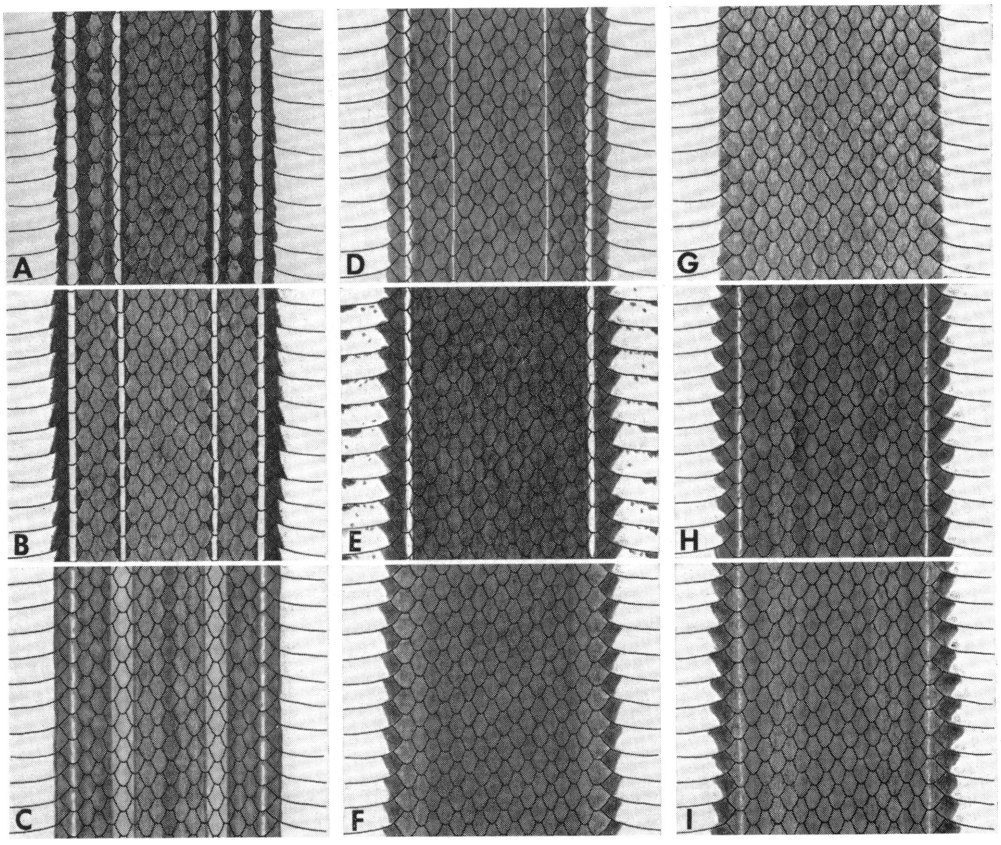


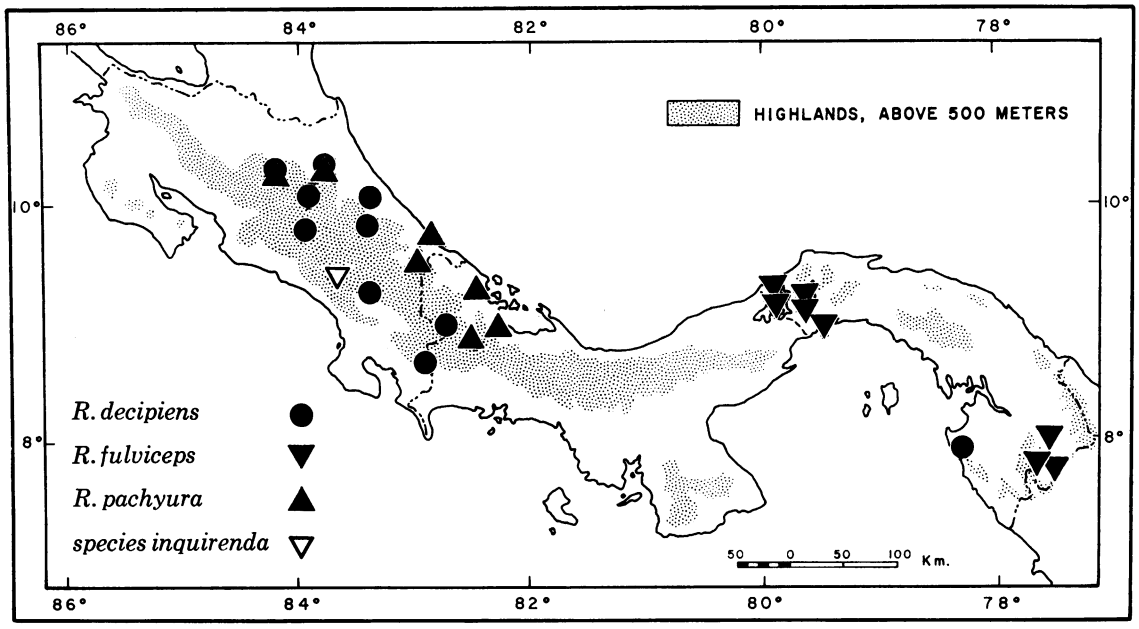
FIG. 41. Midbody patterns in the *lateristriga* group. A. *Rhadinaea guentheri*, USC 209, Costa Rica. B. *R. lateristriga*, UIMNH 55724, Ecuador. C. *R. multilineata*, AMNH 98284, Venezuela. D, E. Both *R. decipiens*, as follows: D. KU 84677, Costa Rica; E. KU 112439, Panama (presence of a ventral pattern is not correlated with either presence or absence of pale line on row 5). F. *R. dumerilii*, AMNH 103823, Colombia. G. *Species inquirenda*, USC 1036, Costa Rica. H. *R. pachyura*, USC 2933, Costa Rica. I. *R. fulviceps*, KU 112453, Panama.

midbody, but the hemipenes are in good condition and the body pattern is discernible. I prefer not to designate a lectotype at this time.

DIAGNOSIS: *Rhadinaea decipiens* is one of several species (all in the *lateristriga* group) with a definite white line on the first row or between the first and second rows of scales. It is distinguished from all other such species, except *R. pachyura* and *R. fulviceps* (which does not always have the line), in that it never has pale ocelli or pale longitudinal lines on the head or nape. Specimens from some populations of *decipiens* have an additional thin white line on the fifth row of scales, and thus differ from *fulviceps* and *pachyura*, which never have such a line, although a broader, ill-defined and diffuse, pale streak may be present. *Rhadinaea decipiens* usually has a narrow or wide, pale orangish, pinkish, or light brown band across the rear of the head and nape; no other member of the *lateristriga* group has a collar (except possibly the juveniles of *R. fulviceps* and *R. pachyura*, on which more data are needed).

Specimens from some populations of *R. decipiens* lack a white line on row 5 and also lack a pale collar. But the supralabials of such specimens are nearly black, except for a conspicuous, longitudinal white line. *Rhadinaea fulviceps* and *R. pachyura* have speckled or brown-spotted supralabials, or brown extensions along the sutures, but no conspicuous white line. Also, the white line on the lower row of body scales seems invariably sharper and more definite in *decipiens* than in the other two species.

Occasional specimens of *R. decipiens* have bold



MAP 14. Locality records for four closely related species of the *lateristriga* group in Costa Rica and Panama. (Two South American records of *Rhadinaea decipiens* are not plotted [Sta. Rita north of Medellin, Colombia, and "Ecuador"]; but see map 15 for southern records of *R. fulviceps*.)

black markings on the ventral midline and thus might be confused with *R. calligaster*, the only other species of *Rhadinaea* that has large and regularly placed ventral markings. But *calligaster* differs in many ways; for example, it lacks white lines on the body, has bold black margins on the supralabials, and has a much shorter tail than *decipiens*.

DISTRIBUTION: Costa Rica to Colombia, as follows: Northeastern and central Costa Rica in the Cordillera Central and adjacent lowlands; central Costa Rica to western Panama in the Cordillera de Talamanca; southeastern Costa Rica (and possibly adjacent Panama) in the Pacific lowlands; eastern Panama in the Serranía del Sapo, and northern Colombia in the Cordillera Central. A questionable record for Ecuador (see Remarks).

Rhadinaea decipiens has been taken at known elevations of 0015–1600 meters in Costa Rica, 910–1620 meters in Panama, and at 2740 meters in Colombia. I have collected it in lower montane rain forest in western Panama (Myers, 1969c, fig. 17), and in cloud forest of the elfin woodland type in eastern Panama (Myers, 1969c, fig. 9). All the known lowland localities are in regions of tropical rain forest.

DESCRIPTION (15 SPECIMENS): See Remarks section for discussion of an additional specimen (holotype of *R. albiceps*) that differs in some respects from the description following.

The largest individual of *Rhadinaea decipiens* examined is a female 569 mm. total length, 225 mm. tail length; the only male having a virtually complete tail (lacking the very tip) is 490 mm. total, 230 mm. tail length. The tail is 46.9 percent of total length in the aforesaid male, and 35.2–46.3 percent in females. The dorsal scales are in 17–17–17 rows; anal ridges are absent. There are 122–140 ventrals (132–137, males; 122, 131–140, females), and 90–121 subcaudals (121, male; 90–114, females). There are eight supralabials (9/8, two specimens), and 10 or in a few cases nine infralabials. There is usually one preocular (1/2, one specimen, 2/2, two), a subpreocular between the third and fourth labials, and two postoculars. Usually there are 1+1 temporals, but a few specimens have 1+2, or (on one side only) 1+1+1.

The body varies from medium brown to black. A narrow, sharply defined, white line originates on the lower side of the neck and extends caudad between rows 1–2 or on the top or middle of row 1; on the tail, the lower edge of this line

tends to merge with the white color of the subcaudals. Specimens from some populations have an additional, usually thinner white line originating on the neck and extending along the middle or top of row 5, and extending well onto the tail.

Specimens having two white lines on each side, as just described, also have a pale band or collar across the nape and rear of the head, with the front part of the head being dark like the body. The anterior edge of the collar lies anywhere from immediately behind the tips of the parietals to immediately behind the posterior apex of the frontal, and the marking extends one to four scales back on the neck. The collar is continuous with the pale throat color, and sometimes with the pale areas of the supralabials.

Some specimens that do not have a dorsolateral line on row 5 also lack the pale collar, both as juveniles and adults (see Geographic Variation). Other individuals lacking the dorsolateral line have, at most, a very narrow or a very faint collar.

The rostral plate is dark around its upper border, and pale on its lower part, often without discrete marking. The dark head color encroaches onto the tops of the supralabials, which may be nearly immaculate white below, or which may have a row of close or actually fused black spots along the edge of the mouth, thus restricting the pale ground color to the form of a horizontal white line across the middle of the labials. The infralabials range from being nearly immaculate to heavily spotted with brown or black. The ventrals and subcaudals are tipped with the dark body color, which forms an almost straight edge on some specimens, and a strongly serrated edge on others. The venter is otherwise white, except that some specimens have dark brown or black spots. These may be scattered irregularly, or arranged in a medial series on the belly, and, in the latter case, with either paired spots or a medial line under the tail.

Complete or partial color notes made before preservation are available for a number of specimens: The band across the rear of the head, when present, has been described by collectors as pink (KU 84677), orange (KU 103893), pale orangish (KU 112441), yellow-orange (USC 8282), yellowish (KU 112439) and dull brown (KU 103892); in preserved material, the collar varies from white to a poorly contrasting brown. The dorsolateral line, when present, is white (USC 8282), gray (KU 103892), or pale yellow (KU 103893); the lateral line and the pale parts of the supralabials seem invariably to be white (KU 103892, 103893, 112439–112441; USC 8282). The venter is white (KU 84677, 103893, 112441) but not always uniformly so: KU 103892 and USC 8282 were pale yellow under the head and throat. KU 112439 and 112440 had white chins, turning yellow under the neck; the latter specimen had a creamy white belly and tail, whereas in the former the belly was greenish white and the underside of the tail bluish white. The iris is dark brown (KU 103893; USC 8282) or reddish brown (KU 112439, 112440), and the tongue is black except for the tips of the fork, which are pure white (KU 103893, 112439–112441; USC 8282). The dorsa of a few specimens (KU 84677, and especially USC 141) are rich, medium brown in preservative and probably are little changed from life. The dorsal body surfaces of fresh material have been noted as dark brown (KU 103893), brownish black (KU 103892), black (KU 112441), and jet black (USC 8282). KU 112439 also had a black dorsum, as did KU 112440 from a few hundred meters lower elevation in the same geographical area, but the latter specimen also had a strong dorsolateral suffusion of light olive-green—the same hue as on the dorsa of some specimens of *Rhadinaea calligaster* from the same region (Cerro Pando, western Panama).

There are 15–17 maxillary teeth, increasing in size posteriorly, followed by a broad diastema and two fangs. The ultimate prediastemal socket lies well anterior to the ectopterygoid process. The fangs are little, if any, enlarged over the posterior prediastemal teeth, but there is a tendency for them to project deeper into the mouth because of the shape of the maxilla. The last fang is offset laterad.

The hemipenis is long and slender. It is single or nearly so; I have detected no divisions in the ends of retracted organs, although the everted hemipenes of one specimen (KU 112440) show a very slight indication of bilobation. The retracted hemipenes of three specimens extended *in situ* to subcaudals 8 (one specimen) and 12 (two), and the everted organs of three additional specimens extended to subcaudals 8 and 9. The retractor muscles of three specimens originated at the levels of subcaudals 22, 29, and 31. The capitulum is small, but its relative size is quite variable, comprising as much as one-third to as

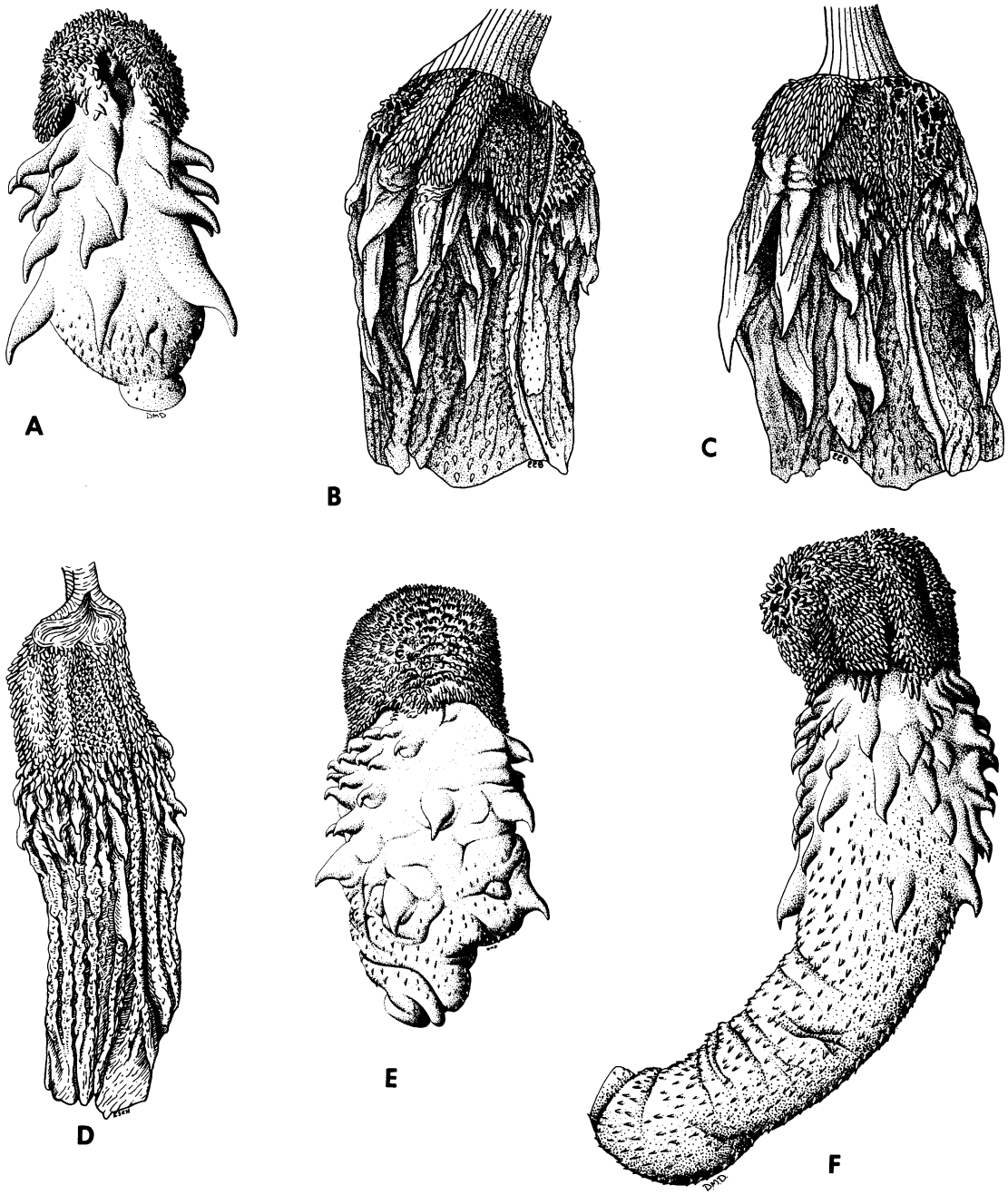


FIG. 42. Hemipenes of the *lateristriga* group. A, B. *Rhadinaea lateristriga*, left everted organ of USNM 151680 and right retracted organ of AMNH 23028. Both ×7.5. C. *R. guentheri*, USC 151, right organ. ×7.5. D. *R. dumerilii*, MNHN 733 (holotype), right organ. ×5. E. *R. fulviceps*, KU 112455, right organ. ×5. F. *R. decipiens*, KU 112440, left organ. ×6.

little as one-fifth of the length of the organ on the sulcate side. The sulcus spermaticus forks slightly above the edge of the capitulum and the branches extend to the end of the retracted organ, but little more than halfway up the capitulum when the organ is everted. The calyces are

spinulate over the asulcate folds and toward the periphery of the capitulum, and papillate on most of the sulcate side. The wall of the capitulum forms a poorly defined, double or partially double fold on the asulcate side of the retracted organ. The hemipenis is only weakly capitate; the edge of the capitulum is fused to the stalk at the base of each half of the asulcate fold. There is a moderately enlarged calyx between the basal parts of the asulcate fold, slightly above the edge of the capitulum; when the hemipenis is everted, this calyx becomes a small but conspicuously deep "pocket" above the edge of the capitulum on the asulcate side. There are about 70–85, or as few as 45 (KU 103893), small to medium, slightly recurved spines below the capitulum, above the basal half of the hemipenis. The spines are small on the sulcate side and become larger toward the asulcate side, where there is a small nude area that is bordered below and on each side by a few medium-sized spines; this area, which lies below the "pocket" in the capitulum, is not especially evident on the everted organ. The largest of the medium-sized spines are at the bottom of the spinose zone. The basal half of the organ is unadorned save for minute spinules. The preceding description is based on retracted hemipenes from BMNH 1946.1.3.96, KU 103893, and USC 94, and on everted organs from KU 103892, 112440 (illustrated), and USC 8292.

Geographic Variation: Populations from the Cordillera Central, and adjacent lowlands of northeastern Costa Rica, are characterized by specimens with two white lines on each side of the body and by a conspicuous collar. Specimens from the lowlands of southeastern Costa Rica, on the Pacific coastal plain (Golfo Dulce region), have the same kind of pattern. Among specimens from these areas, there is a definite tendency for the collar to be palest and to occupy more of the parietal plates in the northeastern lowlands (Limón Province).

Except for an individual (MCZ 15300) from Navarro at the north end of the Cordillera de Talamanca, specimens from the Talamanca Mountains of central Costa Rica (USC 94) and western Panama (KU 112439, 112440) lack a dorsolateral pale line on row 5. The Navarro specimen has a very faint dorsolateral line; it lacks a pale collar and the brown head is conspicuously lighter than the dark brown body. The other specimens, all adults, either lack a pale collar or have only a very faint indication of a narrow one; their heads are dark brown, not much lighter than the blackish bodies. The absence, or virtual absence, of the collar is not the result of ontogenetic change, at least not completely. An adult (KU 112440) from 1450 meters elevation, north of Cerro Pando, western Panama, lacked a collar, as did a juvenile (which later escaped) from a lower elevation (910 meters) on the same slopes. An adult (KU 112439) from the same drainage, at 1620 meters, had the faintest indication of a narrow, yellowish ring across the ends of the parietals.

The only available specimens from the southern part of the range, in eastern Panama (KU 112441) and northern Colombia (BMNH 98.10.27.2), are juveniles, which represent populations that almost certainly are separated from the northern populations and from each other as well. The heads of these two specimens are medium brown, lighter than the blackish bodies, and there is a narrow, pale ring behind the tips of the parietals. In life, the Panamanian specimen had a reddish brown head, pale orangish ring, and a black body. A direct comparison of the preserved specimens indicates that the Colombian juvenile was probably similarly colored in life. There is no pale dorsolateral line.

Populations of *decipiens* below northern Costa Rica are represented by snakes with dark brown or black bodies, whereas the more vividly patterned northern specimens are usually lighter (medium brown), at least in the northeastern

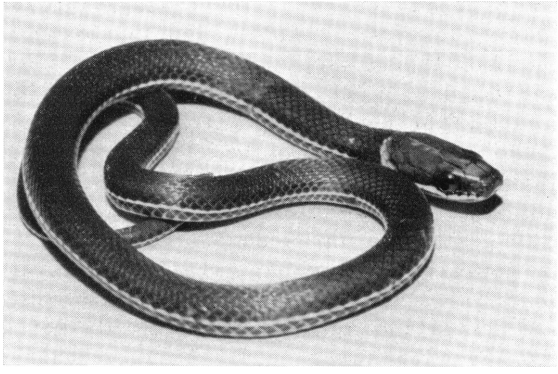


Fig. 43. *Rhadinaea decipiens*, KU 112441, juvenile from isolated population in Darién, Panama. Although very small (107 mm. snout-vent), this individual had already lost greater part of its tail, perhaps to a predator. Few specimens of this long-tailed species have complete tails when collected.

lowlands of Costa Rica. Specimens from the northeastern lowlands also tend to have the supralabials largely white, whereas in other populations, including the disjunct ones in eastern Panama and Colombia, there is considerable dark pigment against which a horizontal white line is conspicuous.

There seems to be little geographic significance in the presence or absence of dark spotting on the venter, except that such markings have been seen only on specimens from the highlands. Regular, median spotting is present on specimens from Cinchona, about 1600 meters elevation, in the Cordillera Central of Costa Rica (KU 35637, 103892), and from 1620 meters in the Cordillera de Talamanca of western Panama (KU 112439). A specimen (USC 94) from an intermediate locality (Navarro, Costa Rica), has irregularly scattered spots.

REMARKS: The name *Rhadinaea albiceps* Amaral (1924) is herein put in the synonymy of *R. decipiens*. The nominal *albiceps* is known only from its holotype, which, according to Amaral, is "probably from Ecuador." The catalogue entry for this specimen (USNM 22446) reads "Colombia? Ecuador?" But letters written by the collector, Mark B. Kerr, in April and May, 1894, indicate (albeit inconclusively) that the snake did indeed come from Ecuador, a supposition also supported by other species in the shipment (*fide* James A. Peters, *in litt.*, 1972). The specimen differs in a few respects from 15 other specimens of *decipiens* that I have examined, so I should not be too insistent in asserting that *albiceps* is not specifically distinct, particularly as its type locality is unknown. For that reason, data from the holotype are not incorporated into the text description of *decipiens* or into tables 16 and 17. The holotype of *albiceps* is briefly redescribed below (most of the information given is supplemental to the original description): The entire head is almost uniformly white, back to a distance of about three scales on the neck; there is, however, a noticeable, longitudinal brown mark between the primary temporal and seventh supralabial, and, much less noticeably, there is a light brown suffusion on the lower postocular and along the tops of the anterior supralabials, and the head plates and some of the nape scales tend to be faintly edged in pale brown. The body is brown, sharply demarcated from the white head, with two distinct white lines on each side—one line originating from the head color and extending along the top of scale row 1, and the other, a thinner line, originating abruptly on the neck, two scales behind the white head, and extending along the middle of row 5; both lines extend virtually to the end of the tail, contrary to a statement in the original description. Ventrals and subcaudals tipped with brown, but venter otherwise immaculate yellowish white. Specimen a subadult male, 339 mm. total length, 152 mm. tail length (44.8 percent); dorsal scales in 17 rows throughout; anal ridges absent; ventrals 120, subcaudals also 120 (given as 121 and 122 in original description); one preocular; a subpreocular situated between labials 3 and 4; two postoculars; temporals 1+2; eight supralabials, with 2–3 touching loreal, 4–5 in contact with eye; nine infralabials, with 1–5 touching anterior genials and 5–6 touching posterior genials; maxillary teeth 15+2. The hemipenis is long and slender. The left retracted organ extends to subcaudal 11 and the retractor muscle originates at subcaudal 29. Only about one-fifth of the length is taken up by the small capitulum, below which is a zone of 35 small spines; the basal three-fifths of the hemipenis is unadorned, save for minute spinules. The asulcate fold of the capitulum was cut during dissection but appears to be doubled. Lack of ossification of papillae on the asulcate fold indicates that the snake is subadult, an assumption also supported by the relatively small size of the snake.

The type specimen of *albiceps* most closely resembles the population of *Rhadinaea decipiens* in the northeastern lowlands of Costa Rica, differing most noticeably in that the entire head is white rather than in the pale color being confined to a band across the rear of the head. The specimen resembles members of the northern population especially in having a moderately light brown body, with two white lines on each side, and in having the pale head sharply demarcated from the body color. It mainly differs from the six other male *decipiens* examined in having a lower number of ventrals and a lower number of spines on the hemipenis. *Rhadinaea decipiens* is still known from relatively few specimens, despite a fairly large range, and I predict that its variational limits will be found to include the characteristics of *albiceps*. If the holotype of *albiceps* actually originated in South America, variation in *R. decipiens* might be analogous to the situation in *R. godmani*, in which terminal populations share similar color patterns that

differ from those of geographically intermediate populations.

Some specimens of *Rhadinaea decipiens* from southern Costa Rica and western Panama resemble *R. pachyura* in lacking the pale collar and dorsolateral line. Dunn's (1942b, 1947) records of "*Rhadinaea pachyura decipiens*" from Finca Lérida, western Panama, are based on specimens of *R. pachyura*; Dunn (1938, 1942b) stated that these snakes intergrade, but he offered no proof except a statement that intergradation was "obvious" because specimens of "*R. pachuyra pachyura* . . . have a faint trace of a light stripe on the first scale row" (Dunn, 1942b, p. 5). This marking is widespread in the *lateristriga* group. Specimens of the real *decipiens* have not been definitely reported from outside of Costa Rica until now.

Rhadinaea decipiens and *R. pachyura* both occur in the highlands of western Panama, but specimens have not been taken sufficiently close to suggest that there is microsympatry. But they evidently are sympatric on the Atlantic slopes of the Cordillera Central and adjacent lowlands of northeastern Costa Rica, where both species have been taken at Cinchona and in the vicinity of Guapiles. It is perhaps meaningful that it is in this region that the color pattern of *decipiens* is most different from the relatively unvarying *pachyura*. However, the differences are not so obvious in the case of juvenile *pachyura*. The young specimen on which Taylor (1954) based the name *Rhadinaea decipiens rubricollis* seems to be in reality a specimen of *R. pachyura*, for reasons given under that species. If my interpretation is correct, this specimen is the only known juvenile of *pachyura* and also the only specimen of that species from the Cordillera Central. The specimen has a pale collar and had me puzzled for a long time, and it is no wonder that Taylor mistook it for *decipiens*. Additional material from the Cinchona area would be very desirable.

The existence of black midventral spotting on some individuals of *R. decipiens* is of interest because of the absolute rarity of such markings within the genus, except in *Rhadinaea calligaster*. Even as remarkable was the dorsolateral suffusion of light olive-green (in an otherwise black ground color) on a specimen (KU 112440) of *decipiens* from western Panama, in a region where some individuals of *calligaster* have a dorsal ground color of an identical hue. Green coloring in *Rhadinaea* is as rare as the large midventral spots. Other aspects of color pattern, as well as major differences in hemipenes and tail length, indicate that *R. calligaster* is not closely related to *R. decipiens*. Although these two species inhabit the same mountain ranges in Costa Rica and western Panama, they have not been collected at the same localities.

The occurrence of midventral spotting in *decipiens* is puzzling, but its existence in a few specimens from northern Costa Rica and from western Panama is strong indication that the represented populations are conspecific, in spite of geographic differences in the presence or absence of the pale collar and dorsolateral line. Identical labial patterns (dark with a white line) in all specimens excepting those from the northeastern lowlands of Costa Rica is an additional factor in considering the widespread populations as conspecific.

Three specimens were found by W. E. Duellman and myself in lower montane rain forest, at 910, 1450, and 1620 meters elevation, on the Atlantic drainage of western Panama, where members of the species seem to forage between spells of rain during the day. Two adults were found as they were crossing trails during sunny periods at midday. The third specimen, a juvenile from 910 meters at Río Claro, north of Cerro Pando, was prowling on the forest floor at about 8 A.M. of a sunny morning; this specimen unfortunately escaped before preservation, but it was noted that it lacked a pale collar and dorsolateral lines. I found another juvenile during a foggy afternoon, in an elfin woodland type of cloud forest in eastern Panama; it was crawling on a root-supported platform of moss and litter, which comprised a second floor a half meter and more above actual ground level. A few specimens have been found dead on roads at night, but the actual times of activity were not known.

The specific epithet is the present participle of *decipio* (to deceive). Günther [1893 (1885–1902), p. 105] meant it as an allusion to the difficulty he had in distinguishing this species from others of the *lateristriga* group, which he had in three different genera.

Rhadinaea dumerilii (Bibron)

Figures 40D, 41F, 42D; map 15

Calamaria dumerilii BIBRON, "1855" [1840?], pl. 26, fig. 1 (watercolor rendition of holotype in lateral view), figs. 2–4 (dorsal, lateral, and ventral aspects

of cephalic scutellation), fig. 5 (ventral scutellation of cloacal region).

Urotheca dumerilii (Bibron): BIBRON, "1843" [184–?], pp. 131, 132. BOULENGER, 1894b, p. 181 (part, not "*Dromicus dumerilii*," see below). AMARAL, 1929b, p. 177. WERNER, 1929, p. 122.

Dromicus dumerilii (Bibron): GARMAN, 1887b, p. 280 (first combination with *Dromicus*, but based on the misidentification of MCZ 9598, a specimen of *Lygophis* [=*Saphenophis*] *boursieri* with erroneous locality, *fide* Myers, 1966, p. 887; 1973).

Rhadinaea dumerillii [*sic*] (Bibron): MAGLIO, 1970, p. 43 (first combination with *Rhadinaea*, with erroneous claim that *dumerilii* is the type species of *Rhadinaea* [see p. 239 n]).

HOLOTYPE: MNHN 733, an adult male. The specimen is well preserved but very faded, and someone has done a poor job of teasing the skin away from the skull. The type locality, originally given as "Cuba," is unknown, but the specimen probably came from Colombia.

DIAGNOSIS: *Rhadinaea dumerilii* is readily identified by its simple, but unique, color pattern: The body is brown and lacks definite markings, except for a small pale spot or ocellus that is above and slightly behind the corner of the mouth. A vague, pale line or stripe originates at the throat and extends along the lower scale rows for a short distance on the neck.

DISTRIBUTION: Known definitely only from the Río San Juan, in Departamento del Chocó, on the Pacific side of northern Colombia. A record (AMNH 35490) from Medellín, Colombia, on the western flank of the Cordillera Central, needs verification.

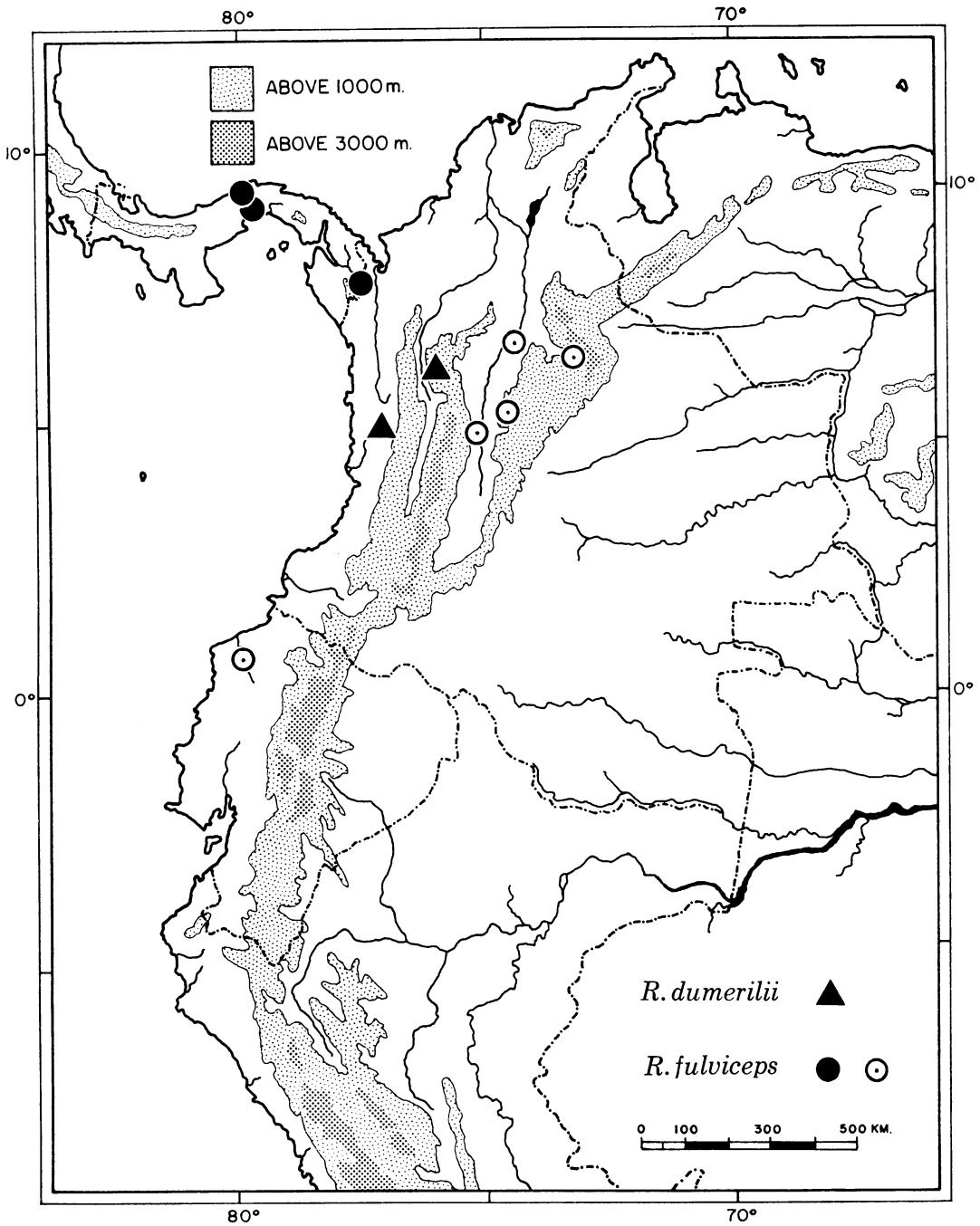
DESCRIPTION (FOUR SPECIMENS): The largest specimen is AMNH 103823, a female 266 mm. snout to vent, plus a broken tail that measures 43 mm.; the holotype, a male, is 238 mm. snout to vent and has an incomplete tail of 82 mm. The holotype, at least, seems to be sexually mature, as indicated by its enlarged and convoluted ducti deferentia and kidney tubules. A juvenile female is 224 mm. total length, of which the tail is 84 mm., or 37.5 percent of the total; this specimen (AMNH 35490) is the only one that has a complete tail.

The dorsal scales are in 17–17–17 rows; anal ridges are absent. There are 128–139 ventrals (128, 129, males; 137, 139, females); the one female with a complete tail has 117 subcaudals. There are eight supralabials, and eight to 10 infralabials (eight in two specimens, and nine and 10 in one specimen each). There is one preocular, except for the holotype which has 1?/2 preoculars. All four specimens have a subpreocular between the corners of the third and fourth labials, and all have two postoculars and 1+2 temporals.

This is a brown or grayish brown snake that has very little pattern. There is a small, partially dark-edged, white spot on each side of the neck; each spot is the size of one or two dorsal scales and borders the ultimate supralabial, being above and slightly behind the corner of the mouth. A poorly defined whitish line or narrow stripe extends from under the angle of the jaws and along the lower one and one-half scale rows of the neck, for a distance of about 12 ventrals. The first scale row remains somewhat paler than the rest of the dorsum for the length of the body. There is a pair of faint, whitish dorsolateral lines on the basal section of the tail, each line lying on the second row of caudal scales and being very poorly defined (these lines are not evident on the holotype, which is badly faded over the entire body). Under magnification, the dorsal scales are seen to be dark around the edges and finely variegated in the centers with dark brown on a paler background.

The top and sides of the head are almost uniform brown and appear slightly lighter than the body, because there is very little dark flecking or variegation on the head. There are no parietal dots and no marking on the rostral. The tops of the supralabials are encroached upon by brown pigment, which tends to form a dark line on the side of the head. The white supralabials and infralabials have brown sutures, and some additional spotting or speckling of light brown may also be present. The venter is white (yellowish in BMNH 1914.5.21.46), except that the ventrals and subcaudals are tipped with dark brown, the edge of which varies from slightly to strongly serrated.

Watercolor illustrations of the holotype (Bibron, "1855" [1840?], pl. 26, fig. 1), in the libraries of the American Museum of Natural History and the University of Kansas, show the following hues: Dorsum dark brown, with lighter brown sides; ventral edges dark brown; venter light brown (KU copy) or light orangish brown (AMNH copy); labials tan wash; poorly defined orangish brown (KU copy) or yellow (AMNH copy) spot behind mouth; whitish line on lower side of neck. The color of the spot on the neck was not mentioned in a printed description



MAP 15. Locality records for *Rhadinaea dumerilii* and *R. fulviceps*. Open symbols represent literature records for *R. fulviceps* in Colombia (Dunn, 1944) and Ecuador (Peters, 1963); see also map 14.

(Bibron, "1843" [184–?], p. 132), but the venter was said to be yellowish orange:

"Esta pequeña serpiente, de un color amarillo naranjado en la parte inferior, es por encima de color de castaña con muchas manchitas negruzcas; además, á lo largo de sus lados se extiendi una raya de un color mas subido dodavía, resultando del ribete negro de la márgen lateral

externa de todas las escutelas ventrales y subcaudales."

It must have taken a fairly long time for the holotype to reach Paris in the early 1800s, particularly since it did not originate in Cuba as originally thought, and any bright colors were probably faded from the effects of the preservative. It is not known who the collector was or whether color notes were made in life, and so it seems useless to speculate on whether the colored plate or the printed description is most accurate. I examined a specimen (AMNH 103823) only a month after it had been preserved, and the venter, labials, and ocelli were white.

There are 15 or 17 maxillary teeth, followed by a diastema and two ungrooved fangs. The ultimate prediastemal socket lies anterior to the front edge of the ectopterygoid process; the last fang is offset laterad. An accurate count could not be made on the holotype because the bones of the mouth are damaged, but there were originally about 16 to 18 prediastemal teeth; the holotype had at least 11 teeth on the palatine and 22 on the pterygoid, and there were about 18 to 20 mandibular teeth.

The hemipenis is single and seemingly not capitate. A retracted hemipenis extended *in situ* to the middle of subcaudal 10, and the retractor muscle originated at the level of subcaudal 24. The distal fourth of the organ bears calyces that are ornamented with unossified papillae; the calyculate area does not extend any farther basad on the sulcate side than on the side opposite. I detected no indication that the calyculate area is set off by an overhang; the organ appeared to be not capitate. The calyculate part of the retracted organ is thrown into a double fold on the asulcate side. The sulcus spermaticus forks directly below the calyculate area (at the end of subcaudal 7 when the organ is *in situ*), and the branches extend to the end of the organ. The quarter sector basad of the calyculate area is heavily spinose. There are 16 moderate-sized, slightly recurved, spines, and about twice as many small spines; the spines are largest toward the asulcate side, where they flank a short, nude strip below the asulcate folds. There is a fairly large spine on the dorsal wall, in the second quarter sector from the base. Except for this isolated spine, the basal half of the hemipenis is ornamented only with minute spinules. The preceding description is based on the left, retracted hemipenis of the holotype, MNHN 733 (illustrated). I examined the hemipenis of this specimen in 1964, and the "detailed" description I wrote at that time now proves to be somewhat inadequate. It remains to be learned whether there is a "pocket" in the edge of the calyculate area, between the base of the asulcate folds. Also, my observation that the organ lacks capitation needs to be verified.

REMARKS: This is the first report of specimens that are conspecific with the holotype of "*Urotheca*" *dumerilii*, except for Boulenger's (1914, p. 816) hesitant identification of a juvenile specimen (BMNH 1914.5.21.46) as *Rhadinaea decorata*. A specimen mentioned by Garman (1887b, p. 280) and Barbour (1914, p. 340) is in reality an example of *Saphenophis* [*Lygophis, auctorum*] *boursieri* (*fide* Myers, 1966, 1973). Statements regarding the dubious locality datum ("Cuba") of the holotype, and ideas about the possible origin and identity of the specimen, were made by the following authors: Barbour and Ramsden (1916, p. 128; 1919, p. 77), Dunn and Bailey (1939, p. 12), especially Dunn (1944, p. 491; 1957, p. 77), Roze (1958, p. 5; 1964, p. 540), Myers (1966, p. 887). Dunn and Bailey had information on the holotype from Roger Conant, who examined the specimen in Paris; Roze also examined the holotype in Paris, but no one published any actual data. The specimen was sent to me from the Paris Museum in 1963, and Dr. Guibé allowed me to retain it until 1964; repeated examination convinced me that the faded type of *dumerilii* represented an otherwise unknown species of the *lateristriga* group of *Rhadinaea*, and that Dunn (1944, 1957) had been at least close to the truth when he suggested the possibilities that it might be a specimen of the later described *R. lateristriga* or *R. fulviceps*. The species was "rediscovered" when I received from the British Museum the Colombian (Chocó) specimen that Boulenger had called *R. decorata*, and when I found a small, badly faded specimen reputedly from Medellín, in a drawer of unidentified snakes at the American Museum. A fourth specimen was obtained in the Chocó by Borys Malkin, who sent it to the American Museum while I was in the process of preparing the present account. These details are offered because of the confused history of this important species, which is the type species of *Urotheca*, a name that technically has priority over the later name *Rhadinaea*. Additional comments are made

in the section Historical Summary and Choice of a Generic Name.

I am following Smith and Grant (1958b) in considering Bibron's illustrations of the holotype as constituting the original "description" of this species (refer to the synonymy). Thus, the name *Calamaria dumerilii*, as used on the plate, was probably published in 1840 according to Smith and Grant, and the combination *Urotheca dumerilii*, as used in the text, was probably published in 1843. Nonetheless, the exact years of publication are by no means certain, and I wonder if parts of the text and certain plates might not have been issued simultaneously. The basis for this thought is that Bibron ("1843" [184–?], p. 131) referred to plate "no. xxvi de la serie de láminas *que acompañan esta parte* erpetológica . . ." (Italics mine.) Bibron (*op. cit.*, p. 132) explained the use of different generic names in combination with the specific epithet: "Por un error que desgraciadamente no hemos notado hasta despues de estampada la lámina de nuestro atlas que representa esta especie, se halla designada con el nombre genérico Calamaria que de ningun modo le conviene, conforme habiamos creido al principio."

An edition of Ramón de la Sagra's "Historia" was published in French, in octavo volumes and consequently with pagination different from the folio edition (Spanish). The French edition seems to have been published at a slightly later date than the Spanish one (*fide* Smith and Grant, 1958b), and so it is not considered here except to note that most workers have credited the name *Urotheca dumerilii* to the French edition; the Spanish and French editions bear the same dates on their title pages.

The specific epithet is a patronym honoring a French herpetologist, presumably the elder Duméril (Andre Marie Constant Duméril, 1764–1860).

Rhadinaea fulviceps Cope

Figures 40C, 41I, 42E; maps 14, 15

Rhadinaea fulviceps Cope, "1885" [1886b], pp. 279, 280; 1887, p. 80; 1900, p. 754. Boulenger, 1894b, p. 179. Werner, 1929, p. 119. Smith and Grant, 1958a, pp. 211, 212.

Coronella fulviceps (Cope): Günther, 1893 (1885–1902), p. 111.

?*Liophis vittatus fulviceps* (Cope): Amaral, 1930, p. 27.

Liophis fulviceps (Cope): Amaral, 1925, p. 7; 1929b, p. 172.

Liophis pachyurus (not of Cope): Dunn, 1931a, p. 163 (part).

Rhadinaea pachyura (not of Cope): Dunn, 1932, p. 1 (part).

R[*hadinaea*]. *d*[*ecipiens*]. *fulviceps* Cope: Dunn, 1942b, p. 5 (*lapsus* for *R. p*[*achyura*]. *fulviceps*).

Rhadinaea pachyura fulviceps Cope: Dunn and Bailey, 1939, p. 10. Dunn, 1944, pp. 492, 493. Peters, 1960, p. 537; 1963, pp. 63, 64. Peters and Orejas-Miranda, 1970, p. 267.

Holotype: USNM 61187, an adult female in fair condition; obtained in Panama by George W. Nelson. Cochran (1961, p. 210) stated that this specimen was "formerly probably 14118," which is the number given in the original description. The specimen agrees well with the type description, except that I counted 138 ventrals (the two preventrals included), whereas Cope recorded 144. But we obtained the same subcaudal counts (109), and our measurements are close (347 mm. total, 151 mm. tail length, compared with 341 and 148 mm. as given by Cope). The three dark brown longitudinal stripes mentioned by Cope are faintly visible, but their exact scale-row relationship cannot now be determined. The first scale row stands out lighter than the rest of the dorsum and, under magnification, is seen to bear a thin, poorly defined and much broken white line.

Diagnosis: A long, thick tail and, on some specimens, a narrow white line or series of dashes on the first scale row, identifies *Rhadinaea fulviceps* as a member of the *lateristriga* group. It is distinguished from other members of the group, except *R. pachyura*, and from all other species of the genus, by its yellow-brown head (red-brown in life), which is sharply contrasted against the brown body (which may show vague, poorly defined stripes). It differs from *pachyura* in that the head coloration extends farther onto the neck (three or four scales in *fulviceps*, one or two scales in *pachyura*), and in that the labials are intensely peppered or blotched with dark pigment (with brown sutures or weakly spotted in *pachyura*); additional differences are given in Remarks under the present species.

I have not seen juveniles of *R. fulviceps*. Conceivably, they might have a pale collar across the nape, rather than a uniform yellow-brown head and nape, in which case they might be confused with specimens from some populations of *R. decipiens*. In this eventuality, the intensely speckled supralabials (either dark with a

horizontal white line or nearly immaculate in *decipiens*) would distinguish the young of *fulviceps*.

DISTRIBUTION: Lowlands of central and eastern Panama, to northwestern Ecuador and the Magdalena drainage of central Colombia. The habitat in Panama is evergreen seasonal forest (monsoon rain forest), from near sea level to about 500 meters elevation.

I have not seen the only known specimen from Ecuador (Peters, 1963), and the species has not yet been taken in the Pacific lowlands of Colombia. Neither have I seen the specimens mentioned by Dunn (1944, p. 492) from the departments of Caldas, Santander, and Boyacá in the Magdalena drainage of central Colombia. The identity of the latter specimens needs confirmation, because some of the localities are at suspiciously high elevations (Muzo, 800–825 meters; San Joaquín, 2003 meters, *fide* Medem, 1965, in list of localities).

DESCRIPTION (18 SPECIMENS): The largest specimen is a male 489 mm. total length, 206 mm. tail length; the largest female is 461 mm. total, 189 mm. tail length. The tail is 41.9–44.6 percent of total length in males, and 39.3–43.5 percent in females. The dorsal scales are in 17–17–17 rows; anal ridges are absent. There are 136–143 ventrals (138–142, males; 136–143, females), and 98–122 subcaudals (112–122, males; 98–109, females). There are eight supralabials, and nine, or occasionally eight, infralabials. There is one preocular (1/2, two specimens), a subpreocular between the third and fourth labials (absent in one specimen), two postoculars, and a basic pattern of 1+2 temporals. These data are for Panamanian specimens. An Ecuadorian specimen (sex?) has 142 ventrals, 108 subcaudals, 10 infralabials, and a single secondary temporal on the right, according to Peters (1963, p. 64).

The body is light to dark brown. The first scale row tends to be lightest, and there is often a thin, ill-defined and much broken white line on this row; this line, when present, disappears on the basal part of the tail. Many specimens have a vague indication of a pattern, especially when immersed in liquid: The body may have a vague marbled appearance, especially anteriorly, caused by the unequal distribution of pale speckling, or "frosting"; or, the fine speckling may be most concentrated dorsolaterally, especially on rows 3–5, causing the snake to have a vague pattern of dark stripes, i.e., a broad dorsal stripe, and a narrower lateral one between the frosting, and the relatively pale, lower row of scales.

The top and upper sides of the head are yellow-brown, and this color extends onto the neck for a distance of three or four scales behind the parietal plates, where it abruptly terminates in sharp contrast to the brown body; the yellow-brown color on some specimens is paler on the neck than on the head. There usually are a few dark specks atop the head, especially on the snout; the yellow-brown color on the neck is often broken by a line of brown pigment on the vertebral row of scales. The rostral plate is pale to medium brown, often with one or more blackish spots. The head color encroaches onto the tops of the supralabials, where it tends to concentrate and form a poorly defined blackish line, especially from the eye to the corner of the mouth. The supralabials and infralabials are basically white, but they are darkened by a dense pattern of blackish specks or small spots, and also by dark pigment along their common sutures. The ventral and subcaudal plates are tipped with blackish brown pigment, which forms a strongly serrated edge. The venter is otherwise white.

I took notes on three live specimens (now KU 112453–112455) in eastern Panama: The head and neck is red-brown in life, and the body is grayish brown, being lightest on the sides. The labials are white, with intense dark speckling, and the narrow, broken line on the first scale row is white. The venter is white, except for a yellowish tinge under the neck. The iris is reddish brown, with a golden tinge above the pupil. The tongue is black, with yellowish gray tips, and the musk from the anal sacs is amber in color.

There are 13–16 subequal maxillary teeth, followed by a distinct diastema and two slightly enlarged fangs. The ultimate prediastemal socket lies well anterior to the front edge of the ectopterygoid process. The last fang is offset laterad.

The hemipenis is single, and when everted, is rather stout. The retracted organ of one specimen extended *in situ* to the base of subcaudal 10, and the retractor muscle originated at the level of subcaudal 24. The everted hemipenes of three individuals extended to the middle or end of subcaudal 7. The capitulum comprises somewhat more than two-fifths to about one-half of

the length of the hemipenis on its sulcate side. The sulcus spermaticus forks less than half of its length up the capitulum, and the branches extend almost to the end of the retracted organ, but little more than halfway up the capitulum when the organ is everted. The calyces are spinulate over the asulcate fold and toward the periphery of the capitulum, and papillate on most of the sulcate side of the capitulum. The wall of the capitulum forms a single, well-defined fold on the asulcate side of the retracted hemipenis. The free edge of the capitulum is twice fused to the stalk on the asulcate side, and, between the fusions, the edge of the capitulum overhangs and conceals a small, deep "pocket." On the retracted organ, the pocket lies to one side and slightly above the basal end of the asulcate fold. The free edge of the capitulum forms a fairly deep overhang on each side of the hemipenis. There are 28–44 small to medium, slightly recurved spines below the capitulum. The uppermost spines toward the sulcate side are small, and the basalmost spines and those on the asulcate side are larger. There is a nude space on the asulcate side, flanked by two rows of two or three spines each; the basal spine in each row is larger than the spine above, but other spines of similar size lie closer to the base of the organ. The basal third, or less, of the hemipenis is unadorned save for minute spinules. The preceding description is based on a retracted hemipenis of MCZ 26647, and on everted hemipenes of AMNH 103779, KU 112455 (illustrated), and UF 7533.

REMARKS: *Rhadinaea fulviceps* has been usually considered a subspecies of *R. pachyura*. Dunn (1931a) stated that the holotypes "are practically identical, and certainly conspecific." Dunn (1942b, p. 5) later considered *fulviceps* as a subspecies of *pachyura*, separating the two by the distance that the light color of the head extends onto the neck. Smith and Grant (1958a) more recently raised *fulviceps* back to specific status, but their assumption that *pachyura* has significantly fewer subcaudals was based on a false notion that the holotype has a complete tail. Actually, however, there are a number of differences. The light head color does consistently extend farther onto the neck in *fulviceps*, which also has intensely speckled labials, and which lacks or has a less well-defined white line on the first row of scales. *Rhadinaea fulviceps* has 1+2 temporals, whereas *pachyura* usually has 1+1. There are slight differences in the relative proportions of parietal and frontal plates. The interparietal suture in *fulviceps* is usually shorter or no more than equal to the length of the frontal, whereas in *pachyura* the suture is usually equal to or longer than the frontal and is only occasionally shorter. *Rhadinaea fulviceps* has, on the average, fewer maxillary teeth. *Rhadinaea pachyura* seemingly attains a larger size. Differences between the hemipenes seem especially important, even though I have seen few examples. The hemipenis of *fulviceps* is rather stout and has a large capitulum, which comprises two-fifths to half of the length of the sulcate side of the organ, and no more than the basal third of the hemipenis lacks spines; the capitulum is only about one-fourth the length of the hemipenis in *pachyura* and over half of the organ lacks spines. It may be assumed that the everted hemipenis of *pachyura* has the same slender appearance as the hemipenis of *decipiens* (compare fig. 42F and 42E, of the everted hemipenes of *decipiens* and *fulviceps*).

The ranges of *R. pachyura* and *R. fulviceps* are probably contiguous in the forested lowlands of the north (Atlantic) coast of Panama, somewhere between Chiriquí Lagoon and the Canal Zone. This is the region in which the rain-forest habitat of *pachyura* gradually changes toward the evergreen seasonal forest that is occupied by *fulviceps* in the eastern half of Panama. The question of conspecificity can be proved or disproved only by specimens from this area.

Dunn (1944, pp. 492, 493) believed that Werner (1899) described a northern Colombian specimen of *Rhadinaea fulviceps* under the name *R. decorata*. Judged from Werner's description, the specimen certainly was not *decorata*. It was said to be a young example, with 17 scale rows, 137 ventrals, 117 subcaudals, one preocular, and a subpreocular. The head was described as reddish brown, followed by a three-scale wide, yellowish white collar, one scale behind the parietals; upper lip yellowish; body blackish brown, with an indication of a dorsal stripe and with a fine, white line on the upper edge of the first scale row. The labial coloration (no horizontal white line), and probably the low elevation of the locality ("Mine Purnio, 350 *m*, bei Honda am Magdalena"), seem to preclude the possibility that the specimen was a young *Rhadinaea decipiens*. Dunn's assignment of the description to *fulviceps* is quite possibly correct,

but I prefer to withhold judgment until it is proved that juvenile *fulviceps* have a pale collar as described above. In the same paper, Werner also described a specimen of "*Erythrolamprus imperialis*," purportedly from the same locality as the "*decorata*"; Dunn (*loc. cit.*) thought that this was really a specimen of *Rhadinaea lateristriga*. A specimen (UMMZ 78263) of *lateristriga* is available from Muzo (Dept. Boyacá, Colombia), a locality for which Dunn (*loc. cit.*) reported specimens of *fulviceps* and *lateristriga* both. So far as I am aware, there is no other indication that either *fulviceps* or *lateristriga* occurs sympatrically with each other or with any other member of the species group. Nonetheless, sympatry between *fulviceps* and *pachyura* is expected in western Panama, and if *fulviceps* occurs in the wet Chocó west of the Andes it might also be sympatric with *dumerilii*. *Rhadinaea fulviceps* is broadly sympatric with *R. decorata*, which belongs to another species group.

A specimen of *Rhadinaea fulviceps* was found crawling on a shaded forest floor at midday, in eastern Panama. Two other specimens from the same area were caught after dark. One fell into a trench that had been dug as a trap (and which had been checked at dusk), and the other was found on the forest floor at 8 P.M.

The specific epithet is a compound of the adjective *fulvus* (reddish yellow, or yellowish brown or tawny) plus the New Latin noun *ceps* (head), in allusion to the head coloration, which differs conspicuously from that of the body.

Rhadinaea guentheri Dunn

Figures 40E, 41A, 42C, 44; map 16

Tachymenis decipiens GÜNTHER, 1895 (1885–1902), p. 163, pl. 53, fig. A (color pattern; name a rejected junior homonym of *Ablabes decipiens* [=*Rhadinaea decipiens*] Günther, 1893 [1885–1902]).

Erythrolamprus decipiens (Günther): BOULENGER, 1896, p. 204.

Coniophanes decipiens (Günther): AMARAL, 1929b, p. 216. TAYLOR, 1951, pp. 141, 142.

Rhadinaea persimilis DUNN, 1938, pp. 197, 198 (holotype: MCZ 19345, from La Loma, 1500 feet elevation, Atlantic slope on trail from Chiriquí Lagoon to Pacific side, Bocas del Toro, Panama; E. R. Dunn and Chester Duryea collectors). TAYLOR, 1951, p. 117; 1954, pp. 743, 744. PETERS AND OREJAS-MIRANDA, 1970, p. 267. (Name a rejected junior homonym of *Liophis persimilis* [=*Rhadinaea persimilis*] Cope, "1868" [1869].) New synonymy.

Rhadinaea güntheri DUNN, 1938, p. 198. (Replacement name for *Tachymenis decipiens* Günther, 1895 [1885–1902], a rejected homonym [see above].)

Rhadinaea guentheri Dunn: PETERS AND OREJAS-MIRANDA, 1970, p. 265 (umlaut deleted following International Commission . . ., 1964, art. 32c).

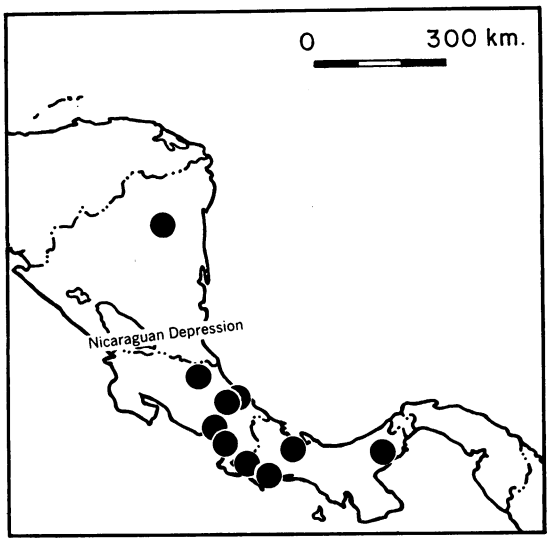
DESIGNATION OF LECTOTYPE: The name *Tachymenis decipiens* is based on three syntypes, BMNH 1946.1.8.13–1946.1.8.15, although the exact number of specimens is not evident in the original description. The type series originally received only two catalogue numbers (94.12.28.2, 94.12.28.3) owing to an error in the original registration (A. F. Stimson, *in litt.*). All three specimens are females according to Dunn (1938) and Stimson (*in litt.*), although Boulenger (1896, p. 204) cited one male and two females; Boulenger (*op. cit.*) seems also to have listed the wrong collector. The best preserved syntype, BMNH 1946.1.8.15, was lent to me and is here designated as lectotype. The specimen is an adult female with 164 ventrals, one preventral, and 27+ subcaudals. The type locality is Irazú, [Cartago or San José Province], Costa Rica; the specimens were obtained by H. Rogers.

The lectotype of *Tachymenis decipiens* is ipso facto the lectotype of *Rhadinaea guentheri*.

DIAGNOSIS: *Rhadinaea guentheri* is a thick-tailed, brownish snake with two conspicuous whitish lines on each side of the body. It can be distinguished from similarly colored specimens of the sympatric *R. decipiens* by the head and neck pattern. *Rhadinaea guentheri* has a pair of white ocelli on the rear of the head (one on the outer side of each parietal plate, behind the upper postocular); there is usually an ocellus or else an enlarged terminus of the dorsolateral white line, on each side of the neck, and usually there is a conspicuous median ocellus or white line on the nape. *Rhadinaea decipiens* lacks the ocelli and in many cases has a pale band across the rear of the head and nape; available evidence indicates that *guentheri* has a red belly in life and *decipiens* a white one.

Specimens from some populations of the South American *R. lateristriga* have a total color pattern similar to that of the Central American *R. guentheri*, except for a white labial line that is lacking in *guentheri*. There are also differences in hemipenes and in number of preoculars and maxillary teeth, as discussed under Remarks in the account of *lateristriga*.

DISTRIBUTION: Northern Nicaragua (a presumed gap in southern Nicaragua), and northern



MAP 16. Locality records for *Rhadinaea guentheri* in lower Central America.

Costa Rica to central Panama. Records are very spotty, but show the species to be present in the Atlantic lowlands and adjacent mountains (below 1000 meters) of Costa Rica and Panama, and on the Pacific slopes (to 2100 meters) of the Cordillera de Talamanca of southwestern Costa Rica, and in the adjacent Golfo Dulce lowlands of Costa Rica–Panama. The principal habitats are presumably tropical and lower montane rain forest.

DESCRIPTION (14 SPECIMENS): The largest of four specimens with unbroken tails is a male 438 mm. total length, 187 mm. tail length; but the snout-vent length of this specimen is only 251 mm., whereas a large female with an incomplete tail has a body length 399 mm. According to Günther [1895 (1885–1902), p. 163], one of the [female] syntypes is even larger, with a snout to vent length of 19 inches (483 mm.). The tail is 38.5 and 42.7 percent of total length in two males, and 36.3 percent in a small female. The body of another small female (USC 277) is somewhat mutilated, but, even so, the tail is only about 27–28 percent of the total length; this individual also has the lowest number of subcaudals (82).

The dorsal scales are in 17–17–17 rows; a few males have anal ridges. Ventrals are 135–176 (135–164, males; 147–176, females); specimens with complete tails have 82–110 subcaudals (98, 110, males; 82, 98, females). A majority of specimens have seven supralabials, but eight is also a common number; one of the syntypes (*fide* Dunn, 1938) has only six supralabials. All specimens examined have eight infralabials. There is one preocular (2/1, one specimen) and two postoculars; several specimens have a small subpreocular. Temporals are normally 1+1, except in the lectotype [and other two syntypes *fide* Günther, 1895 (1885–1902), and Dunn, 1938], where the formula is 0+1. The types have the single temporal separated from the postoculars by a supralabial-parietal contact (except on one side of one specimen *fide* Dunn, 1938).

The body is light to dark brown and there are two conspicuous, somewhat variably positioned, white lines on each side, extending from the neck to the end of the tail. The lowermost line originates anteriorly from the pale color of the throat, and extends caudad along the middle of the first scale row, or along the upper half of row 1 and adjacent edge of row 2, or along equal parts of rows 1 and 2; on the tail, the lower part of this line tends to merge with the white subcaudal surface. The uppermost line lies on the middle of row 5, or it is shifted slightly up or down to encroach onto either adjacent row, or it occupies equal parts of rows 5 and 6. These white lines are bordered with dark brown or blackish brown, and the intervening spaces are lighter brown. One specimen (LSU 8761) has a faint, median dark line on the vertebral row of scales.

The anterior terminus of the dorsolateral white line lies a few scales behind the parietal plates and is usually expanded to form a circular or elongated white spot, which, in some specimens, is broken off as a discrete ocellus. The anterior end of the line is not expanded, nor is there an ocellus, in a few specimens (ANSP 24252, KU 31939, USC 7108). There is usually a median white spot or short white line (lacking in FMNH 83480), on the nape three to five scales behind the parietal suture. There is a pair of white ocelli on the rear of the head, each ocellus lying on the outer edge of a parietal plate close behind the upper postocular. The rostral plate is pale tan, except for a brown ∩-shaped mark, spot, or horizontal bar, and usually there are two extensions of tan backward onto the prefrontals, fusing or not fusing with a tan line on each supraocular and in some cases connected with a tan crossbar on the front edge of the frontal. The top of the head is mostly brown like the body, except that in many cases there is

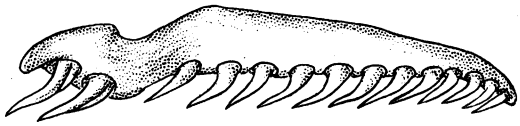


FIG. 44. Right maxilla of *Rhadinaea guentheri*, LSU 8761, ventrolateral view. × 12.

some darker brown mottling. A blackish line edges the tops of the supralabials, which, like the infralabials, are mostly white, with or without a row of blackish spots, especially on the anterior plates. The venter is white, except that the ventrals and subcaudals are tipped with blackish brown from the sides of the body.

The venter is red in life according to Dunn (1938) and Taylor (1954, pp. 743, 744); it is noted as orange-red on the field tag of LSU 8761. The ocelli and white lines are presumably whitish in life.

There are 11 to 13 subequal maxillary teeth followed by a broad diastema and two fangs that are about one and one-half to two times larger than the prediastemal teeth. The ultimate prediastemal socket is well anterior to the ectopterygoid process. The diastema is large, about equivalent to the space occupied by the last two to three prediastemal teeth. The two fangs usually (seven of 10 specimens) bear weak to moderate grooves on the basal two-thirds of the anterior face, but the grooves are in many cases difficult to see without proper magnification and lighting. The last fang is offset laterad.

The hemipenis is single and extends to the base of subcaudal 7 (two cases) or the end of subcaudal 9 (one) in the retracted organs of three specimens, and to subcaudals 5/6 in the case of the everted organs of a fourth individual. The retractor muscle originates at the level of subcaudal 21 or 22. The capitulum comprises from about two-fifths to nearly half of the length of the hemipenis on its sulcate side. The sulcus spermaticus forks at the edge of the capitulum and the branches extend to the end of the retracted organ, but less than halfway up the capitulum when the organ is everted. The calyces are spinulate over the asulcate fold and toward the periphery of the capitulum, and papillate on most of the sulcate side of the capitulum. The wall of the asulcate side of the capitulum forms a well-defined fold when the organ is retracted; this fold is single except for a short division of the basal part, where the free edge of the capitulum is twice interrupted by fusions to the stalk. When the hemipenis is everted, the area between the fusions becomes a small but conspicuously deep "pocket" in the edge of the capitulum on the asulcate side; the free edge of the capitulum forms a conspicuous overhang on each side of the hemipenis, between the sulcate and asulcate surfaces. There are 22–29 small to large, slightly recurved spines below the capitulum. The spines are small on the sulcate side and become larger toward the asulcate side, where there is a nude region that is flanked by two rows of three spines each; this nude area extends basad from the "pocket" in the edge of the capitulum, and becomes relatively broad and flat when the hemipenis is everted. The basalmost spine in each of the aforesaid rows is rather large, and there is an unpaired moderate-sized to large-sized spine on the dorsal wall (=side of the everted organ) at the bottom of the spinose zone. About the basal fourth to third of the organ is unadorned save for minute spinules. The preceding description is based on the everted hemipenes of USC 7108, and on retracted organs of AMNH 7412, KU 31939, and USC 151 (illustrated).

REMARKS: *Rhadinaea guentheri* is a replacement name given by Dunn (1938) for *Tachymenis decipiens* Günther, the latter name being a junior homonym of *Ablabes decipiens* (=*Rhadinaea decipiens*) Günther. Dunn (*loc. cit.*) correctly placed both of Günther's species in *Rhadinaea*, thus creating the homonymy. In the same paper, Dunn named a supposed new species, *Rhadinaea persimilis*, which he noted to be, "almost identical in coloration with *Tachymenis decipiens* [*R. guentheri*] . . ." and that "some might maintain that *persimilis* specimens are merely the males of *decipiens* [*guentheri*]." Presumed differences were grooved rear maxillary teeth in *guentheri* versus smooth teeth in *persimilis*, more ventrals in *guentheri* (165–173, three females) than in *persimilis* (137–143, four males), and one or two labials in contact with the parietal on one or both sides of the head of *guentheri*. However, Dunn stressed only the presence or absence of grooves on the rear fangs. I can distinguish only one species in the 14 specimens that I have examined, including the holotype and two paratypes of *persimilis*, and a syntype of *guentheri*. Moderate to faint grooves are visible under proper magnification and lighting in at least seven specimens, including specimens with the lowest as well as the highest numbers of ventrals (135, 136,

males; 176, female); however, the grooves on the fangs of some specimens are so weak that it was no surprise not to be able to distinguish grooves in three other specimens. Ventrals range from 135 to 164 in males and 147 to 176 in females. The contact of labials and parietals occurs only in the three syntypes of *guentheri*, and doubtlessly is an anomaly that occurs (or occurred) at high frequency at the type locality, whether because of genetic or environmental reasons.

Thus, I regard the names *Rhadinaea guentheri* Dunn, 1938, and *Rhadinaea persimilis* Dunn, 1938, as belonging to one and the same species. There is no difficulty in making a choice of which name to use, because the latter is a junior homonym of *Liophis persimilis* Cope, "1868" [1869], which I recognize as a valid species of *Rhadinaea*. The holotype of Cope's *Liophis persimilis*, however, is lost. Should it ever be proved that Cope's species is not congeneric with Dunn's *R. persimilis*, then the latter name would again become available. To prevent unnecessary name changes in this eventuality, I take the prerogative of "first reviser" and direct that the name *R. guentheri* Dunn be given priority over *R. persimilis* Dunn, by any worker who considers these names synonymous.

Rhadinaea guentheri is very close to *R. lateristriga*, and comparisons are given under the latter species. A Costa Rican record of *lateristriga* by Viquéz S. (*fide* Taylor, 1951, p. 17) might conceivably have been based on *guentheri*.

Taylor (1954, p. 744) obtained a juvenile specimen by digging at the base of a rotting tree. A few specimens have been found on roads, but very little is known about this species. The specific epithet honors Albert Günther, whose description and illustration of "*Tachymenis decipiens*" forms the legal basis for the replacement name that is here considered the valid name of the species.

Rhadinaea lateristriga (Berthold)

Figures 4, 5, 40G, 41B, 42A, B; map 17

Liophis lateristriga BERTHOLD, 1859, pp. 180, 181.

Dromicus temporalis COPE, 1860b, p. 370 (holotype: probably MCZ 297 [*fide* Barbour, 1914, p. 338], erroneously recorded as "probably Cuba").

Liophis (*Cosmiosophis*) *lateristriga* Berthold: JAN, 1863, pp. 289, 303 [pp. 79, 93, in reprint]. JAN AND SORDELLI, 1866 (1860–1881), vol. 2, livr. 18, pl. 5, fig. 1 (details of color pattern and scutellation of holotype).

Dromicus frenatus PETERS, 1863, pp. 278, 279 (holotype: formerly ZMB 2126, now lost [*fide* Günther Peters, *in litt.*], from "Guayaquil," Ecuador, obtained by Consul C. Reiss).

Dromicus multilineatus PETERS, 1863, pp. 279, 280 (part, variety B, from Bogotá [variety A=lectotype of *Rhadinaea multilineata*]; syntype formerly in ZMB, now lost *fide* Günther Peters, *in litt.*).

Dromicus nuntius JAN AND SORDELLI, 1867 (1860–1881), vol. 2, livr. 24, pl. 5, fig. 1 (details of color pattern and scutellation of holotype [not seen], from "Andes de l'Equateur—Musée de Munich").

Dromicus lateristriga (Berthold): COPE, 1868, pp. 103, 104.

Liophis temporalis (Cope): BOULENGER, 1894b, p. 143. Werner, 1929, p. 113.

Urotheca lateristriga (Berthold): BOULENGER, 1894b, p. 181 (part: not *Dromicus multilineatus* [=*Rhadinaea multilineata*], nor *Ablabes decipiens* [=*Rhadinaea decipiens*]). AMARAL, 1929b, p. 178. WERNER, 1929, p. 122.

Urotheca coronata STEINDACHNER, 1901, p. 196 (abstract); 1902, p. 106, pl. 1, figs. 3, 3a (color pattern of head and anterior body, and cephalic scutellation in ventral aspect, of holotype [not seen]: Prince Bayern Collection No. 58 [possibly in Vienna Museum], from the vicinity of Babahoyo, [Los Ríos Province], Ecuador).

Erythrolamprus labialis WERNER, 1909, pp. 237, 238, fig. 10 (color pattern of dorsal and lateral aspects of head and neck; two syntypes [not seen], Hamburg Museum no. 117 [*fide* Peters, 1960, p. 537), from Boliche, Ecuador; F. von Buchwald, collector).

Leimadophis temporalis (Cope): BARBOUR, 1914, p. 338. AMARAL, 1929b, p. 168.

Coniophanes labialis (Werner): AMARAL, 1929b, p. 217.

R[*hadinaea*]. *lateristriga* (Berthold): DUNN, 1942b, p. 5.

Rhadinaea lateristriga lateristriga (Berthold): DUNN, 1944, p. 493. PETERS, 1960, pp. 536, 537. PETERS AND OREJAS-MIRANDA, 1970, p. 266.

HOLOTYPE: Lost; evidently not in the Zoologisches Museum Göttingen (*fide* Medem, 1965, p. 304). Few workers who have dealt with this species seem to have had access to the original description (Berthold, 1859, pp. 180, 181), which is consistently cited as having been published in the "Göttingen Anzeiger" or "Göttingen Gelehrte Anzeiger," a nonexistent journal so far as I have been able to determine. The complete description is as follows: "L. micans, supra ater, infra stremineus, striga laterali a naso versus caudam alba; capite planiusculo, rostro prominulo; scuto frontali lato; scutellis praeocularibus 3; seriebus squamarum laevium 17; scutis 151, anal. 2. —ex Nova-Granada."

Georges Jan (1863, p. 303) was in correspondence with Berthold and provided some additional details on the holotype, which he had borrowed from Göttingen for illustration in the "Iconographie Générale" [Jan and Sordelli, 1866 (1860–1881), vol. 2, livr. 18, pl. 5, fig. 1]. The type locality originally was given only as New Granada (Colombia), but Berthold evidently told Jan (*loc. cit.*) that the specimen came from Popayán, in the present Departamento de Cauca.

DIAGNOSIS: *Rhadinaea lateristriga* is a thick-tailed, brown snake with a white line or series of dashes on row 1 (or rows 1–2), and usually with a similar line on row 5 (or, in some cases an ill-defined pale streak on rows 4–6). The species is immediately recognizable in the southern part of its geographic range by a thin, sometimes broken, white neck-ring, which is formed from a posterodorsad extension of each white supralabial line. This marking is lacking in northern specimens, which might be confused with related species that have a white line on the first scale row: The dorsal head coloration is about the same hue as the body in *lateristriga*, but the heads of *R. decipiens*, *R. fulviceps*, and *R. pachyura* are distinctly paler than the body. Some *R. lateristriga* have a pair of short white lines or ocelli on the rear sides of the head, and a similar but unpaired marking on the nape. *Rhadinaea guentheri* has similar markings and invariably has two white lines on each side of the body, but it lacks the white supralabial line of *lateristriga*. *Rhadinaea multilineata* may have the medial ocellus (or line) on the nape, but the head markings are continuous lines from the eye to the body.

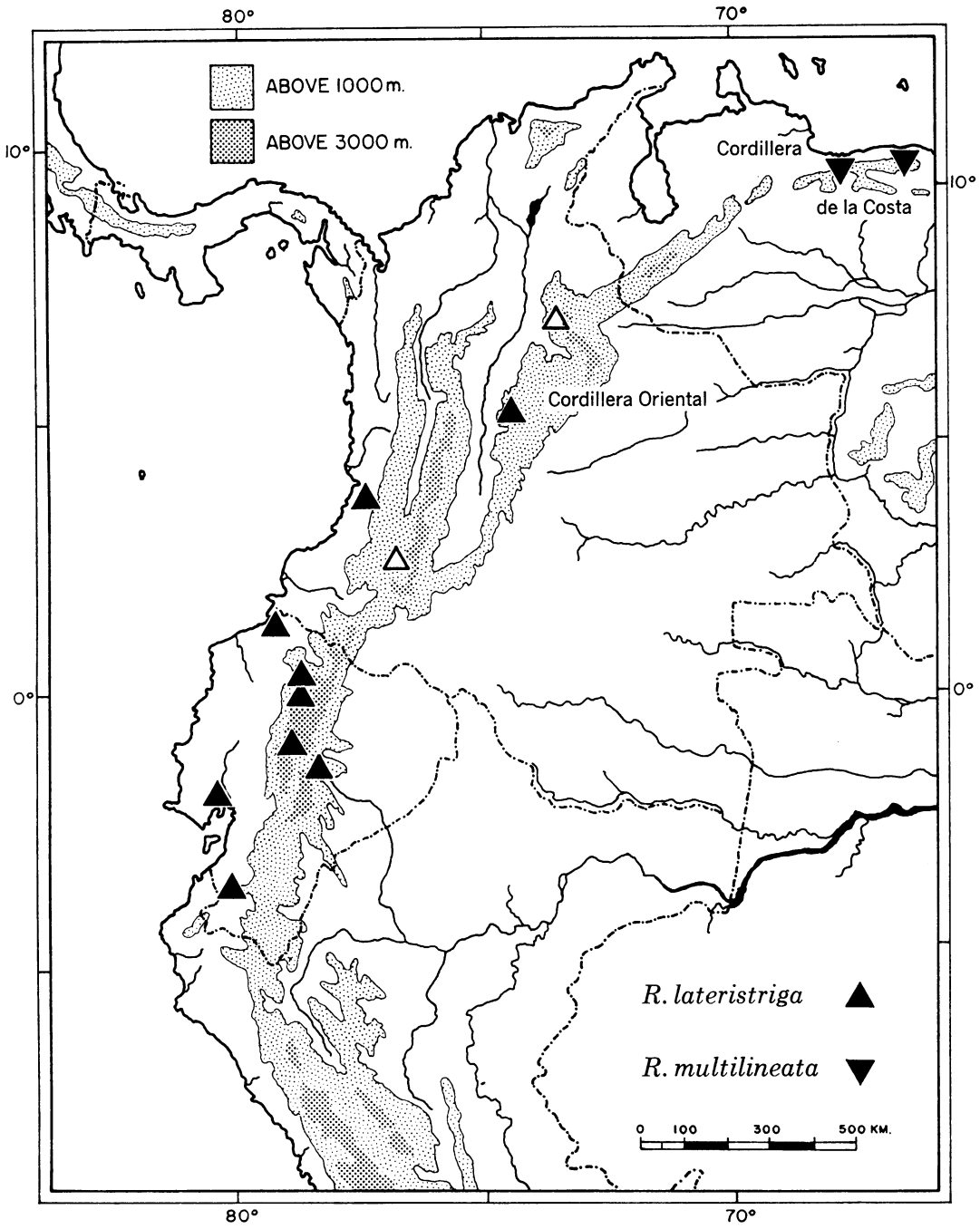
Rhadinaea lateristriga normally has two preoculars (three, counting the subpreocular); all other species in the genus normally have one preocular.

DISTRIBUTION: The Andean cordilleras of Colombia, and south in Andean and Pacific-side Ecuador to "Peru" (ANSP 5581, no definite locality). Specimens lack definite elevational data, and nothing has been recorded about habitats.

DESCRIPTION (12 SPECIMENS): The largest complete specimen is a female 622 mm. total length, 201 mm. tail length (another female, with an incomplete tail, is longer by 21 mm. snout to vent); the largest male is 405 mm. total, 131 mm. tail length. The tail is 32.0 and 32.3 percent of total length in two males, and 32.3 and 33.3 percent in two females. The dorsal scales are in 17–17–17 rows; anal ridges are absent. There are 144–167 ventrals (144–162, males; 153–167, females); specimens with complete tails have 82–92 subcaudals (87, 92, males; 82, 87, females). There are eight supralabials (7/7, 8/7, two specimens) and eight, or occasionally nine, infralabials. There are two preoculars, or three counting a relatively large subpreocular between the corners of the third and fourth supralabials; the loreal is fused with the lower preocular and extends to the eye in two individuals. There are two postoculars (1/2 in one) and 1+1 temporals.

The body is brown, with one or two usually conspicuous white lines on each side, extending from the neck well onto the tail. The most constant marking is a white line or series of dashes on the first scale row or the adjacent edges of rows 1–2; this line originates either abruptly on the lower side of the neck or from the pale throat color, and, on the tail, it tends to merge with the white subcaudal surface. There is usually a dorsolateral marking that involves row 5: This may be a white or tan line or series of dashes on row 5; or it may be a broader, ill-defined, diffused stripe of white or tan on row 5 and adjacent parts of row 4 and/or row 6; or (in UMMZ 78263) it may even be a dark-edged, well-defined tan stripe covering row 5 and the adjacent thirds of rows 4 and 6. One specimen (ANSP 5600) has a distinct, pale dash on each scale in rows 4–8; those dashes in rows 4–6 are largest and form the diffused dorsolateral stripe. The white lines or pale stripes are either edged with dark brown or not; occasional specimens have vague, dark brown stripes bordering the pale markings. There is sometimes a median brown line, slightly darker than the ground color, on the vertebral row and edges of the paravertebrals.

The supralabials are mostly dark or blackish brown, except for a white line that extends along the middle. In some populations, the posterior ends of the white lines extend posterodorsally from the lips and up the sides of the neck, fusing or not on the nape, several scales behind the parietals. If the extended supralabial lines fail to meet, or if they do not extend onto the neck, there is often a small ocellus or short, dark-edged white line on the midline of the nape. The anterior end of the dorsolateral line or stripe (when present), may fuse with, or end behind,



MAP 17. Locality records for *Rhadinaea lateristriga* and *R. multilineata* in northern South America. Open symbols are literature records (for *lateristriga*) for Bucaramanga (Nicéforo María, 1942, p. 92) and Popayán (type locality), Colombia.

the neck-ring or ends of the supralabial lines; if there is no neck-ring, the dorsolateral line or stripe (when present) ends abruptly or else fuses with a whitish blotch that rises dorsad from the pale throat color of some individuals. One specimen (USNM 151680) lacks dorsolateral lines

but has a small ocellus on the side of the neck, where a dorsolateral line would normally originate; usually there is no tendency for the formation of ocelli on the neck. The head is brown above, in many cases with dark spots on internasals and prefrontals. Usually there is a pair of small ocelli, or short, dark-edged white lines, on the rear of the head, each marking lying on the upper postocular and outer edge of a parietal plate. The pale supralabial lines in many cases meet on the rostral plate, above a ∩-shaped dark mark, the ends of which may be continuous with dark pigment along the upper edges of the mouth. Other parts of the rostral plate are pale tan, and usually there are two posterior barlike extensions of this color; each tan bar crosses an internasal, prefrontal, and supraocular, and is usually connected to its fellow by one or more tan crossbars.

The infralabials and genials are usually heavily mottled, spotted, or speckled with brown. The venter is white, except for the ends of the ventrals and subcaudals, which are tipped either with the brown coloring of the body or with blackish brown; a dark ventrolateral stripe is formed in the latter case. Cope (1868, p. 104) described the venters of recently preserved specimens as deep orange-red.

There are 11 teeth that increase in size posteriorly, followed by a broad diastema and two fangs, which are up to twice as large as the ultimate prediastemal tooth. The last prediastemal tooth is well anterior to the front edge of the ectopterygoid process. The last fang is offset laterad.

The hemipenis is single. The retracted organ of one specimen extended *in situ* to the middle of subcaudal 7, and the retractor muscle originated at the level of subcaudal 22. The everted organ of another individual extended to the base of subcaudal 6. The capitulum comprises about one third of the length of the hemipenis on its sulcate side. The sulcus spermaticus forks below the edge of the capitulum and the branches extend to the end of the retracted organ, but less than halfway up the capitulum when the organ is everted. The calyces are spinulate over the asulcate folds and toward the periphery of the capitulum, and papillate on most of the sulcate side of the capitulum. The wall of the capitulum forms a well-defined, double fold when the organ is retracted. The free edge of the capitulum is interrupted by a fusion to the stalk at the base of each half of the asulcate fold, and the capitulum is indented between these fusions. When the hemipenis is everted, the indented place becomes a small but conspicuously deep "pocket" in the edge of the capitulum on the asulcate side; the free edge of the capitulum forms a deep overhang on each side of the hemipenis, between the sulcate and asulcate surfaces. There are 22–33 small to large, slightly recurved spines below the capitulum. The spines are small on the sulcate side and become larger toward the asulcate side, where there is a nude region that is flanked by two rows of three (or four) spines each; this nude area extends basad from the "pocket" in the edge of the capitulum and is most conspicuous when the organ is everted. The basalmost spine in each of the aforesaid rows is the same size or larger than the spine immediately above, and there is an unpaired moderate or large-sized spine on the dorsal wall (=one side of the everted organ), at the bottom of the spinose zone. The basal third, or more, of the organ is unadorned save for minute spinules. The preceding description is based on an everted hemipenis of USNM 151680 (illustrated), and on retracted organs of AMNH 23028 (right organ illustrated) and ANSP 5600.

GEOGRAPHIC VARIATION: Specimens from the southern half of the range, that is, from the level of Quito south to Peru, have a partial or complete neck-ring that results from posterodorsad extensions of the white supralabial lines. The nominal *Dromicus frenatus*, *Dromicus temporalis*, *Erythrolamprus labialis*, and *Urotheca coronata* were based on specimens of *Rhadinaea lateristriga* having this kind of pattern.

In northwestern Ecuador (BMNH 78.1.25.51, UIMNH 55723, 55724) and in Colombia, there seems to be no tendency for the formation of such a collar, although the supralabial lines are distinct. The names *Liophis lateristriga* and *Dromicus nuntius* are based on specimens that lack the collar described above, as indicated by the illustrations in the "Iconographie Générale des Ophidiens" (but see below).

The specimen of "*Dromicus nuntius*" seems to have the beginning of a collar, but I think that this is caused by a pale blotch arising from the white throat, low on the side of the neck. The lateral body lines and the supralabial line flow into this blotch. This type of pattern is present in the available specimens (see above) from northwestern Ecuador. However, the specimen of

nuntius is not depicted in full lateral view [Jan and Sordelli, 1867 (1860–1881), vol. 2, livr. 24, pl. 5, fig. 1], and the ventral part of the blotch is not shown, so possibly I have misinterpreted the nature of the marking. Unfortunately, the type locality of *Dromicus nuntius* was given only as the "Andes de l'Equateur."

Some of the other variability that is indicated in the description of color pattern is possibly influenced by geographic factors, but too few specimens have been seen to permit a satisfactory analysis of pattern variation in this distinctive Andean species. Although I rather doubt that it is conspecific with *Rhadinaea multilineata*, additional specimens are needed from the Cordillera Oriental of Colombia before a definite statement can be made. A specimen of *lateristriga* (UMMZ 78263) from Muzo, about 100 kilometers north of Bogotá, is the only one examined from there, and it has a well-defined tan dorsolateral stripe as in *multilineata*, although the stripe (on row 5 and adjacent thirds of 4 and 6) is not continuous to the eye as in *multilineata*). I have not seen additional northern Colombian specimens mentioned by Dunn (1944, p. 493) and Nicéforo María (1942, p. 92).

There seems to be remarkably little variation in scutellation and number of maxillary teeth.

REMARKS: *Rhadinaea lateristriga* is most closely related to *R. guentheri* and *R. multilineata*, as revealed, for example, by the unusual tan markings on the snouts of specimens of each species; the tendency for this pattern of interconnected tan bars, on top of the muzzle, is found nowhere else in the genus. Although *R. lateristriga* and *R. multilineata* otherwise have different color patterns (but see Geographic Variation), their hemipenes are much alike and both species are remarkable in having little or no variation in the number of maxillary teeth (11+2 in nine *lateristriga* and 10 *multilineata*). Some specimens of *lateristriga* have a color pattern on the head and body similar to that of the Central American *guentheri*, but the latter species has a variable number of maxillary teeth (11+2–13+2, nine specimens) and the hemipenis differs in one important aspect. There is a single, thick fold on the capitulum of the retracted hemipenis of *guentheri*, whereas there is a well-defined double fold on the retracted organs of *lateristriga* and *multilineata* (compare fig. 42B with 42C). Most specimens of *guentheri* have weak grooves on the maxillary fangs, and this feature should be watched for in *lateristriga*.

Nothing seems to have been recorded of the habits or habitats of *Rhadinaea lateristriga*. Some records indicate that the species may descend virtually to sea level on the Pacific side of Ecuador, but specific data are not available and I do not care to even guess at the elevational range.

Dunn (1944, p. 493) expressed the belief that Werner (1899) described a specimen of *Rhadinaea lateristriga* under the name *Erythrolamprus imperialis*.

The specific epithet is formed from the genitive of *latus* (the side or flank) plus the noun *striga* (streak). This is in allusion to the pale line on the first row of scales, as the holotype did not have a dorsolateral line.

TABLE 17
NUMBER OF MAXILLARY TEETH IN THE *lateristriga* GROUP

Species	N[a]	No. of Teeth							Range
		11+2	12+2	13+2	14+2	15+2	16+2	17+2	
decipiens	14	—	—	—	—	4	9	1	15+2–17+2
dumerilii	3	—	—	—	—	1	2	—	15+2–16+2
fulviceps	11	—	—	1	3	6	1	—	13+2–16+2
guentheri	9	2	5	2	—	—	—	—	11+2–13+2
lateristriga	9	9	—	—	—	—	—	—	11+2
multilineata	10	10	—	—	—	—	—	—	11+2
pachyura	7	—	—	—	—	1	5	1	15+2–17+2
species inquirenda	1	—	—	—	—	—	—	1	17+2
Combined	64	21	5	3	3	12	17	3	11+2–17+2

[a]One maxilla from each specimen.

Rhadinaea multilineata (Peters)

Figures 40F, 41C; map 17

Dromicus multilineatus PETERS, 1863, pp. 279, 280 (part, variety A [variety B=*Rhadinaea lateristriga*]).

Urotheca lateristriga (not of Berthold): BOULENGER, 1894b, p. 181 (part).

Rhadinaea lateristriga multilineata (Peters): DUNN, 1944, p. 67. PETERS AND OREJAS-MIRANDA, 1970, p. 266.

Urotheca lateristriga multilineata (Peters): ROZE, 1959, p. 4; 1964, p. 540; 1966, pp. 236, 237, fig. 56 (poorly reproduced photograph of a preserved specimen).

DESIGNATION OF LECTOTYPE: The specimen here designated was described as variety "A" by W. Peters (1863, p. 280), from "Puerto Cabello und Caracas," Venezuela. According to Günther Peters (*in litt.*), the specimen was formerly ZMB 2108 but is now lost. I take the unusual course of designating a lost specimen as lectotype in order to insure conformance to recent usage of the name *multilineata* (see Remarks); a neotype can be designated later if there seems to be a real need.

DIAGNOSIS: *Rhadinaea multilineata* is one of several species (all in the *lateristriga* group) that have a white line on the first row of scales. It differs in having a pale temporal line that is continuous from the eye to the body, whereas the other species lack temporal markings or have only an ocellus or short, discrete line behind the upper rear edge of the eye. Another distinguishing feature is a usually well-defined tan stripe on row 5 and part of each adjacent row; some specimens of *lateristriga* have a tan stripe in this position, but usually it is vague and lacks sharply delineated edges.

DISTRIBUTION: Montane forest of the Cordillera de la Costa, 800–2000 meters elevation, northern Venezuela. The habitat at Rancho Grande is cloud forest (Test, Sexton, and Heatwole, 1966, p. 44).

DESCRIPTION (18 SPECIMENS): The largest specimen, a female, is 582 mm. total length, 217 mm. tail length; the largest male is 443 mm. total, 190 mm. tail length. The tail is 36.8–42.9 percent of total length in males, and 34.7–37.3 percent in females. The dorsal scales are in 17–17–17 rows; anal ridges are absent. There are 133–151 ventrals (133–146, males; 142–151, females), and 88–103 subcaudals (99–103, males; 88–100, females). There are eight supralabials, and eight infralabials (in a few cases nine or seven on one side). There is one preocular, and usually a subpreocular between the third and fourth labials, and two postoculars. There are 1+1 temporals, except for one aberrant individual that has 1+1+2/2+1+2.

The middorsum, i.e., the median five rows and adjacent half-rows, is brown or grayish brown, usually with a slightly darker line on the vertebral row and edges of the paravertebral rows. In a few cases, there is a vague dark line between rows 7 and 8. A tan stripe borders the dorsal color on each side, lying on row 5 and adjacent halves (more or less) of rows 4 and 6; this stripe usually has sharp, blackish edges, but the dark edges may be somewhat diffused and less distinct in large individuals. The lower sides are brown, darker than the dorsum, and there is a conspicuous white line or series of dashes on the first scale row, usually near the middle of the row.

The tan dorsolateral stripe narrows and in many cases tends to form a small ocellus behind the head. A black-edged, whitish line extends posteriorly from the rear of the eye into the dorsolateral body stripe or into the expanded, ocellus-like terminus of the stripe; there is only in few cases a slight gap between these markings. There is a short, black-edged, whitish line on the nape, in front of the anterior terminus of the dark vertebral line. The rostral plate is pale tan, except for a ∩-shaped dark mark, bar, or spot, and there is an extension of the tan color up on the muzzle and back onto each supraocular, where the tan bar in some cases skirts the top of the eye and merges with the pale postocular line. The top of the head is mostly brown like the dorsum of the body, except that there is dark mottling or spotting in some specimens. A blackish line edges the tops of the white supralabials, and there is a series of dark spots along the edge of the mouth; these spots are sometimes nearly fused, causing the appearance of a white line across the middle of the supralabials. The infralabials are variably spotted or speckled with dark pigment. The ventral surfaces are white, except that the ventrals and subcaudals are tipped with dark brown from the sides of the body. In a few cases there are a few brown spots scattered about the venter, or a narrow zigzag line or row of spots under the middle of the tail.

Test, Sexton, and Heatwole (1966, p. 44) stated that a specimen from Rancho Grande had an orange-yellow venter. The middorsum was said to be dark gray, the dorsolateral stripe dusky light brown, and the lower sides dark gray

with a white line, which was bordered below by black [on ventral tips and lower edge of first scale row].

There are 11 subequal teeth, followed by a broad diastema and two enlarged fangs. The ultimate prediastemal tooth is well anterior to the front edge of the ectopterygoid process. The last fang is offset laterad.

The hemipenis is single. The retracted organ of one specimen extended *in situ* to the end of subcaudal 7, and the retractor muscle originated at the level of subcaudal 19. The capitulum comprises about two-fifths of the length of the hemipenis on its sulcate side. The sulcus spermaticus forks slightly above the edge of the capitulum and the branches extend not quite to the end of the retracted organ. The calyces are spinulate over the asulcate folds and toward the periphery of the capitulum, and papillate on most of the sulcate side of the capitulum. The wall of the capitulum forms a well-defined, double fold when the organ is retracted. The free edge of the capitulum is interrupted by a fusion to the stalk at the base of each half of the asulcate fold, and the capitulum is indented between these fusions. (When the hemipenis is everted, the indented place doubtlessly becomes a conspicuously deep "pocket" in the edge of the capitulum on its asulcate side.) There are 20 small to large, slightly recurved spines below the capitulum. The spines are small on the sulcate side and become larger toward the asulcate side, where there is a nude region that is flanked by two rows, each with three large spines, of which the basalmost spine is largest in one row and the middle spine is largest in the other row; this nude area extends basad from the "pocket" in the edge of the capitulum. There is a large, unpaired spine on the dorsal wall (=one side of the everted organ) at the bottom of the spinose zone. The basal third of the organ is unadorned save for minute spinules. The preceding description is based on a retracted hemipenis of AMNH 98284.

REMARKS: *Dromicus multilineatus* Peters, 1863, was a composite name based on a Venezuelan snake and on Colombian *lateristriga*. Dunn (1944, pp. 65, 67) seems to have been responsible for the present-day restriction of the name *multilineata* to the Venezuelan populations, although a lectotype has not been designated until now. Dunn (*loc. cit.*) treated *multilineata* as a subspecies of *Rhadinaea lateristriga*, but I prefer to regard it as a distinct species, at least until more is known about *lateristriga* from the northern part of the Cordillera Oriental of Colombia, where intermediate populations might be expected. I have seen only one specimen of *lateristriga* from this cordillera, from a locality about 100 kilometers north of Bogotá, but Nicéforo María (1942, p. 92) recorded it from as far north as Bucaramanga. *Rhadinaea multilineata* exhibits much less variation in color pattern than *R. lateristriga*. The temporal marking, which is continuous from the eye to the body, and the dorsolateral tan stripe, which is more than a vague suffusion of pigment and which usually has well-defined edges, combine to give *multilineata* a distinctive appearance. *Rhadinaea multilineata* has fewer ventrals and preoculars, and more subcaudals, than *lateristriga*.

Rhadinaea multilineata is at least partly diurnal in the cloud forest at Rancho Grande (Test, Sexton, and Heatwole, 1966, p. 44), and I should not be surprised if it were almost completely so. The specific epithet is formed of the prefix *multi-* (many) plus the noun *linea* (line) plus the suffix *-atus* (provided with), in reference to the striped pattern.

Rhadinaea pachyura (Cope)

Figures 40B, 41H; map 14

Contia pachyura COPE, 1875a, pp. 145, 146. GÜNTHER, 1893 (1885–1902), p. 104. BOULENGER, 1894b, p. 267. AMARAL, 1929b, p. 181. WERNER, 1929, p. 149.

Liophis pachyurus (Cope): DUNN, 1931a, p. 163 (part).

Rhadinaea pachyura pachyura (Cope): DUNN, 1938, p. 198; 1942b, p. 5. TAYLOR, 1951, pp. 117, 118. PETERS AND OREJAS-MIRANDA, 1970, p. 267.

Rhadinaea pachyura (Cope): DUNN, 1932, p. 1 (part). TAYLOR, 1954, p. 679. SMITH AND GRANT, 1958a, p. 212.

Rhadinaea decipiens rubricollis TAYLOR, 1954, pp. 739, 740 (holotype: KU 31956, from Cinchona, *ca.* 5500 feet elevation, Volcán Poás, Costa Rica; Edward H. Taylor, collector). PETERS AND OREJAS-MIRANDA, 1970, p. 264. New synonymy.

HOLOTYPE: USNM 30618, an adult male in poor condition, obtained by William M. Gabb at Sipurio, [near Suretka, Limón Province], Costa Rica. The specimen seems to have been dried at one time; accurate measurement is now impossible, and even dorsal scale counts cannot be made with confidence. I counted 135 ventrals (including the preventral) and 50 caudals, the

same figures obtained by Cope. The tail is incomplete, a fact not mentioned in the original description, which has caused some confusion in the literature (i.e., Smith and Grant, 1958a, p. 212). The dorsal ground color is brown, and I presume that it may have been dark brown originally, although Cope described the specimen as being black. Cope stated that the scales were generally poreless but that some had one pore; I was unable to find any apical pits and suspect that he was looking at an occasional air bubble trapped beneath a scale.

DIAGNOSIS: *Rhadinaea pachyura* is one of several species (all in the *lateristriga* group) with a definite white line or series of dashes on the first row of scales. It is distinguished from other such species, except *R. decipiens* and *R. fulviceps*, by the absence of pale ocelli or pale lines on the head or nape.

Rhadinaea pachyura and *R. fulviceps* both have yellow-brown heads (may be reddish brown in life) against a brown body, but the head coloration extends only one or two scales onto the neck (behind the parietal tips) of *pachyura*, and three or four scales back on *fulviceps*. The latter species has intensely speckled labials (weakly spotted in *pachyura*) and may lack the white line on the first scale row; *R. pachyura* has a long, slender hemipenis with a relatively small capitulum, whereas in *fulviceps* the hemipenis is stouter and the capitulum comprises nearly half of the length of the organ on the side with the sulcus spermaticus. Additional differences are given in the Remarks, under *R. fulviceps*.

Rhadinaea pachyura lacks a thin, white dorsolateral line (although a broader, ill-defined and diffused streak may be present), and adults do not have a collar across the nape. The lack of both of these features (or only of the thin line in juveniles) distinguishes *pachyura* from northern populations of sympatric *R. decipiens*. But the dorsolateral line is lacking in some populations of *decipiens*, and some individuals from these populations also lack a collar. Such specimens can be distinguished from *pachyura* by the presence of a horizontal white line on dark supralabials; the labials of *pachyura* are weakly spotted with brown or have brown sutures. Also, *pachyura* seems invariably to have a brown body (at least in preservative), whereas available specimens of weakly patterned *decipiens*, from the southern populations, are black.

DISTRIBUTION: Principally in the Atlantic lowlands, from northern Costa Rica to western Panama, but also in adjacent highlands, to about 1600 meters (in both the Cordillera Central of Costa Rica and the Cordillera de Talamanca of Panama, where it evidently crosses onto the upper slopes of the Pacific drainage, between the Cordillera de Talamanca and the Serranía del Tabasará). This is principally a tropical and lower montane rain-forest distribution, except on the Pacific slopes of Panama, where the montane forest is exposed to a winter dry season.

DESCRIPTION (NINE SPECIMENS): A large female is 516+ mm. (384 mm. snout-vent, 132 mm. of incomplete tail); the largest male is 435+ mm. (259 mm. snout-vent, 176 mm. of incomplete tail). ANSP 23880 (head and neck only, sex unknown), must have been much larger than either of the foregoing, judged from the size of its head. The tail is 40.9 percent of total length in a juvenile male (the holotype of *R. decipiens rubricollis*); no other measurable specimen has a complete tail. The dorsal scales are in 17–17–17 rows; anal ridges are absent. There are 130–138 ventrals (130–134, males; 132–138, females), and 104 (female) and 124 (male) subcaudals. There are eight supralabials, and nine or 10 infralabials. There is usually one preocular (2/1, 2/2, two specimens), a subpreocular between the third and fourth labials, two postoculars, and 1+1 temporals (1+2 on one side of one specimen).

The body is medium or dark brown, or grayish brown. A thin white line, or series of white dashes, originates on the lower side of the neck and extends along the middle or top of scale row 1 on the body, and gradually disappears on the basal section of the tail. There is in some cases a pale frosting on the upper sides, especially on rows 4 and 5, where the frosting appears as a definite, but diffused, whitish streak. Less concentrated pale speckling may also occur higher on the body, where scale rows (especially row 6) that are relatively free of the frosting cause, on some specimens, the appearance of very vague, dark lines or stripes.

The top and upper sides of the head are yellow-brown, and this color extends one or two scales behind the ends of the parietal plates, to abruptly terminate in usually sharp contrast to the brown body; on some specimens, the head color extends back for an additional scale or two in the vertebral row. One small male of 198 mm.

total length, the only known juvenile of *pachyura*, has a whitish collar across the rear of the head; the posterior edge (one and one-half scales behind the parietals) is sharply defined against the body color, but anteriorly there is a gradation to the yellowish brown color on the rear of the parietals (see below for the color of this specimen in life). The rostral plate varies from brown above and pale below to nearly uniform brown. The head color encroaches onto the tops of the supralabials, where the pigment tends to concentrate and form a dark brown line, especially from the eye to the corner of the mouth. The white supralabials and infralabials usually have concentrations of brown pigment along their sutures, but in some cases a few plates have medial brown spots close to the border of the mouth. The ventrals and subcaudals are tipped with the dark body color, which usually forms a strongly serrated edge. The venter is otherwise white, in some cases with a few scattered dark specks. Taylor (1954, pp. 739, 740, under the name *R. decipiens rubricollis*) described the pale colors of the only known juvenile as follows:

"In life . . . head reddish brown; a reddish band across back of parietals and nape . . . supralabials lavender . . . chin and infralabials pink . . . first scale row with small paper-white spots that form a dotted line . . . venter for four fifths of its length flesh white; remainder of body and subcaudal region bluish white." The body color was said to be black, but it is brown in preservative. The coloration of living adults is not known. Presumably there is an ontogenetic change in which the pale collar changes to the anterior color of the head.

There are 15–17 maxillary teeth, increasing in size posteriorly, followed by a distinct diastema and two slightly enlarged fangs. The ultimate prediastemal socket lies anterior to the front edge of the ectopterygoid process, sometimes only barely so. The last fang is offset laterad.

The hemipenis is long, slender, and single. A retracted organ extended *in situ* to about the middle of subcaudal 10, and the retractor muscle originated at the level of subcaudal 28. The capitulum comprises only about one-fourth of the length of the hemipenis on its sulcate side. The sulcus spermaticus forks at a point about half of its length up the capitulum, and the branches extend virtually to the end of the retracted organ. The calyces are spinulate over most of the asulcate folds and toward the periphery of the capitulum, and papillate on most of the sulcate side of the capitulum. The wall of the capitulum forms a well-defined, double fold on the asulcate side of the retracted organ. The hemipenis is rather weakly capitate. The free edge of the capitulum is fused to the stalk at the base of each half of the asulcate fold. Several calyces between the asulcate folds are rather large, but I do not know if these would form a "pocket" when the organ is everted (i.e., as in *R. decipiens*, see fig. 42F). There are 46 small to medium, slightly recurved, spines below the capitulum. The spines, all of which are rather stubby, are small on the sulcate side and become larger toward the asulcate side, where there is a short nude region that is flanked by two rows of spines; each row contains three spines and extends basad from the bottom of an asulcate fold. The basalmost spine in each of the aforesaid rows lies slightly to one side and is larger than the spines above; also, these are the largest and lowest spines on the entire organ. More than the basal half of the organ is unadorned save for minute spinules. The preceding description is based on a retracted hemipenis from KU 112458. I also examined a retracted, *in situ* hemipenis of the holotype, but my notes on it are not adequate for my more recent standards of description; however, the organ extended to the end of subcaudal 10, and so is about the same length as the one described.

REMARKS: *Rhadinaea pachyura* is similar to *R. fulviceps* in some characters and to *R. decipiens* in others. It is very much like *fulviceps* in coloration, but more like *decipiens* in hemipenial structure. All three species have been considered conspecific. *Rhadinaea pachyura* and *fulviceps* might conceivably prove to be conspecific, when specimens, especially males, become available from between the presently known ranges, but I believe that *pachyura* and *decipiens* are distinct species, a situation that I think has been misinterpreted because of the great geographic variability of *R. decipiens*.

Taylor (1954) described *Rhadinaea decipiens rubricollis* on the basis of a juvenile snake from Cinchona, in the Cordillera Central of northern Costa Rica. This specimen has a nape collar somewhat as in *decipiens*, but in several other respects it is typical of *pachyura* and does not agree with two adult specimens of *decipiens* now available from the same locality. The following

characteristics cause me to put the name *rubricollis* in the synonymy of *Rhadinaea pachyura*: 1) There is no narrow white line on row 5 as in all northern *decipiens*, but there is a whitish frosting on rows 4 and 5, resulting in the weak, diffused stripe that is often seen in adult *pachyura*; 2) the white line on row 1 is formed from a series of dots and dashes and is not so sharply defined as in *decipiens*, and it disappears on the basal part of the tail; 3) the labials are mostly white and have brown pigment along their sutures, as is common in *pachyura*, whereas the two *decipiens* from Cinchona have darkened supralabials with a horizontal white line. I believe that the collar of this specimen is a juvenile feature of *pachyura* (or a geographic variation), but additional material is needed to confirm this. No other juveniles, of either species, are available for comparison, except for two specimens of *decipiens* from eastern Panama and Colombia, which is far from the range of *pachyura*.

Norman Scott told me that he found a specimen of *Rhadinaea pachyura* under a log, at Cahuita, in Limón Province, Costa Rica. Nothing else seems to be known of its habits. The specific epithet is a combination of the adjective *pachys* (thick) plus the noun *oura* or *ura* (tail), in reference to the thickness of the basal part of the tail, a characteristic of the *lateristriga* group in general.

Rhadinaea, species inquirenda

Figures 40H, 41G; map 14

INTRODUCTION: I have been unable to assign one specimen of the *lateristriga* group to a named species. The specimen is from the southern slopes of Cerro de La Muerte, in the vicinity of Finca de Jardín, 6 miles [9.6 kilometers] south of Villa Mills. This locality is in the Cordillera de Talamanca, Cartago Province, central Costa Rica.

DESCRIPTION (USC 1036): It is a juvenile or subadult male (the hemipenial spines are not ossified) 350 mm. total length, of which the nearly complete tail is 144 mm., or 41.1 percent of the total. There are 17–17–17 rows of dorsal scales and no anal ridges. The specimen has 132 ventrals and 119 subcaudals, although one or a few pairs of subcaudals may be missing because of breakage at the extreme tip of the tail. There are eight supralabials, 11/10 infralabials, one preocular, a subpreocular in a notch between the third and fourth labials, 2/3 postoculars (bottom one on right is tiny), and 1+2/1+1 temporals. There are two extra scales lying side by side above the sixth supralabial, on each side of the head.

The body is uniform dull brown (gray under the stratum corneum) in general aspect. Close examination reveals that the basal part of a scale is paler than the edges and apex; this contrast is most pronounced on the scales on the sides and posterior part of the body. The top and upper sides of the head are uniform medium brown, somewhat lighter than the color of the body. The color of the head extends one to two scales behind the parietals and terminates abruptly, but the contrast between it and the body coloration is not great. There is a vague ∩-shaped blackish mark on the brown rostral plate. The brown head color encroaches onto the supralabials, the first three and the last two being almost completely suffused with pale brown. There is a row of blackish brown spots along the lower parts of the supralabials, and these spots set off a white ground color above, on labials 4–6, but there is not sufficient contrast to give the impression of a horizontal white line; there is no pigmentation along the common sutures of the labials. There is a tinge of brown on the chin, and there are some vague blackish spots on the first five or six infralabials. The ventrals and subcaudals are tipped with dark pigment, which forms a straight border (not noticeably serrated) between the dark dorsal coloration and the pale venter, which is immaculate yellowish white.

There are 17 subequal maxillary teeth, which are followed by a diastema and two fangs that are little (if any) larger than the prediastemal teeth. The ultimate prediastemal socket lies anterior to the front edge of the ectopterygoid process. The last fang is offset laterad.

The hemipenis is single. The right retracted hemipenis extended *in situ* to the middle of subcaudal 10, and the retractor muscle originated at the level of subcaudal 29. The capitulum is small, comprising only about one-fifth of the total length of the organ on its sulcate side. The sulcus spermaticus forks at the edge of the capitulum, and the branches extend nearly to the end of the organ. The wall of the capitulum forms a poorly defined double fold on the asulcate side. There are 40+ small to medium, stubby spines below the capitulum; the spines

are largest basally and toward the asulcate side, where there is a small nude area (below the folds of the capitulum) that is flanked by two rows of three spines each and bordered by another spine below. The largest of the medium-sized spines lie at the bottom of the spinose area, well below the spines that border the aforesaid nude space. More than the basal half of the organ is unadorned, save for minute spinules. It is difficult to see all the detail because the organ is from a young snake; there has been no ossification of the spines or of papillae on certain calyces.

REMARKS: This specimen is reminiscent of *Rhadinaea pachyura* in the uniform head coloration, but it is slightly like some specimens of *R. decipiens* in the pattern of markings on the supralabials. Some specimens of *decipiens* do lack a pale collar but, even so, there tends to be a blotching and unevenness of the color of the head, and the labial markings are more intense, causing a definite impression of a white line on a blackish ground. Details of the hemipenis are more like those in *decipiens* than in *pachyura*. The sulcus spermaticus forks near the edge of the capitulum rather than halfway up; the small nude area on the asulcate side is bordered by a basal spine, which is absent in *pachyura*, and the spines around the nude space are not the largest and basalmost spines on the organ. The specimen differs from all specimens of both species in that it lacks a white line on the first row of scales.

The specimen possibly represents an undescribed species, but it seems equally possible to me that it is a geographical variant or even a totally aberrant specimen of either *R. decipiens* or *R. pachyura*. Neither of these species can be said to be well known; too few specimens are in collections. An important feature of the specimen is its almost total lack of a pattern. It is perhaps worth noting that a specimen of *R. godmani* is unique among Costa Rican specimens of its species in also having a nearly unicolor body, and this specimen is also from Cerro de La Muerte, although on the side opposite from where the *decipiens-pachyura*-like specimen was collected. There is no particularly close relationship between the *godmani* and *lateristriga* groups, but the existence of a nearly patternless specimen of each group, from the same mountain, may be more than coincidence.

THE *brevirostris* GROUP

The *brevirostris* group, which is restricted to South America, is comprised of six species: *Rhadinaea affinis*, *R. bilineata*, *R. brevirostris*, *R. occipitalis*, *R. persimilis*, and *R. poecilopogon*. One species (*brevirostris*) is widespread along the foot of the Andes and in the Amazonian basin, and the others occur south of the basin, especially in the southern Brazilian highlands. The group is defined especially by the following combination of characters (see also table 3): The hemipenis is single, or either single or bilobated within the same species, but the insertion of the retractor muscle is slightly divided in any case. There are enlarged soft papillae on the asulcate calyces, and short stubby spinules above the large papillae in two species; capitation of the hemipenis varies from present to absent. Two species show either partial or complete reduction of from 17 to 15 scale rows. Anal ridges and a subpreocular are invariably absent. Only supralabial 2 (not 2–3) normally touches the loreal. There are 7 or 8 supralabials, and, in the latter case, labials 3–5 enter the orbit (rather than generic norm of 3–4). Color pattern is extremely variable, but all except one species have either a pale canthal-temporal line or else some form of pale postocular marking.

The *brevirostris* group is one of greatest diversity. *Rhadinaea occipitalis* is the most extreme form, with its anterior blotching and 15 scale rows. Although *occipitalis* does not look like a *Rhadinaea*, it is connected with *brevirostris* through hemipenial features, and with *poecilopogon* through head pattern.

Rhadinaea affinis (Günther)

Figures 45F, 46A; map 19

Enicognathus Melanocephalus DUMÉRIL, BIBRON, AND DUMÉRIL, 1854, pp. 330–332 (part: one of the syntypes of *E. melanocephalus* [MNHN 7863, probably from Brazil], an unavailable name because its lectotype=*Sibynophis subpunctatus*).

Dromicus affinis GÜNTHER, 1858, pp. 128, 129 (part, specimens *a*, *b*).

R[*hadinaea*]. *obtusa* (not of Cope). Part: COPE, 1868, p. 132, and 1875a, p. 139 (reference to a syntype [MNHN 7863] of *Enicognathus melanocephalus*, see above; Cope also refers to an illustration in Jan and Sordelli, but the specimen figured is *Rhadinaea persimilis*).

Coronella Iheringii BOULENGER, 1885, pp. 194, 195 (three syntypes [not seen]: BMNH 1946.1.4.32–1946.1.4.34 [formerly 82.10.4.65–82.10.4.67], from the state of Rio Grande do Sul, Brazil; H. von Ihering, collector); 1886, p. 431.

TABLE 18

ASPECTS OF INTERSPECIFIC VARIATION[a] IN THE *brevirostris* GROUP

Species	N	Ventrals		Subcaudals		Tail Length as a Percentage	
		Males	Females	Males	Females	Males	Females
affinis[b]	6	144–172 (3) 158.3	170–183 (3) 176.3	66–75 (3) 70.3	64–68 (3) 66.3	22.1–30.9 (3) 27.1	20.8–24.0 (3) 22.7
bilineata	1	138 —	— —	75 —	— —	27.6 —	— —
brevirostris[c]	55	142–166 (33) 152.3±1.18	141–166 (21) 150.9±1.47	44–61 (26) 51.5±0.73	36–57 (19) 43.8±1.22	19.4–24.8 (23) 22.4±0.31	16.7–22.8 (17) 19.3±0.40
occipitalis[b]	25	161–184 (15) 175.3±1.77	179–192 (10) 184.6±1.22	66–80 (14) 75.4±0.98	64–74 (8) 69.8±1.29	21.8–27.6 (14) 25.6±0.43	20.6–24.9 (10) 23.0±0.49
persimilis[d]	1	128 —	— —	58 —	— —	26.4 —	— —
poecilopogon[b]	5	151, 158 154.5	159–160 (3) 159.3	76, 79 77.5	65–71 (3) 68.7	28.7, 29.9 29.3	25.6–27.9 (3) 26.9
Combined ranges	93	128–184	141–197	44–80	36–74	19.4–30.9	16.7–27.9

[a]The following statistics are given if the sample is sufficiently large: Above, range followed by number of specimens in parentheses (if more than two); below, mean and standard error of the mean.

[b]See the text description for additional data compiled from the literature.

[c]A geographical breakdown is given in the species account.

[d]See table 20 for additional data compiled from the literature.

TABLE 19
NUMBER OF MAXILLARY TEETH IN THE *brevirostris* GROUP

Species	N[a]	No. of Teeth 10+2	11+2	12+2	13+2	14+2	15+2	16+2	17+2	18+2	19+2	20+2	Range
affinis	6	2	—	—	—	2	—	—	1	1	—	—	10+2–18+2
bilineata	1	—	—	—	—	—	—	—	—	—	—	1	20+2
brevirostris	38	—	—	2	22	5	9	—	—	—	—	—	12+2–15+2
occipitalis	15	—	—	—	5	6	3	—	1	—	—	—	13+2–17+2
persimilis	1	—	—	—	—	—	—	—	1	—	—	—	17+2
poecilopogon	5	—	—	—	1	3	—	1	—	—	—	—	13+2–16+2
Combined	66	2	—	2	28	16	12	1	3	1	—	1	10+2–20+2

[a]A single maxilla from each specimen.

Rhadinaea affinis (Günther): BOULENGER, 1894b, pp. 172, 173 (part: not the reference to a figure of *Enicognathus melanocephalus* [=*Rhadinaea persimilis*, see above]). WERNER, 1929, p. 117. PRADO, 1943, pp. 12, 13, 15; 1945a, pp. 74, 75. PETERS AND OREJAS-MIRANDA, 1970, p. 263.

Liophis affinis (Günther): AMARAL, 1926b, p. 104; 1929a, p. 87; 1929b, p. 170; 1936, p. 113; 1944, pp. 55, 56 (*Liophis* by implication, but listed as *Rhadinaea affinis*).

DESIGNATION OF LECTOTYPE: Two syntypes are BMNH 1946.1.5.80, 1946.1.9.5, from Rio de Janeiro, Brazil; presented to the British Museum by A. Fry and G. Busk. A third syntype (BMNH 55.4.18.15, not seen), from Brazil, was assigned to the later described *Rhadinaea poecilopogon* by Boulenger (1894b, p. 173). A fourth specimen that was tentatively assigned to *affinis* in the original description is from Jamaica and is most likely a specimen of *Alsophis ater* probably being specimen "B.*d*" in Boulenger (1894b, p. 122), according to data supplied by A. F. Stimson.

I have examined BMNH 1946.1.5.80 and here designate it as lectotype. It is a male with 144 ventrals, one preventral, and 70 subcaudals.

DIAGNOSIS: *Rhadinaea affinis* is a large member of the *brevirostris* group and agrees with *R. persimilis*, *R. bilineata*, and *R. poecilopogon* in having 17–17–17 scale rows and a dark line on row 4 (or dark sides up onto row 4). *Rhadinaea affinis* differs from these species in having a pale marking, usually triangular or wedge-shaped, behind each eye. See the Remarks section for additional comparisons with *R. persimilis*, the closest ally.

Rhadinaea cuneata of Mexico is the only other species of *Rhadinaea* characterized by a wedge-shaped, postocular marking, although such a marking occurs as a variation in the South American *R. occipitalis*, which is immediately distinguished on account of its spotted pattern.

DISTRIBUTION: Southeastern and southern Brazil, from the state of Minas Gerais south into Rio Grande do Sul.

DESCRIPTION (SIX SPECIMENS): The largest specimen is a female 712 mm. total length, 148 mm. tail length; the largest male is 606 mm. total, 148 mm. tail length. The tail is 22.1–30.9 percent of total length in males and 20.8–24.0 percent in females. Prado (1943, table) gave a maximum size of 731 mm. total length, 159 mm. tail length, for a female. Calculating from Prado's (*loc. cit.*) measurements of 26 specimens gives a range of 18.4–29.8 percent (mean 24.5) for the tail length of 16 males, and 16.9–26.1 percent (mean 21.6) for 10 females.

The dorsal scales are in 17–17–17 rows; anal ridges are absent. There are 144–183 ventrals (144–172, males; 170–183, females), and 64–75 subcaudals (66–75, males; 64–68, females). Prado (*loc. cit.*) gave 156–181 ventrals [males 156–176, mean 167.1; females 169–181, mean 176.5], and 42–74 subcaudals [males 63–74, mean 69.9; females 42–72, mean 63.2]. There is one preocular, no subpreocular, two postoculars, 1+2 temporals, seven supralabials, and eight infralabials.

The body is medium brown. There is a broken, blackish brown vertebral line, in which most of the dark pigment tends to be concentrated toward the apexes of the vertebral scales. A lateral line of blackish dashes extends along the lower edge of row 4, sometimes overlapping onto the top of row 3. The lateral dark line is edged above by a whitish line near the middle of the fourth row. The dark lines originate from the dark head color and the lateral whitish line

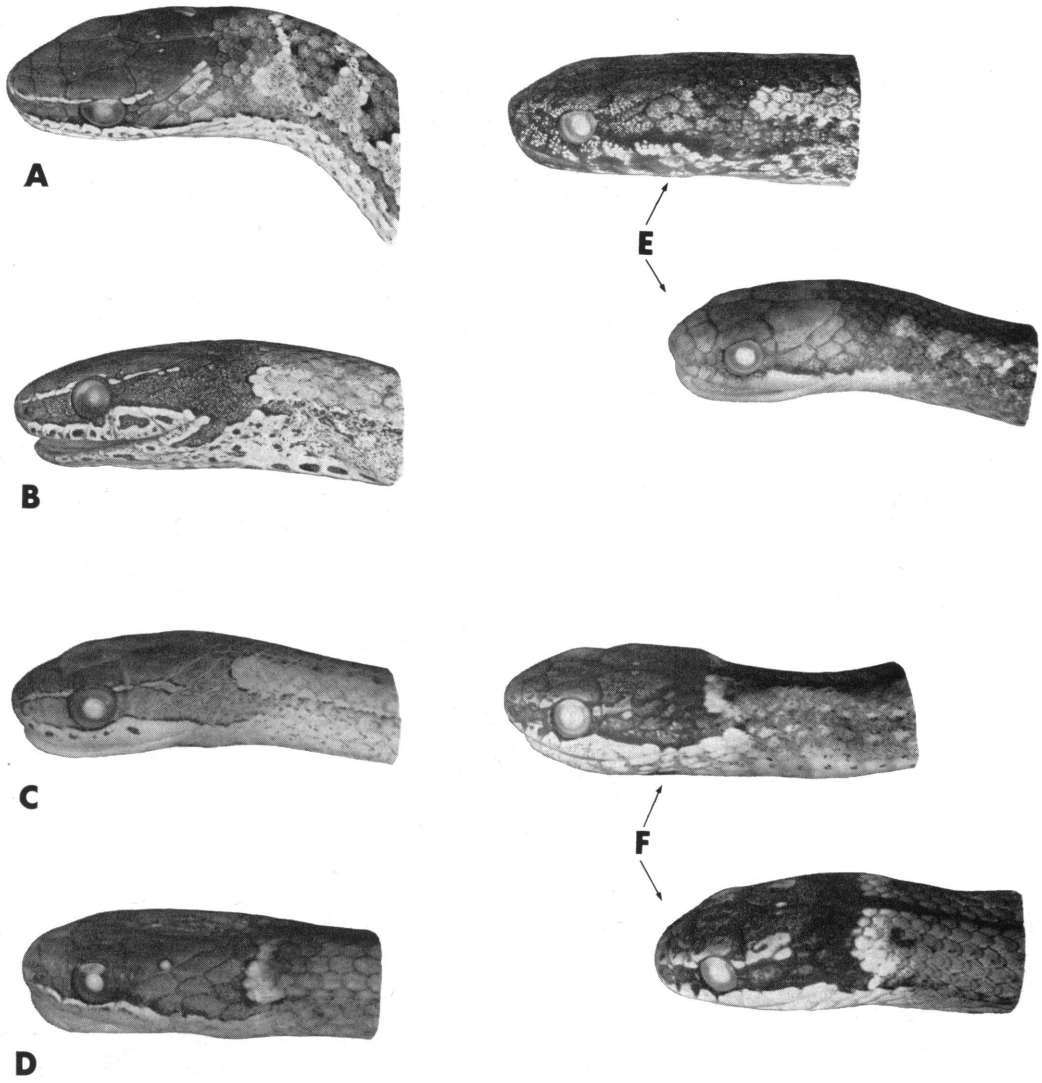


FIG. 45. Head patterns in the *brevirostris* group. A. *Rhadinaea occipitalis*, USNM 120833, Brazil. B. *R. poecilopogon*, ANSP 27344, Uruguay. C. *R. bilineata*, SMF 19052, Brazil. D. *R. persimilis*, SMF 32457, Brazil. E. *R. brevirostris*—upper, KU 119391, Ecuador; lower, BMNH 1946.1.1.9 (syntype of *Dromicus viperinus*), Peru. F. *R. affinis*, Brazil—upper, BMNH 1946.1.5.80 (lectotype); lower, ZIUS 3966.

originates on or behind the neck, and all lines extend to the end of the tail. The dark vertebral line anteriorly interrupts a narrow (one or two scales) whitish collar that crosses the nape a scale-length behind the parietals and which terminates at the lateral dark line on each side of the neck. The top and sides of the head are blackish brown in general aspect, in marked contrast to the lighter body, but the dark coloring anteriorly breaks into spots or extends as a kind of scrollwork on the supraoculars, prefrontals, internasals, and rostral, which are basically paler brown. A pair of pale parietal dots is in some cases present. Behind each eye, there is a pale marking that is usually wedge-shaped and lies mainly on the parietal, with the apex of the wedge at the eye (on the upper postocular) and with the lower rear corner on the temporals. This postocular mark is only vaguely wedge-shaped in MCZ 17930 because of irregular borders; in MNHN 7863, the marking is reduced to a dark-edged pale line on the outer

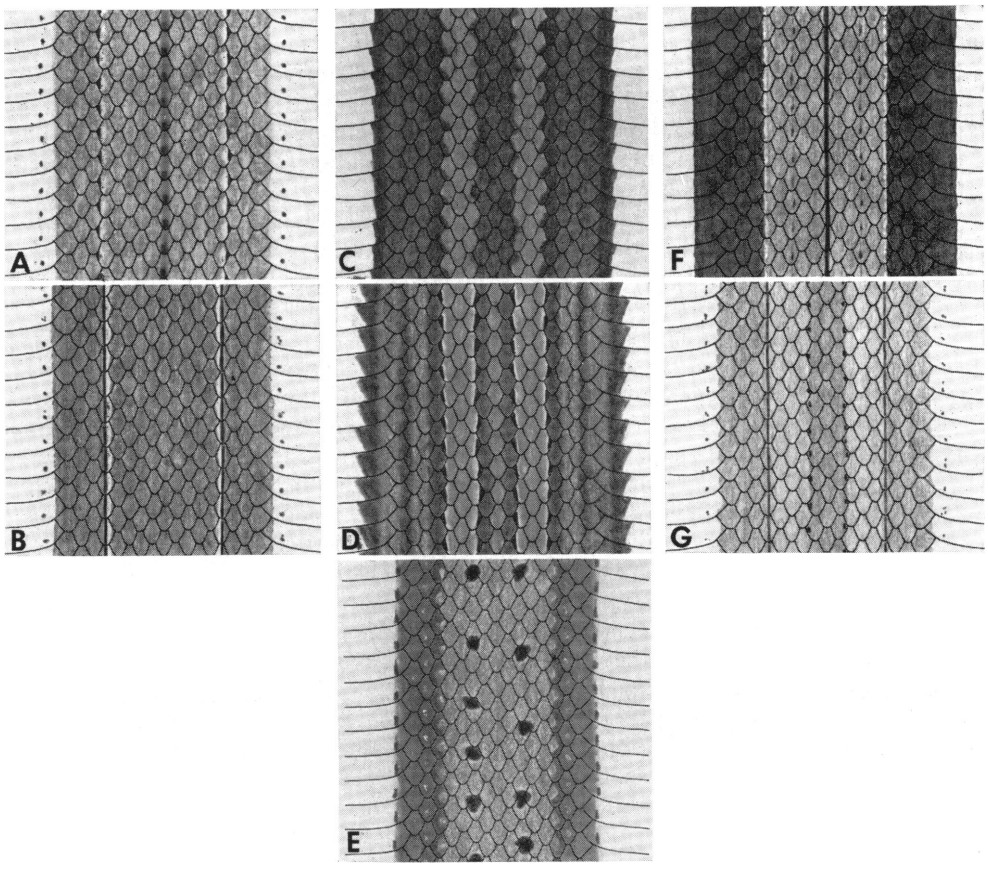


FIG. 46. Midbody patterns of the *brevirostris* group. A. *Rhadinaea affinis*, BMNH 1946.1.5.80 (lectotype), Brazil. B. *R. persimilis*, SMF 32457, Brazil. C, D. Both *R. brevirostris*, Ecuador, as follows: C. UMMZ 82881; D. AMNH 23289. E. *R. occipitalis*, SMF 19059, Brazil. F. *R. poecilopogon*, BMNH 82.10.4.78, Brazil. G. *R. bilineata*, SMF 19052, Brazil.

edge of the parietal and, representing the lower corner of the wedge, a discrete white spot on the upper secondary temporal. The postocular markings are grayish to whitish on preserved specimens, but possibly were pale tan in life. There is a tendency for a black line to run across the posterior supralabials from the eye to the corner of the mouth. The supralabials and entire underside of the head are yellowish white, immaculate or with a dense marbling of light, grayish brown. The venter is pale yellow. The brown dorsal color encroaches slightly onto the ends of the ventrals and subcaudals, and there is a conspicuous line of black dots (a double line in MCZ 17930) on each side of the venter, from the throat onto the tail; the line of dots may terminate after just a few subcaudals or extend nearly to the end of the tail.

There are 10–17 maxillary teeth, followed by a broad gap and two enlarged fangs. The ultimate prediastemal socket lies anterior to the front edge of the ectopterygoid process. The last fang is offset laterad. Two specimens (BMNH 89.12.16.117; USNM 76339) with the formula 10+2 have all the teeth relatively short and thick compared with four other specimens, in which the range is 14+2–18+2.

A retracted hemipenis extended *in situ* to the end of subcaudal 6, and the retractor muscle originated at subcaudal 23. The hemipenis is single, but there is a short (less than half a subcaudal) division in the insertion of the retractor muscle, on the lateral wall. The hemipenis is noncapitate, except for a distinct overhang in the middle of the asulcate side, slightly below the tip. There are large calyces on the tip of the

organ, and somewhat smaller calyces on about the distal third of the sulcate side; the calyces are papillate, without spinules. The sulcus spermaticus forks more than halfway up the hemipenis and its branches extend to the tip of the organ; there is a thick, solid wall of tissue between the branches for nearly half of their length, gradually giving way to calyces distally. There are some large, rather flaplike papillae below the calyces on the asulcate side of the tip. There are more than 70 small to medium, slightly recurved spines below the calyces. Many of the spines on the asulcate side are arranged in two long, parallel rows below the distal overhang of large papillae. Between the distal halves of these two rows of spines is a low ridge of tissue that bears several papillae and which is connected to the adjacent spines by small ribs of tissue that form a weak pattern on the retracted organ. There are some scattered spinules near the basalmost spines, and an obvious cluster of spinules near the base of the organ, on the sulcate side. The preceding description is based on the left retracted hemipenis of the lectotype, BMNH 1946.1.5.80. This organ is similar to the one illustrated for *Rhadinaea persimilis* (fig. 47C), except that in *affinis* the calyculate area is somewhat more extensive on the sulcate side, there is a sign of capitation on the asulcate side, and there are smaller and more numerous spines in the rows toward the asulcate side. The hemipenis of a second specimen of *affinis* differs only in a few respects from that of the lectotype: The retracted organ of USNM 76339 is a bit shorter, extending to the middle of subcaudal 5, and the short division of the retractor insertion can be distinguished on the medial wall as well as on the lateral; there are more than 80 spines and the asulcate ridge of tissue bears papillae on its entire length and is less conspicuous, with the "ribs" being almost absent.

REMARKS: Judging from characteristics of the hemipenis and color pattern of the body, *Rhadinaea affinis* is most closely related to the evidently sympatric *R. persimilis*. I think that these represent distinct species, albeit my material has been very limited. *Rhadinaea affinis* is larger, has a more distinctly calyculate and partly capitate hemipenis, has fewer maxillary teeth, has a wedge-shaped marking behind each eye, lacks an enamel-white line on the supralabials, has the supralabials and underside of the head either immaculate or densely marbled with dark pigment (rather than speckled), and has more ventrals and subcaudals.

One of the syntypes of *Enicognathus melanocephalus* Duméril, Bibron, and Duméril proves to be a specimen of *Rhadinaea affinis*. This is the same specimen (MNHN 7863) later identified as "*Rhadinaea obtusa*" by Cope (1868, p. 132), who stated that, "It is figured by Jan in his Iconographie, as the second specimen of *R. melanocephala*" [Cope's reference is to Jan and Sordelli, 1866 (1860–1881), vol. 1, livr. 16, pl. 1, fig. 4*]. It is not clear whether Cope was referring to the species generally or thought that MNHN 7863 was actually the same specimen figured in Jan and Sordelli, but, in any case, their specimen evidently was from the Milan Museum (as indicated in the plate index for livr. 16) and should be recognizable, if still extant, by an azygous scale between the fifth and sixth supralabials on the right side of the head. I consider the Jan and Sordelli figure to be based on a specimen of *Rhadinaea persimilis*.

Müller (1968, p. 39) provided an interesting record of *Rhadinaea affinis* (misidentified as "*Liophis poecilopogon*") from São Sebastião Island, Brazil; the specimen was found in a banana plantation at the edge of a forest. São Sebastião Island is close to the mainland, as are the few other islands on which species of *Rhadinaea* have been found.

The specific epithet is a form of *adfinis* (related, adjacent), possibly in allusion to a resemblance between the types and *Leimadophis melanostigma*, a specimen of which was described (as "*Dromicus pleii*") in the same place (Günther, 1858, p. 128).

Rhadinaea bilineata (Fischer), new combination

Figures 45C, 46G; map 19

Enicognathus bilineatus FISCHER, 1885, pp. 98, 99, pl. 3, fig. 5 (dorsal, lateral, and ventral aspects of cephalic scutellation and color pattern of holotype).

Rhadinaea poecilopogon (not of Cope): BOULENGER, 1894b, p. 173 (part: specimen *d*, the holotype of *Enicognathus bilineatus*). PETERS AND OREJAS-MIRANDA, 1970, p. 267 (part).

HOLOTYPE: Not seen, BMNH 1946.1.5.77 (formerly BMNH 86.5.15.19, and originally no. 858 in Fischer's private collection), a male (*fide* Boulenger, 1894b, p. 173) from Santos, [Brazil]; purchased from a dealer by J. G. Fischer.

DIAGNOSIS: *Rhadinaea bilineata* is a weakly

striped species of the *brevirostris* group, in which *bilineata* agrees with *R. occipitalis* and *R. poecilopogon* in having a narrow, pale line along the canthus rostralis to the temporal region. It differs from *occipitalis* (*q.v.*) in body pattern and in having 17 rows of scales rather than 15. It differs from *poecilopogon* in lacking conspicuously darkened sides and a dark vertebral line, in having a relatively weak labial pattern, and in not having a wedge of dark head color extending around and under the corner of the mouth. Additional comparisons with *poecilopogon*, probably the closest relative, are given in the Remarks section.

DISTRIBUTION: Southern Brazil, from the state of São Paulo south into Santa Catarina.

DESCRIPTION (ONE SPECIMEN): The specimen is a juvenile male 185 mm. total length, of which the tail comprises 51 mm. (27.6 percent). The dorsal scales are in 17–17–17 rows; anal ridges are absent. There are 138 ventrals and 75 subcaudals. There is one preocular, no subpreocular, two postoculars, 1+2 temporals, seven supralabials, and eight infralabials. The male holotype was described as having 140 ventrals and 82 subcaudals; it measured 325 mm. total length, 96 mm. tail length [29.5 percent].

The body is light brown. There is a slightly darker, poorly defined brown stripe from the head to the end of the tail, on the median five scale rows of the body. The darkest (median) part of the aforesaid stripe is enclosed between two rows of dark brown dots, which are aligned along the outer edge of each paravertebral row of scales. There is a thin, dark brown line on the middle of row 4, from the side of the head to the end of the tail; the melanophores in the ground color are very sparse along the upper edge of the lateral dark line, but there is no conspicuous or well-defined pale border to the line. The top and sides of the head are dark brown for a distance of two scales behind the ends of the parietals, where there is a vague whitish spot on each side of the broad dorsal stripe. The dark head cap posteriorly has a fine dark edge that is continuous with the two longitudinal rows of dark dots, which are fused into solid lines for a length of several scales on the nape. The dorsal body stripe is particularly dark (i.e., the same hue as the top of the head) between the lines on the neck, for a distance of about five scales behind the interparietal suture, and this area encloses a dark-edged, white line on the midline of the nape. A dark-edged cream line is continuous around the tip of the snout and extends along the canthus rostralis, through the top of the eye, and terminates behind the eye on the mid-temporal region. The dark head is inconspicuously speckled and vermiculated with pale brown, and there is a pair of white parietal dots. The dark sides of the head are demarcated by a blackish line that extends along the tops of the anterior supralabials and through the posterior labials to the corner of the mouth. The lower parts of the supralabials and the ventral surfaces are white. There is a dark brown spot on each of the first five supralabials, and a few dots on the tip of the chin. The dorsal brown color encroaches only slightly onto the tips of the ventrals and subcaudals, but there is a line of dark brown dots on each side of the venter, each line originating under the neck and disappearing under the base of the tail.

There are 20 subequal maxillary teeth followed by a broad diastema and two enlarged fangs. The ultimate prediastemal socket lies well anterior to the front edge of the ectopterygoid process. The last fang is offset laterad.

The left retracted hemipenis extends to subcaudal 6 and the retractor muscle to subcaudal 24. The organ is single, possibly with a short division in the insertion of the retractor muscle. The tiny hemipenis was dissected *in situ*, but owing to the lack of ossification of the spines not enough detail was discernible for an adequate description.

REMARKS: The name *Enicognathus bilineatus* was early placed in the synonymy of *Rhadinaea poecilopogon*, where it has remained until this time. My resurrection of the name *bilineata* must be considered tentative, pending a better understanding of intraspecific variation in *R. poecilopogon*. The single specimen (SMF 19052) here assigned to *bilineata* agrees generally with the description and illustrations of the holotype, with the chief differences being that the vague nape spots and the dorsal rows of dark dots are not indicated for the type specimen. The specimen examined by me is light brown with a slightly darker stripe on the dorsum, whereas the holotype was described as reddish gray with a bluish stripe; these differences in color are probably due mainly to state of preservation and loss of the stratum corneum in the holotype. The head is dark brown in SMF 19052, rather than black as described for the type.

The similarities between SMF 19052 and the holotype of *bilineata* (based on Fischer's original description and illustrations) seem more important than the few differences indicated above, and suggest to me that *bilineata* may be a valid species differing from *poecilopogon* in the following ways: *R. bilineata* seems first of all to be a much less vividly marked species, lacking the conspicuously darker sides and sharp vertebral line of *poecilopogon*, as well as the bolder labial pattern and dark wedges of color under the corners of the mouth that contribute to give *poecilopogon* a very distinctive appearance. *Rhadinaea bilineata* is, in contrast, just another small brown rhadinaea without much to call attention to itself. The lines of ventrolateral dots originate at about the level of the third ventral as virtually parallel rows in the two known specimens of *bilineata*, whereas in the specimens called *poecilopogon* the two rows originate close together, at or in front of the first ventral, and are markedly divergent before becoming parallel under the neck. Also, the ventrolateral dots remain posteriorly distinct in *bilineata*, whereas the dots tend to fuse into solid lines that edge (or disappear into) the blackish pigment that so boldly encroaches onto the ventral tips in *poecilopogon*. The number of teeth was not reported for the holotype of *bilineata*, but there are 20+2 on the right maxilla of SMF 19052, compared with 13+2–16+2 in the specimens examined of *poecilopogon* [Prado (1943, p. 13), however, records 20+2 teeth for a specimen of *poecilopogon*]. *Rhadinaea bilineata* possibly has a lower number of ventrals than *poecilopogon*, and a higher number of subcaudals, but the data are scant.

Some of the supposed differences between *Rhadinaea bilineata* and *R. poecilopogon* are possibly due to the small sample sizes, but, in the available specimens, I find no reason to suppose that only a single species is involved. Fischer was perhaps unaware of the name *R. poecilopogon*, but he did compare his new species with Jan's description of *Enicognathus elegans* [=*poecilopogon*]. The specific epithet is formed of the prefix *bi-* (two) plus *lineatus* (lined), evidently in reference to the dark lateral lines.

Rhadinaea brevirostris (Peters)

Figures 45E, 46C, D, 47A; map 18

Coronella decorata (not of Günther): GÜNTHER, 1859, p. 412.

E[*nicognathus*]. *taeniolatus* JAN, 1863 (March 31), pp. 266, 272, 273, 327 (pp. 56, 62, 63, 117, in reprint), (holotype [not seen] from Brazil, in Hamburg Museum). JAN AND SORDELLI, 1866 (1860–1881), vol. 1, livr. 16, pl. 2, fig. 4 (color pattern and details of scutellation of holotype). *Nomen oblitum.*

Dromicus brevirostris PETERS, 1863 (June 29), pp. 280, 281.

Dromicus viperinus GÜNTHER, 1868, pp. 418, 419 (two syntypes: BMNH 1946.1.1.9, 1946.1.1.10, from Pebas [Amazon River, northeastern Peru]; John Hauxwell, collector).

Rhadinaea taeniolata (Jan): COPE, "1869" [1870?], p. 154.

Rhadinaea nicaga (not of Cope, 1868): COPE, "1885" [1886a], pp. 102, 103.

Coronella taeniolata (Jan): BOETTGER, 1888, p. 195.

Rhadinaea undulata (not of Wied). Part: BOULENGER, 1894b, pp. 174, 175 (various names in synonymy and specimens *c–e*); 1896, p. 635. NICÉFORO MARÍA, 1942, p. 91.

Taeniophallus nicagus (not of Cope, 1868): COPE, 1895, p. 201, pl. 27, fig. 4 (drawing of hemipenis; also reproduced in Cope, 1900, pl. 25, fig. 4).

Liophis undulatus (not of Wied): AMARAL, 1929b, p. 174 (part). PETERS AND OREJAS-MIRANDA, 1970, p. 180 (part).

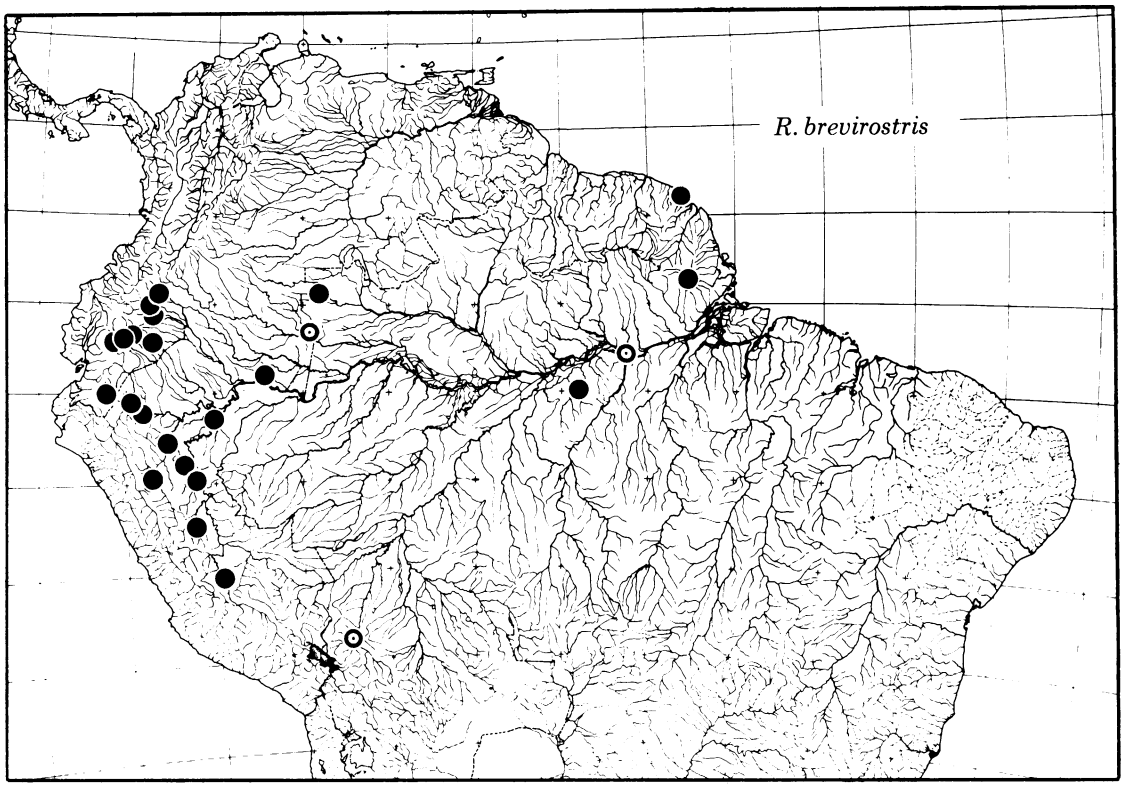
Rhadinaea brevirostris (Peters): SHREVE, 1934, pp. 127–129. DUNN, 1944, pp. 493, 494. PETERS, 1960, p. 536. PETERS AND OREJAS-MIRANDA, 1970, p. 264.

Liophis brevirostris (Peters): PARKER, 1935, pp. 521–522.

Urotheca brevirostris (Peters): HOGE AND BELLUOMINI, "1959" [1960], p. 16.

HOLOTYPE: Formerly ZMB 3869 (*fide* J. A. Peters, 1960, p. 536), but now lost (*fide* Günther Peters, *in litt.*), from "Quito"; purchased. I agree with J. A. Peters (*loc. cit.*) that the locality given is almost certainly erroneous; consequently, I regard the type locality as unknown.

DIAGNOSIS: *Rhadinaea brevirostris* is unique in the genus in having 17–17–15 dorsal scale rows. Most other species have 17 rows, or more, throughout the body; the only species with a lower number is the distinctly spotted *R. occipitalis*, which has 15–15–15 or 15–15–13 rows. A frequently useful feature in the identification of *brevirostris* is the broad middorsal dark stripe, which in most cases has undulating and/or serrated edges, in contrast to the straight-edged stripes of other *Rhadinaea*. Based only on dorsal scale count, this species might be taken for a *Leimadophis*, except that the stripes extend the length of the body and do not anteriorly disappear or break into spots.



MAP 18. Locality records for *Rhadinaea brevirostris* in Amazonian region of South America. Open symbols are literature records for Brazil (Hoge and Belluomini, "1959" [1960]), Colombia (Dunn, 1944), and Bolivia (Boettger, 1888).

DISTRIBUTION: Below 1500 meters along the eastern foot of the Andes, from Southern Colombia to Bolivia, and eastward through the Amazon Basin to French Guiana and Pará, Brazil.

DESCRIPTION (55 SPECIMENS): The longest individual is a male 472+ mm. (the incomplete tail is 100+ mm.); the next largest male is 420 mm. total, 88 mm. tail length; the largest female is 418 mm. total, 85 mm. tail length. The tail is 19.4–24.8 percent of total length in males, and 16.7–22.8 percent in females. Dorsal scales are in 17–17–15 rows in all specimens, with the reduction occurring between ventrals 84–113 in 23 specimens checked for this character. Method of scale-row reduction is by fusion of rows 3+4 (10 specimens) or 4+5 (six), or, by loss of row 4 (four); three additional specimens each showed a fusion of 3+4 on one side of the body, and either a fusion of 4+5 or loss of row 4 on the other side. Anal ridges are absent. Relatively large, unpigmented scale organs ("pits") are normally evident on the plates bordering the eye (i.e., preocular, supralabials 3–5, and postoculars), with the usual exception of the supraocular. About 16 percent of all specimens examined have apical "pits" on some of the scales on the neck; the pits, when present, are either single (and positioned off center) or paired, and are of variable size.

There are 141–166 ventrals (142–166, males; 141–166, females), and 36–61 subcaudals (44–61, males; 36–57, females). There is one preocular (1/2, 2/2, two specimens), no subpreocular, and two postoculars (1/2, 3/2, two specimens). There are eight supralabials (rarely 7/8 or, in one, 6/7), and nine or occasionally eight infralabials (7/8, 8/10, 9/10, three specimens). Temporals are basically 1+2, with occasional individuals showing a fusion of the primary temporal with the upper plate in the second row; other deviations, such as 1+1+2 or 2+2+2, are rare.

A broad, dark brown dorsal stripe originates at the rear of the head, sometimes from a transverse blotch, and extends to the end of the tail, occupying the median three scale rows and up to half of each adjacent row. This marking is occasionally no more than a unicolored streak with poorly defined edges (e.g., AMNH 15207), but usually there are blackish, undulating or serrated edges. The dorsal stripe in many cases is undulatory on the neck and serrated posteriorly, although either condition may obtain throughout the length of the body; the stripe tends to be straight-edged on the tail, but only rarely does it have straight edges on the body. It is not uncommon for the dorsal stripe to be broken by a thin, pale grayish vertebral line. The dorsolateral ground color is grayish brown to yellowish brown, in many cases with little contrast to the adjacent dorsal and lateral dark areas. The sides tend to be dark brown, especially posteriorly, up onto row 4 and the lower part of row 5, with an irregular serrated or undulatory upper margin. In many cases there is differentiation within the dark sides of a still darker stripe, involving all or part of row 4 and part of row 5 and/or row 3, and there may additionally be development of a dark line between rows 1 and 2. These dark lateral markings, when present, may extend the length of the body or else be developed only on the posterior part. The body may be marked with whitish flecks, which are most likely to be conspicuous on the dark sides.

A few individuals in the sample have light yellowish brown heads, in marked contrast to the darker brown body. Such specimens have a thin black line from the eye to the corner of the mouth, below which the supralabials and underside of the head are whitish, either immaculate or with only a few dark specks. Specimens are found that are intermediate between the aforesaid head coloration and the opposite (and most common) extreme, in which the head is as dark brown as the dorsal stripe, the black postocular line is wider and in some cases extends forward to the snout, and, most noticeably, the supralabials and entire underside of the head are very dark, being densely speckled and blotched with gray or brown. Dark-headed specimens often have other distinctive markings—black spots atop the head, especially anteriorly, and/or vivid white dots distributed over the dark labials or even over the entire head, and/or a spotless white postocular line, below the black one, from the eye to the corner of the mouth. Many dark-headed individuals have a pair of variably sized, tan or grayish spots (sometimes vague ocelli) on the rear of the head, each spot lying partly on the outer rear edge of a parietal plate and partly on the posterior temporal region. Individuals with any type of head coloration may have an inconspicuous pair of pale parietal dots.

The dark color under the head, in specimens so marked, extends a short distance back under the neck. The anterior ventral plates have a dark brown or black spot on each side. These spots usually fuse posteriorly, forming a solid blackish ventrolateral line that is normally darker than the dark sides of the body; the inner edges of the ventrolateral lines usually are nearly straight, but, rarely, they are strongly serrated. The rest of the venter is white or light yellow, usually immaculate or occasionally dotted or sparsely spotted with grayish. One specimen (AMNH 101972) is unique in having dense grayish brown mottling and speckling across the basal half of each ventral and along the subcaudal sutures, with the consequence that the white ground color is greatly obscured.

There are 12–15 subequal maxillary teeth, followed by a distinct diastema and two slightly enlarged fangs. The ultimate prediastemal socket is anterior to the front edge of the ectopterygoid process, except in a few specimens with 15 prediastemal teeth where part of the ultimate socket lies posterior. The last fang is offset laterad.

The retracted hemipenis is single or very slightly bilobated, extending *in situ* to subcaudals 10–14; an everted organ extended to subcaudal 12. The bilobation, when present, is less than the length of a subcaudal and possibly is not evident in the everted state. There is a short division in the insertion of the retractor muscle, regardless of whether or not there is a corresponding bifurcation of the hemipenis itself. The retractor muscle is stout and extends relatively far back, originating at subcaudals 29–36 (i.e., 16–22 subcaudals from the tip of the tail). Capitation is weak, with no (or very little) indication of an overhang on the asulcate side. The "capitulum" comprises from one-third to nearly half the length of the organ on its sulcate side. The sulcus spermaticus forks below the calyculate region at a point no more than (sometimes

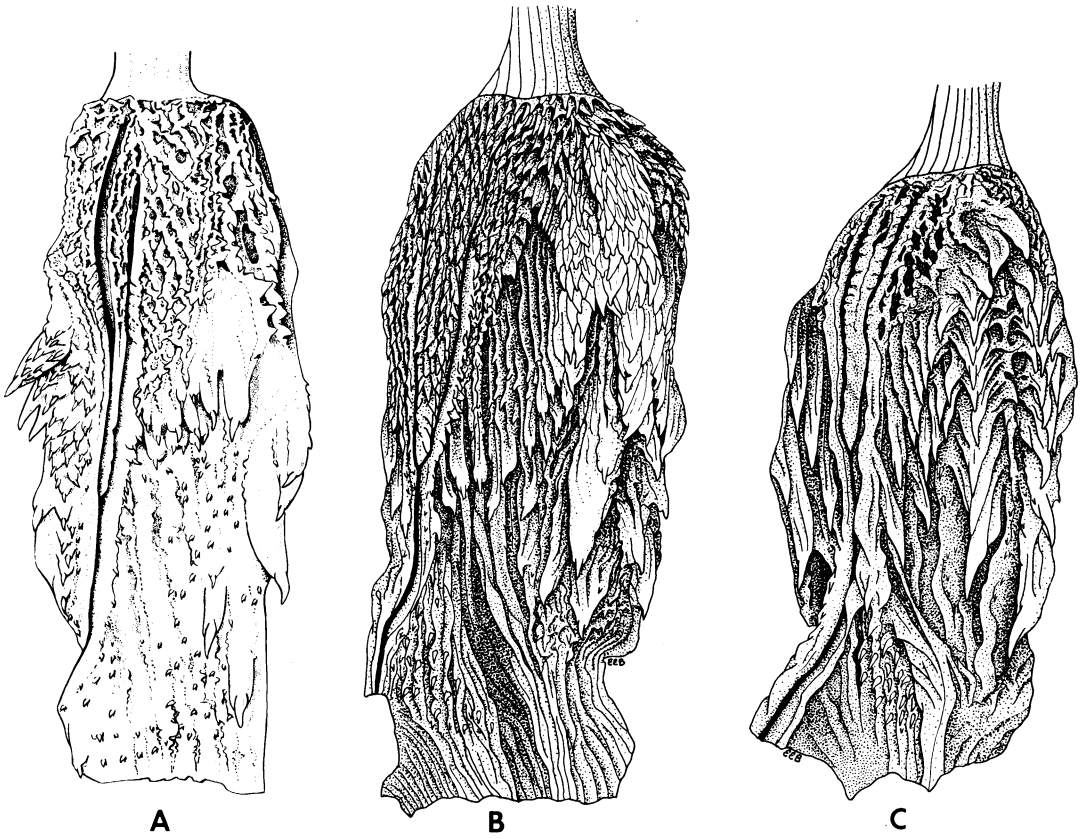


FIG. 47. Hemipenes of the *brevirostris* group. A. *Rhadinaea brevirostris*, AMNH 49171, left organ. ×6.4. B. *R. occipitalis*, USNM 120833, left organ. ×9.6. C. *R. persimilis*, SMF 32457, left organ. ×10.2.

conspicuously less than) half of its length up the hemipenis. The branches of the sulcus are long, and one of them extends to the very tip of the retracted organ, whereas the other branch is separated from the tip by several calyces (this seemed to be the case even in one bilobated organ examined for this feature, with one of the branches failing to reach the tip of the dorsal lobe); the branches extended nearly to the end of the one everted organ seen, and here also it was evident that the branches are not quite equivalent in length. The asulcate wall of the capitulum forms a short, single fold on the retracted hemipenis. The calyces on, and immediately to each side of, the aforesaid fold are much larger than the calyces on the sulcate side, and the papillae that adorn the calyces are also larger on the asulcate fold; some of the large papillae on the asulcate fold are replaced by thick, knoblike spinules in some specimens. At the lower edge of the asulcate fold is a gigantic calyx that forms a large naked pocket, whose lower edge is continuous with a low ridge of tissue that bears papillae and interrupts an otherwise nude area below the calyculate region. The giant calyx, or pocket, and the associated, fringed ridge are especially obvious on the everted hemipenis, but their nature is easily destroyed if care is not taken in dissecting the retracted organ. There are several medium to large spines staggered down the asulcate side of the hemipenis, basad from the nude region below the capitulum. There are small spines bordering the calyculate region on the sulcate side. The spines extend onto the basal fourth or fifth of the organ; there are scattered, inconspicuous spinules below the spines. The preceding description is based especially on the left everted and right retracted hemipenes of KU 119389, and also on retracted organs from AMNH 23289, 28799, 49171 (illustrated), 101973, BMNH 1946.1.1.9, 1946.1.1.10, KU 97877, 105427, and UMMZ 82880 and 92018.

GEOGRAPHIC VARIATION: It is difficult to

detect precise trends because the majority of available specimens are from the foot of the Ecuadorian and Peruvian Andes, and the vast reaches of the Amazon Basin are sparsely represented indeed.

A specimen from the Amazonian lowlands of north-central Brazil (AMNH 101972: Rio Manjura, latitude 4°S, longitude 57°W) has an extremely dark venter, as described above. Possibly this represents a localized trend, although a second specimen (AMNH 101973), from the same locality, has a much paler venter, with relatively sparse, dark speckling across the bases of the ventral plates. A specimen (KU 97877) from eastern Brazil (Amapá) north of the Amazon has a pale belly, except that the ventral plates are more broadly tipped with black than in most other available specimens.

Several specimens (AMNH 4462 and the BMNH syntypes of *Dromicus viperinus*) are distinctive in having relatively pale, yellowish brown heads and virtually immaculate white labials. These specimens, which are from localities some 500 kilometers apart (Pebas, Peru, to Caruru [near Río Vaupes at Colombian border], Brazil), are possibly indicative of the situation in a large section of the western part of the Amazonian lowlands, although specimens from the Río Ucayali drainage (south-southwest of Iquitos) have dark heads. Specimens with intermediately colored heads have been seen from scattered localities along the Andean foothills, from Colombia to Peru.

There is possibly a clinal pattern in reduction of ventrals, subcaudals, and tail length, from north to south along the base of the Andes. A rough breakdown of the data, between Ecuador and Peru, shows the following:

ECUADOR

Ventrals: 156.5±1.79 (148–166, 12♂); 156.1±1.93 (150–166, 9♀)

Subcaudals: 53.6±1.03 (50–61, 10♂); 48.6±1.27 (46–57, 8♀)

Tail length as a percentage: 22.9±0.41 (21.5–24.8, 9♂); 20.6±0.40 (18.9–22.8, 8♀)

PERU

Ventrals: 147.6±1.04 (142–154, 13♂); 147.0±1.39 (141–158, 11♀)

Subcaudals: 49.0±1.11 (44–55, 9♂); 40.6±0.96 (36–45, 10♀)

Tail length as a percentage: 21.9±0.64 (19.4–24.6, 9♂); 18.2±0.36 (16.7–19.8, 9♀)

The preceding tabulation does not include the three specimens with light-colored heads ("*viperinus*" type) from farther east in the Amazonian Basin. These specimens, all males, have ventral counts (158, 159, 159) and subcaudal counts (55, 56, —) higher than the means for Ecuador and Peru. A few snakes from eastern Brazil, the easternmost specimens examined, on the other hand, show the reverse in having lower counts more like the situation in Peru: KU 97877 (male), 149 ventrals, 51 subcaudals; AMNH 101972 (female), 147 ventrals, 37 subcaudals.

I cannot say if there is geographic variation in the hemipenis, as too few organs have been examined. Of particular interest is the occurrence in some specimens, but not others, of stubby, ossified knobs on the asulcate side of the capitulum. These are present in the two syntypes of *Dromicus viperinus* (Pebas, Peru) and in UMMZ 82880 (Santiago-Zamora, Ecuador). These individuals also seem to have more strongly capitate hemipenes than do other specimens, and a geographic correlation seems possible.

REMARKS: Duméril, Bibron, and Duméril named *Enicognathus melanocephalus* on the basis of specimens from "Guadeloupe" and Brazil, in 1854. Cope (1868, p. 132) stated that: "In the description of this last species, three are mingled, as I have ascertained both from a reading of the same, and from an examination of the originals in Mus. Paris. One of these is our *R. obtusa*, the other is the true *R. melanocephala*, which should be described as follows, and the third is a species as yet undescribed, which I call *Lygophis nicagus* Cope." Cope restated these remarks several years later (1875a, p. 139), and their authenticity was not denied by the next person to consider the matter (Bocourt, 1886 [1870–1909], p. 630). The syntype that was redescribed as a new species by Cope (1868), under the name *Lygophis nicagus*, looks like a specimen of *Rhadinaea brevirostris*, as will be commented on in a later paragraph. Of first concern is the identity of the *melanocephalus* syntype called by Cope "the type of the species" and redescribed by him under the name *Rhadinaea melanocephala* (Duméril, Bibron, and Duméril), an action clearly to be regarded as the designation of a lectotype of *Enicognathus melanocephalus*. The lectotype [MNHN 7503] is readily separated from the other syntypes [MNHN 55 and 7863] by several attributes, including the temporal

formula described by Cope as 2+2+2 (1+2 in the other specimens); the positioning of the lower temporal in row 1 would have caused Boulenger (1893, p. 187) to consider it a supralabial (seventh on left side, eighth on right) that is narrowly excluded from the labial margin. The lectotype is a male (hemipenis not dissected) with about 46 small teeth on each maxilla, 1–2 oculars, 8/9 supralabials (4–5/4–6 in eye), ? infralabials, 17–17–17 scale rows, four preventrals, 157 ventrals, slightly angular ventrolateral edges, divided anal, 59+ subcaudals, and a total length of 305+ mm. (tail 77+ mm.); this old specimen is very faded, but a few elements of the pattern described by Cope are still discernible, including a pale line on the vertebral scale row, with a dark dot on an occasional vertebral scale, a dark collar about six scales long, and dark-dotted ventral and subcaudal tips. The specimen belongs to the Asiatic genus *Sibynophis*, as recognized by Boulenger (1893, p. 186) when he placed *Enicognathus melanocephalus* (part) and *Rhadinaea melanocephala* in the synonymy of *Polydontophis* (=*Sibynophis*) *subpunctatus*; Cope had been misled by the erroneous locality datum ("Guadeloupe") and evidently did not examine the dentition, or he would not have placed the specimen in *Rhadinaea*. This Asiatic snake was named *Oligodon subpunctatum* by Duméril, Bibron, and Duméril (1854, p. 58) in the same work in which they described *Enicognathus melanocephalus*. Boulenger (*op. cit.*) probably was the first reviser and, if so, his choice of names firmly fixes *subpunctatus* as the valid name, with *E. melanocephalus* becoming (by virtue of Cope's lectotype designation) a "junior" subjective synonym that is unavailable for a species of *Rhadinaea*, and a *nomen oblitum* in any case. The syntype of *E. melanocephala* referred by Cope to *Rhadinaea obtusa* is really a specimen of *Rhadinaea affinis* (*q.v.*).

After *Enicognathus melanocephalus*, the next oldest name to be taken up in a nomenclatural analysis of *Rhadinaea brevirostris* is *Enicognathus taeniolatus* Jan, which was published in March, 1863; the exact date of publication evidently was March 31, according to the title page of the reprint. The name *brevirostris* was first published in the combination *Dromicus brevirostris* Peters, in a paper in the "Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin." The title page for the volume of papers "Aus dem Jahre 1863" is dated 1864, but, presumably, different parts of the bound volume were issued in 1863; indeed, Peters himself (1871, p. 400) gave 1863 as the date of publication of his *Dromicus brevirostris*. The earliest possible date for *brevirostris* is June 29, 1863, as indicated in the running head, "Sitzung der physikalisch-mathematischen Klasse vom 29. Juni 1863." The name *E. taeniolatus*, therefore, has seniority by nearly three months at the very least. The holotype of *Enicognathus taeniolatus* is illustrated in Jan and Sordelli [1866 (1860–1871), vol. 1, livr. 16, pl.2, fig. 4]. The distinctive color pattern of the holotype, as well as details of scutellation, fall within the range of variation in my sample of *brevirostris*, except that the relatively pale vertebral line has more contrast than is usually the case. Only one species seems to be involved. Both names were placed in the synonymy of "*Rhadinaea*" *undulata* by Boulenger (1894b). Shreve resurrected *brevirostris* in 1934, and this name has been used for the species since that time. The name *taeniolatus* has been included in the synonymy of *brevirostris* (see Shreve, 1934; Parker, 1935) without consideration of its evident seniority, but *taeniolatus* appears not to have been used as a correct name for a valid species since 1888 (Boettger). The name *Enicognathus taeniolatus* is accordingly suppressed as a "forgotten name" (International Commission on Zoological Nomenclature, 1964, art. 23b).

Dromicus viperinus Günther (1868) is based on specimens having yellowish brown heads and unmarked labials. This name was first placed in the synonymy of *brevirostris* by Peters (1871). I find no correlated characters to substantiate the validity of *viperinus*, and there are specimens with intermediate head coloration.

As shown in a preceding paragraph, the earlier name *Enicognathus melanocephalus* is not available for *Rhadinaea brevirostris*. But the *melanocephalus* syntype that Cope (1868, p. 132) later made the holotype of *Lygophis nicagus* looks very much like a specimen of *brevirostris*. The names *nicagus* and *brevirostris* were placed in the synonymy of the composite *Rhadinaea undulata* by Boulenger (1894b); Shreve (1934) considered one of Cope's ("1885" [1886a]) references to *nicagus* to be based on misidentified specimens of *brevirostris*; Parker (1935) agreed with Shreve's action but went a step farther and placed *Enicognathus melanocephalus* (part) and *Lygophis nicagus* as subjective synonyms of *brevirostris*. The proper

identity of Cope's *nicagus* is of importance because it is the nominal type species of the monotypic genus *Taeniophallus* Cope, 1895. The *melanocephalus* syntype—*nicagus* holotype is MNHN 55 and, as noted by Cope, it is illustrated by Jan and Sordelli (1866 [1860–1881], vol. 1) as the upper specimen in figure 4 of plate 1, livraison 16; proof of this is the presence in both specimen and figure of an azygous temporal scale between the primary temporal and the parietal on the left side of the head. The specimen is very faded and lacks precise locality, but it agrees with my present description of *Rhadinaea brevirostris* in almost all respects. It is a male, with 17–17–15 scale rows that reduce by loss of rows 4 at ventrals 100/97, 14+2 maxillary teeth, 8 supralabials (second in loreal, 3–5 in eye), ? infralabials, 1–2 oculars, indication of large "pits" on the oculars and labials adjacent to the eye, 1+2 temporals (or 2+2 on left side if azygous scale is counted, see above), two preventrals, 166 ventrals, divided anal, 56 pairs of subcaudals, and a total length of 367 mm., of which the tail is 77 mm. (21 percent). The specimen is almost completely faded, except for a dark line from eye to corner of mouth, a posterior trace of a dorsal undulatory stripe, and the dark edging of ventrals and subcaudals. The original color pattern of this specimen, as illustrated by Jan and Sordelli (*loc. cit.*), does not precisely match any specimen of *brevirostris* that I have seen, but, conceivably, it might have been based on a somewhat faded example. Thus, except for a slight reservation regarding the original color pattern, the characteristics just cited would lead me unhesitatingly to identity MNHN 55 as a specimen of *Rhadinaea brevirostris*. Dissection of the hemipenis, however, reveals that the specimen is 1) not a *Rhadinaea*, and 2) probably not a South American snake. The hemipenis differs most importantly from *Rhadinaea* and most other xenodontines in having an undivided sulcus spermaticus. The inverted hemipenis extends *in situ* to subcaudal 11 and the retractor muscle inserts at subcaudal 30; the organ is noncapitate and very slightly bilobate, with the simple sulcus extending into the dorsal lobe; the distal three-tenths of the hemipenis is calyculate except for a longitudinal cluster of small spines on the asulcate fold, which is single and (unlike *Rhadinaea*) extends the full length of the retracted organ (probably it would expand and disappear during inflation); there is a spinose region below the calyces. There is nothing about this hemipenis that seems aberrant, and I must conclude that the holotype of *nicagus* is not a *Rhadinaea*. I do not know to what genus it properly belongs; although *nicagus* is the nominal type species of *Taeniophallus*, I do not think that it should even be associated with that name, as I comment on below.

The remarkable similarity of Cope's *Lygophis nicagus* to *Rhadinaea brevirostris* led him ("1885" [1886a], pp. 102, 103) to apply the name *Rhadinaea nicaga* (Cope) to genuine specimens of *brevirostris* from the upper Amazon drainage. Furthermore, Cope's illustration (1895, pl. 27, fig. 4; 1900, pl. 25, fig. 4) of the hemipenis of "*Taeniophallus nicagus*" seems to be that of a *brevirostris*, and his concept (1895, p. 201) of the monotypic *Taeniophallus* is thus based largely on *Rhadinaea brevirostris* rather than on *Lygophis nicagus*; in this context, it is worth noting that the hemipenes of the unique specimen of *nicagus* had not been examined prior to my dissection. The type species of *Taeniophallus* will have to be designated by the International Commission on Zoological Nomenclature, in accordance with article 70(a), but, in the meantime, the interest of stability is best served by maintaining the name in the synonymy of *Rhadinaea* and considering *brevirostris* as the type species. Therefore, I would recommend that the Commission use its plenary powers and adopt choice "(i)" under article 70(a); before submitting such a petition, I hope to publish illustrations and a full redescription of the holotype of *Lygophis nicagus*.

Aleman (1953, p. 215; see also Roze, 1966, p. 236) provisionally reported *Rhadinaea brevirostris* from northwestern Venezuela, on the basis of specimens from the Río Negro, between Lake Maracaibo and the Sierra de Parijá; this geographically improbable record is based on *Leimadophis melanotus* (MHNS 927 and 1298). A record (Rendahl and Vestergren, 1940) of *brevirostris* from the upper Río Cauca valley of southern Colombia is based on specimens of *Saphenophis sneiderni* Myers, 1973. The only reliable record from outside of the Amazonian drainage proper seems to be the specimen of *brevirostris* (NMB 1485) mentioned by Parker (1935, p. 522), from Cayenne, French Guiana; I examined this specimen after the present account was written and the following data are not included in the text or tables: female, 399 mm. total, 86 mm. tail length; 17–17–15

scale rows reducing by fusion of rows 3+4 at ventral 99; some single apical pits on neck; 166 ventrals, 55 subcaudals; supralabials 8, with 3–5 in eye; infralabials 8/9; oculars 1–2, with large "pits," temporals 2+2; head dark, with hint of white line below postocular dark line, and with labials and underside of head speckled with dark; lower four scale rows of body darkened and ventral tips darker still; middorsal dark stripe with strongly undulating edges that anteriorly tend to enclose some dorsolateral light areas.

Parker (1935, p. 522) stated that *R. brevirostris* rarely has 17 scale rows before the vent (i.e., no posterior reduction in the number of rows), an observation that I have been unable to substantiate.

The specific epithet has its basis in the words *brevis* (short) and *rostrum* (snout), and is descriptive of the relatively short muzzle.

Rhadinaea occipitalis (Jan)

Figures 45A, 46E, 47B, 48; map 20

Coronella elegans (not of Tschudi): GÜNTHER, 1858, p. 38.

E[*nicognathus*]. *occipitalis* JAN, 1863, pp. 266, 267 (pp. 56, 57 in reprint). JAN AND SORDELLI, 1866 (1860–1881), vol. 1, livr. 16, pl. 1, fig. 1 (color pattern and details of scutellation of syntype).

Dromicus (*Lygophis*) *Wuchereri* GÜNTHER, 1863, pp. 325, 326, fig. (dorsal, ventral, and lateral details of cephalic color pattern and scutellation of holotype: BMNH 1946.1.5.70, formerly BMNH 63.10.10.5 [not seen], from Bahia [Baía, Brazil]; O. Wucherer, collector).

Dromicus miolepis BOETTGER, 1891, pp. 345, 346 (holotype [not seen] originally in Lübeck Museum, from Sorata, Bolivia; Ernesto Guenther, collector).

Rhadinaea occipitalis (Jan): BOULENGER, 1894a, p. 347; 1894b, pp. 175, 176; 1896, p. 635. BOETTGER, 1898, p. 67. DEVINCENZI, 1925, pp. 35, 36. WERNER, 1929, p. 119. PRADO, 1945a, p. 75; 1945b, pp. 105–107.

Liophis occipitalis (Jan): AMARAL, 1929a, p. 89; 1929b, p. 174; 1936, p. 115. BERTONI, 1939, p. 47. PETERS AND OREJAS-MIRANDA, 1970, p. 179.

SYNTYPES: Jan based the name *occipitalis* on a specimen from Bahia [=Baía, Brazil] in the Geneva Museum, and on a second specimen from Brazil in the Zoologisches Museum in Hamburg. The latter specimen was the one figured by Jan and Sordelli and would, for that reason, probably make the best lectotype, but I have not tried to ascertain if either specimen is still extant.

DIAGNOSIS: *Rhadinaea occipitalis* is identifiable at a glance by its color pattern, which includes a dark head with a white line from the canthus rostralis through the eye, and dark blotches on the neck that are posteriorly replaced by pairs of small spots (see illustrations). It is the only species of *Rhadinaea* with 15–15–15 or 15–15–13 rows of scales; the only other species approaching such a low number is *R. brevirostris*, which has 17–17–15 rows and a different color pattern.

DISTRIBUTION: Northeastern Peru southeastward through Bolivia and Paraguay to northern Argentina, Uruguay, and southern Brazil, thence northward along the coast to northeastern Brazil (see Remarks). Apparently absent from the greater part of the Amazon Basin.

DESCRIPTION (25 SPECIMENS): The longest individual is a female 570 mm. total length, 136 mm. tail length; the largest male is 504 mm. total, 125 mm. tail length. Prado (1945b, table) gave a maximum size of 587 mm. total, 131 mm. tail length, for a female. The tail is 21.8–27.6 percent of total length in males, and 20.9–24.9 percent in females. Calculations from Prado's measurements (*loc. cit.*) of 41 additional specimens gives a range of 23.9–29.4 (mean 26.3) percent for 10 males, and 17.0–27.1 (mean 23.8) percent for 31 females.

Dorsal scales are in 15–15–15 or 15–15–13 rows; posterior reduction, when it occurs, is by fusion of rows 2 and 3. Anal ridges are absent. There are 161–192 ventrals (161–184, males; 179–192, females), and 64–80 subcaudals (66–80, males; 64–74, females). Prado (*loc. cit.*) gave 160–194 ventrals [males 161–181, mean 174.7; females 160–194, mean 182.7], and 55–81 subcaudals [males 67–81, mean 74.7; females 55–79, mean 70.3]. There is one preocular, no subpreocular, and two postoculars. There are eight supralabials (in some cases seven or nine, usually on one side only), and nine infralabials (in some cases eight on one side). The temporal plates are rather variable in arrangement, and counts of 1+2 and 2+2 are about equally common; some deviations, usually on one side of the head only, include 0+2, $1+\frac{2}{1}$, 2+1+2, and 2+2+2.

The body is light brown (gray after loss of stratum corneum). There are two to 18 dark brown saddle-markings on top of the neck; on some specimens these markings are connected by a dark brown vertebral stripe and a brown

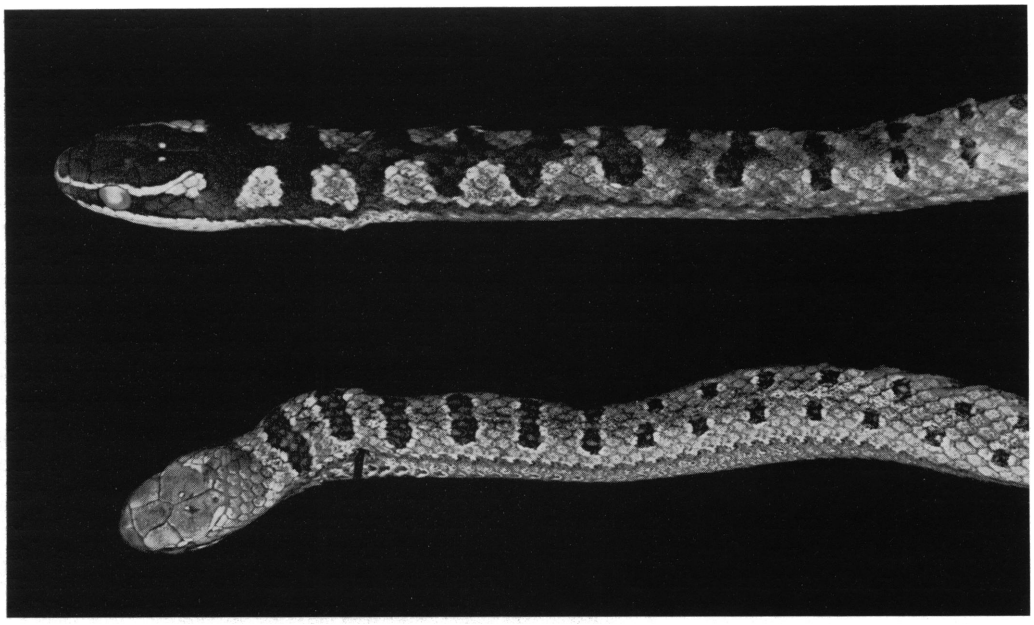


FIG. 48. Variation in anterior body pattern of *Rhadinaea occipitalis*. *Top*: SMF 19060, Sorata, Bolivia. *Bottom*: SMF 19059, central Brazil.

lateral stripe, the stripes being confined to the neck and confluent with the dark head color (fig. 48, top). The anterior blotches are two or three scales wide on the longitudinal axis of the body, but the posterior ones are reduced to one scale and then are replaced by 10–90 pairs of small spots, which are positioned on each side of the midline of the body, sometimes in a staggered arrangement. Usually there are spots along the length of the body and an additional number on the tail; on some individuals a median dark streak forms on the rear of the body and becomes a narrow, well-defined stripe on the tail, thus connecting and obscuring the spots. On one specimen (SMF 19058) the spots become tiny and disappear behind midbody, although there is a narrow, dark vertebral stripe on the end of the body and the tail. The lower three scale rows and edges of the ventrals and subcaudals are usually darker brown than the dorsal ground color—slightly darker anteriorly on the body and conspicuously darker posteriorly. There is a tendency for this dark lateral band to be bordered above by a series of whitish dots or dashes on top of the third scale row; occasionally there is a narrow whitish streak on the first scale row. Some specimens have the sides little darker than the dorsum and the white dots are weakly developed or absent.

The top and sides of the head are dark brown. A vivid cream line is continuous around the tip of the snout and extends along the canthus rostralis through the top of the eye and terminates a short distance behind the eye on the side of the parietal. There is a pair of closely spaced, white parietal dots, and in many cases there is a pair of larger cream spots, one on each side of the rear of the head. Each of these larger spots, when present, lies partly on the rear edge of the parietal, and partly on the upper secondary temporal and one or more adjacent body scales; several specimens have each of the spots confluent with the anterior white line, thus forming an elongated wedge-shaped marking behind each eye (fig. 48, top). The dark head color is in many cases continuous with the first dark blotch on the nape.

There is a tendency for a dark brown or black line across the top edges of the anterior supralabials and through the posterior labials to the corner of the mouth. The lower parts of the supralabials, and the underside of the head, are white—immaculate, weakly dotted with black, or heavily mottled with blackish brown. The venter is white or pale yellowish. Some individuals, even those with weakly marked labials and chins, have a profusion of black dots under the neck. The ventrals and subcaudals are

slightly edged with brown pigment from above, and some specimens additionally have a line of black dots or dashes along each side of the venter.

There are 13–17 subequal maxillary teeth, followed by a distinct diastema and two slightly enlarged fangs. The ultimate prediastemal socket lies either anterior or posterior to the front edge of the ectopterygoid process, the position being correlated with low and high numbers of prediastemal teeth, respectively. The last fang is offset laterad.

The retracted hemipenis is either single or (in FMNH 35644) very slightly bilobed, extending *in situ* to subcaudals 7–10. The bilobated organ extended to the base of subcaudal 7 and was divided from about the middle of subcaudal 6, with the two slips of retractor muscle merging near the end of subcaudal 7. Slight divisions of the retractor muscle can be seen in some specimens that have nonbilobated hemipenes; the retractor muscle originates at the level of subcaudals 22–30. The capitulum comprises more than half the length of the retracted organ on its sulcate side but is much shorter on the other side. The sulcus spermaticus forks at the lower edge of the capitulum and its long branches extend virtually to the tip. The calyces are papillate except near the middle of the asulcate fold, where there are some short, thick, knoblike spinules. The asulcate wall of the capitulum forms a distinctly to weakly doubled fold or a thick, single fold. The papillae on the calyces are compressed and flaplike, and those on the lower edge of the asulcate fold are very large and overhang a nude space that extends deeply under the edge of the capitulum. There are two nearly parallel, double-rows of medium-sized spines that extend basad from the asulcate fold to about the middle of the organ. Between the two double-rows is a low ridge of soft tissue (nude or bearing a few spinules) that extends from the cavity under the capitulum to the base of a large, thick spine, which arises between and slightly below the aforesaid rows. There are several spines below and to each side of the large one; these extend quite close to the base on some organs, and are intermediate in size between the big spine and those in the parallel rows. There are several small spines across the middle of the organ on the sulcate side. There are some scattered, inconspicuous spinules below the spines on the asulcate side, and a usually distinct cluster of spinules close to the base of the organ near the sulcus spermaticus. There are some smooth places between the basal ridges of tissue, but none forms a conspicuous, broad depression, and none is very likely to be obvious when the hemipenis is everted. The preceding description is based on retracted hemipenes from AMNH 54593, ANSP 11124, FMNH 35644, SMF 19058, 19060, and USNM 120833 (left organ illustrated). I have not seen an everted hemipenis.

REMARKS: The color pattern of the body of *Rhadinaea occipitalis* is somewhat reminiscent of the usual condition (anterior blotches, posterior stripes) in the unrelated genus *Leimadophis*, but the head pattern is similar to that of *Rhadinaea poecilopogon*, another member of the *brevirostris* group. The placement of *occipitalis* in this group of *Rhadinaea* seems clearly indicated by similarities between the hemipenes of *R. occipitalis* and *R. brevirostris* (fig. 47A, B, and descriptions in text)—including the knoblike spinules present in *occipitalis* and some specimens of *brevirostris*, and also the intraspecific variability in presence or absence of bilobation (table 2). The low dorsal scale formula of *occipitalis* continues the reduction trend set by *brevirostris*, and these two species are probably much more closely related than external appearance would suggest.

Little is known about *Rhadinaea occipitalis*, despite its broad geographic range. Information is especially needed on the ecological distribution of this species, particularly in the dry region of northeastern Brazil. The northernmost Brazilian records in map 20 are plotted on the authority of Amaral (1934, pp. 186, 187; Areia, Estado Parahyba) and Prado (1945b, p. 107; Teresina, Estado Piauí); the latter locality is arbitrarily shown as a disjunction in the generic range (map 1), primarily to draw attention to this problem. *Rhadinaea occipitalis* seems less restricted to humid-forest environments than any other member of the genus, but habitat notes are lacking. Lönnberg (1902) recorded a specimen from a locality (Tatarenda, Caiza, Bolivian Chaco [not plotted in map 20]) characterized as "on the border between the dry woods and the subtropical forest, partly broken up in groves separated by grassy areas."

The occurrence of this primarily lowland species at Sorata, in the Bolivian highlands, needs to be verified. Sorata is the stated type locality of *Dromicus miolepis* Boettger, and also the stated provenance of SMF 19060 [=No.

8175, lc in Boettger's (1898, p. 67) catalogue], here shown as the upper specimen in figure 48. I have not seen the *miolepis* holotype, but Boettger himself (*loc. cit.*) accepted Boulenger's action in synonymizing *miolepis* with *occipitalis*.

Rhadinaea occipitalis is known as *cobra jericoá* in northeastern Brazil (Amaral, 1934, p. 187), and it is one of several snakes that are called *ñuasó* in Paraguay (Gatti, 1955, pp. 96, 97). The specific epithet is formed from the noun *occipitium* (the back of the head) plus the adjective-forming suffix *-alis* (pertaining to), probably in allusion to the color pattern.

Rhadinaea persimilis (Cope), new combination

Figures 45D, 46B, 47C; map 19

E[nicognathus]. melanocephalus (not of Duméril, Bibron, and Duméril): JAN, 1863, pp. 266, 269, 270 (pp. 56, 59, 60 in reprint; part: specimens from Brazil in Milan and Monaco Museums). JAN AND SORDELLI, 1866 (1860–1881), vol. 1, livr. 16, pl. 1, fig. 4 (part: fig. 4*, color pattern and details of scutellation of Milan Museum specimen from Brazil).

Rhadinaea obtusa (not of Cope). Part: COPE, 1868, p. 132, and 1875a, p. 139 (reference to Jan and Sordelli's figure 4* [see above] only; the syntype of *Enicognathus melanocephalus* referred here by Cope is a specimen of *Rhadinaea affinis, q.v.*).

Liophis persimilis COPE, "1868" [1869], p. 308.

Rhadinaea poecilopogon (not of Cope): BOULENGER, 1894b, p. 173 (part). PETERS AND OREJAS-MIRANDA, 1970, p. 267 (part).

Liophis insignissimus AMARAL, 1926b, pp. 103, 104 (pp. 9, 10 in reprint), pl. 1, figs. 7–9 (dorsal, lateral, and ventral renditions of anterior part of holotype: IB 3172 [not seen], from Estação Biologica, Serra de Cubatão, São Paulo, Brazil; Domingos de Lemos, collector); 1929a, p. 88; 1929b, p. 172; 1936, p. 114. New synonymy.

Rhadinaea insignissima (Amaral): WERNER, 1929, p. 118.

Rhadinaea beui PRADO, 1943, pp. 13, 14, plate (dorsal and ventral photographs of holotype or paratype; holotype is IB 4730 [not seen], from Curitiba, Paraná, Brazil); 1945a, p. 75. PETERS AND OREJAS-MIRANDA, 1970, p. 264. New synonymy.

Rhadinaea insignissimus (Amaral): PETERS AND OREJAS-MIRANDA, 1970, p. 266.

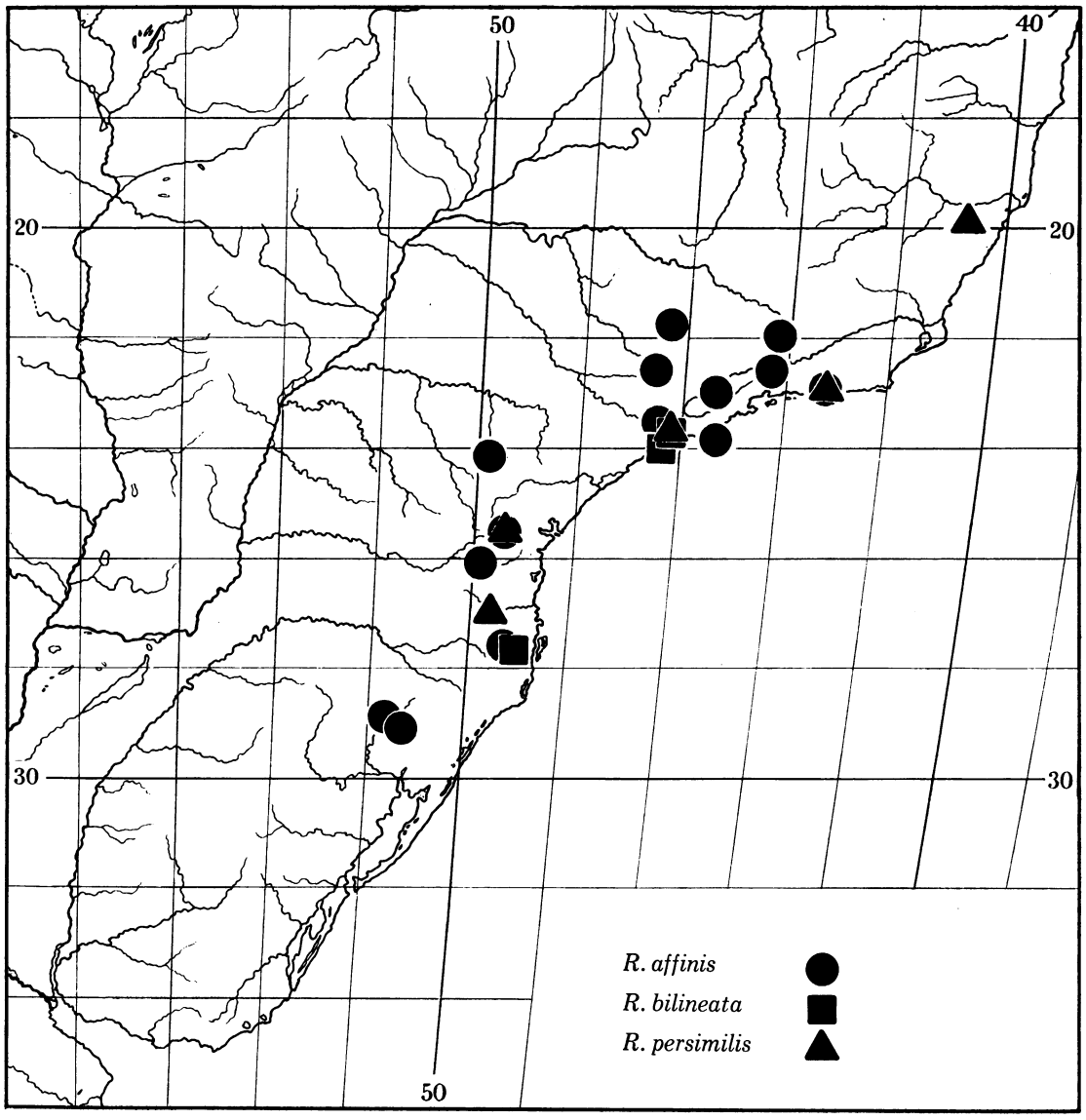
HOLOTYPE: Formerly MCZ 436, now lost (*fide* Barbour and Loveridge, 1929, p. 297; Ernest E. Williams, *in litt.*). "From Rio de Janeiro; brought by the Thayer expedition" (Cope "1868" [1869], p. 308).

DIAGNOSIS: *Rhadinaea persimilis* is a small-headed and evidently diminutive member of the *brevirostris* group and agrees with *R. affinis*, *R. bilineata*, and *R. poecilopogon* in having 17–17–17 scale rows and a dark line on row 4 (or dark sides up onto row 4). It lacks the conspicuous white line that extends along the canthus rostralis and through the top of the eye in *bilineata* and *poecilopogon*, and it lacks the wedge-shaped postocular marking that characterizes *affinis*. Additional comparisons are given in the Remarks section under *R. affinis*.

DISTRIBUTION: Southeastern Brazil, from the state of Espiríto Santo south to Santa Catarina.

DESCRIPTION (ONE SPECIMEN): This individual (SMF 32457) is a male 254 mm. total length, of which the tail is 67 mm. (26.4 percent) of the total; it evidently is an adult as the hemipenial spines are ossified. Dorsal scales are in 17–17–17 rows; anal ridges are absent. There are 128 ventrals and 58 subcaudals. There is one preocular, no subpreocular, two postoculars, 1+2 temporals, seven supralabials, and nine infralabials.

The body is medium brown, being somewhat darker on the sides (especially posteriorly) below a blackish brown line that runs along the middle of row 4. The dark line is bordered above by a whitish line on the upper part of row 4, both lines originating on the neck as a series of dashes and extending to the end of the tail. There is a faint trace of a dark line on the vertebral row of scales, especially on the neck, where it interrupts a narrow whitish collar that crosses the nape a scale-length behind the parietals. The collar, which is one to two scales wide, stops short of running into the white throat and is partly edged in black on its anterior and lower sides. The head is a darker brown than the body. There is a pair of faint, white parietal dots and, on the same horizontal plane, a pair of tiny, black-rimmed, white ocelli. Each ocellus lies on the outer, middle edge of a parietal plate, above the junction between the primary and secondary temporals. A black-edged, enamel-white stripe undulates along the tops of the supralabials, from the nostril to the corner of the mouth, where it becomes faint and disappears. The lower parts of the supralabials, and the infralabials, are yellowish white, with a fine speckling of brown. The venter is pale yellowish. The brown dorsal color encroaches slightly onto the ends of the ventrals and subcaudals, and there is a conspicuous line of brown dots on each side of the belly, from the throat to the anal plate.



MAP 19. Locality records for three species of *Rhadinaea* (*brevirostris* group) endemic to southeastern Brazil. Symbols represent specimens examined, and literature records from the following sources: Prado (1943) for *R. affinis*; Fischer (1885) for type locality of *R. bilineata*; Amaral (1926b, as *Liophis insignissimus*), Cope "1868" [1869], and Prado (1943, as *R. beui*) for *R. persimilis*.

There are 17 subequal maxillary teeth, followed by a broad gap and two enlarged fangs. The ultimate prediastemal socket lies well anterior to the front edge of the ectopterygoid process. The last fang is offset laterad.

A retracted hemipenis extended *in situ* to the end of subcaudal 6, and the retractor muscle originated at the level of subcaudal 24. The organ is single, but there is a slight division (about the length of half a subcaudal) in the retractor muscle. The hemipenis seems to be noncapitate. There are large calyces on the tip, and somewhat smaller calyces on the distal fourth of the sulcate side of the hemipenis; the calyces are papillate, without spinules. The sulcus spermaticus forks a little more than halfway up the hemipenis and its branches extend to the tip of the organ; there is a thick, solid wall of

tissue between the branches for most of their length, gradually giving way to calyces near the end. There are several very large, flaplike papillae below the calyces on the asulcate side of the tip. There are about 50 small to medium, slightly recurved spines below the calyces. Those spines on the asulcate side are arranged in two long, parallel rows below the distal overhang of large, flaplike papillae. Between these two rows of spines is a low ridge of tissue that bears several papillae on its distal half and which is connected to the adjacent spines by small ribs of tissue that form a distinctive pattern, at least on the retracted organ. There are a few scattered spinules near the basalmost spines, and an obvious cluster of spinules more basally, on the sulcate side. This description is based on the left retracted hemipenis of SMF 32457 (illustrated).

VARIATION: The specimen pictured by Jan and Sordelli [1866 (1860–1881), vol. 1, livr. 16, pl. 1, fig. 4*] has much darker sides than the one that I examined. Cope ("1868" [1869], p. 308) indicated that the holotype had dark sides also. The types of *Rhadinaea beui* (=*persimilis*) evidently are more like the specimen that I examined in this regard, judged from the description and photograph (Prado, 1943), although the latter is poorly reproduced.

There evidently is variation in the white parietal dots and small white ocelli on the back part of the head. Jan and Sordelli (*loc. cit.*) showed two pairs of white dots on the parietals, one pair behind the other. The specimen that I describe has four markings in a straight line across the head. Such pale markings were not mentioned by Cope (*loc. cit.*), Prado (*loc. cit.*), or Amaral (1926b, as *Liophis insignissimus*); Cope and Amaral also did not mention the pale nuchal marking. Cope stated that the holotype had a black dot on the end of each subcaudal ("scutellum"), as well as on each ventral plate ("scutum"), but, in the other known specimens, the dark dots terminate at the anal plate.

At least the type specimen of *Liophis insignissimus* (=*persimilis*), as well as the specimen examined, have a conspicuous horizontal white line on the upper parts of the supralabials, although in the former specimen the marking is confined to those labials posterior to the eye (Amaral, 1926b, pl. 1, fig. 8). Cope (*loc. cit.*) mentioned that the holotype of *persimilis* had the labials "white edged above," a description that also seems to apply to the specimen figured by Jan and Sordelli (*loc. cit.*). Prado (*loc. cit.*) did not mention such a marking in the description of *Rhadinaea beui* (=*persimilis*).

Aspects of variation in scutellation and size are given in table 20; all known specimens are listed except the two recorded in the older literature (see synonymy) under the name *Enicognathus melanocephalus*. Conceivably, more than one species is represented by the specimens in table 20, but, if so, it is not readily apparent. The table was compiled mainly from inadequate literature sources, and, pending further investigation, it seems best to consider all the specimens under only one of the available names, the oldest of which is *Rhadinaea persimilis* (Cope).

TABLE 20

SCALE COUNTS, SIZES (IN MILLIMETERS), AND PROPORTIONS OF SOME SPECIMENS OF *Rhadinaea persimilis*

Character	Holotype[a] ♂?	SMF 32457 ♂	IB 4730[b] ♂	IB 8519[c] ♂	IB 3172[d] ♀?
Ventrals	131	128	126	126	136
Subcaudals	70	58	51	55	58
Supralabials	7	7	7	?	7
Infralabials	7	9	?	?	?
Total length	[286][e]	254	330	368	395
Tail length	[82][e]	67	90	94	100
Tail length, as a percentage	28.7	26.4	27.3	25.5	25.3

[a]Data from Cope ("1868" [1869], p. 308).
[b]Holotype of *Rhadinaea beui*. Data from Prado (1943, p. 14).
[c]Paratype of *Rhadinaea beui*. Data from Prado (*loc. cit.*).
[d]Holotype of *Liophis insignissimus*. Data from Amaral (1926b, pp. 103, 104, and [for supralabials] pl. 1, fig. 8).
[e]Originally given as: 11 inches, 3 lines total length; 3 inches, 3 lines tail length.

REMARKS: The name *Rhadinaea persimilis* (Cope, "1868" [1869]) seemingly has not been used since its inception, except by Boulenger (1894b) as a tentative synonym of *R. poecilopogon*. If Cope's data are correct, which is not a safe assumption, the lost holotype of *persimilis* had a relatively high number of subcaudals (table 20). One other puzzling aspect of Cope's description is the mention of black dots on the ends of the subcaudals but, with so few specimens known, this might well be a variable feature (as in the related *R. affinis*). Although it has never been used as a senior synonym, the century-old name *Liophis persimilis* cannot be suppressed under the *nomen oblitum* rule of the International Code (1964, art. 23b), because the junior synonyms (*insignissimus* and *beui*) are themselves less than 50 years old. But the junior names are not well known either, having been used only a few times each, mainly in the original descriptions and in checklists that have not added new information; all citations are listed in the synonymy. The species has been nicely figured by Jan and Sordelli under the name *Enicognathus melanocephalus* Duméril, Bibron, and Duméril, a name which properly belongs in the synonymy of an Asiatic species of *Sibynophis*, as explained in the discussion under *Rhadinaea brevirostris*.

The single specimen (SMF 32457) on which the present description of *Rhadinaea persimilis* is based was described by Mertens (1930) under the name *Liophis insignissimus* Amaral. Although Amaral (1929b, p. 172; 1936, p. 114) accepted Merten's designation, I do not feel particularly secure in placing Amaral's *insignissimus* into synonymy without having seen the holotype, which is depicted in the original description (Amaral, 1926b, pl. 1, figs. 7–9) as having a somewhat more pronounced head than the specimen at hand, which, in general habitus, agrees with published photographs (Prado, 1943) of *Rhadinaea beui* (=*persimilis*). The doubt probably could be resolved by direct comparison of the type specimens of *Liophis insignissimus* and *Rhadinaea beui*, which are in the collection of the Instituto Butantan. Prado (1943) makes no reference to *insignissimus* in his description of *Rhadinaea beui* or in his account of *Rhadinaea affinis*, although the latter species (as "*Liophis*" *affinis*) was said by Amaral (1926b, p. 104) to be related to *Liophis insignissimus*. Peters and Orejas-Miranda (1970, p. 266) stated that the holotype of *Liophis insignissimus* "seems unquestionably a *Rhadinaea*," but Werner (1929, p. 118) was actually the first author to combine the specific epithet with the name *Rhadinaea*.

The closest relative of *Rhadinaea persimilis* is perhaps *R. affinis*, but there are many differences as indicated under the latter species. The specific epithet is a word meaning "very similar," in allusion to the resemblance in color pattern of *R. persimilis* to *Coniophanes fissidens*, a species of Middle America and northwestern South America.

Rhadinaea poecilopogon Cope

Figures 45B, 46F; map 20

Dromicus affinis GÜNTHER, 1858, p. 129 (part: specimen *c*).

Rhadinaea poecilopogon COPE, 1863 ("April"), pp. 100, 101. BOULENGER, 1894b, p. 173 (part: not *Liophis persimilis* [=*Rhadinaea persimilis*], nor *Enicognathus bilineatus* [=*R. bilineata*]). DEVINCENZI, 1925, pp. 34, 35. WERNER, 1929, p. 118. PRADO, 1943, pp. 13, 15; 1945a, p. 75. PETERS AND OREJAS-MIRANDA, 1970, pp. 267 (part), 268.

E[*nicognathus*]. *elegans* JAN, 1863 ("March 31"), pp. 266, 268, 269 (pp. 56, 58, 59 in reprint; two syntypes [not seen], from Montevideo and Buenos Aires, formerly in the museums of Milan and Torino). JAN AND SORDELLI, 1866 (1860–1881), vol. 1, livr. 16, pl. 1, fig. 3 (color pattern and details of scutellation of Milan Museum specimen from Buenos Aires). *Nomen oblitum.*

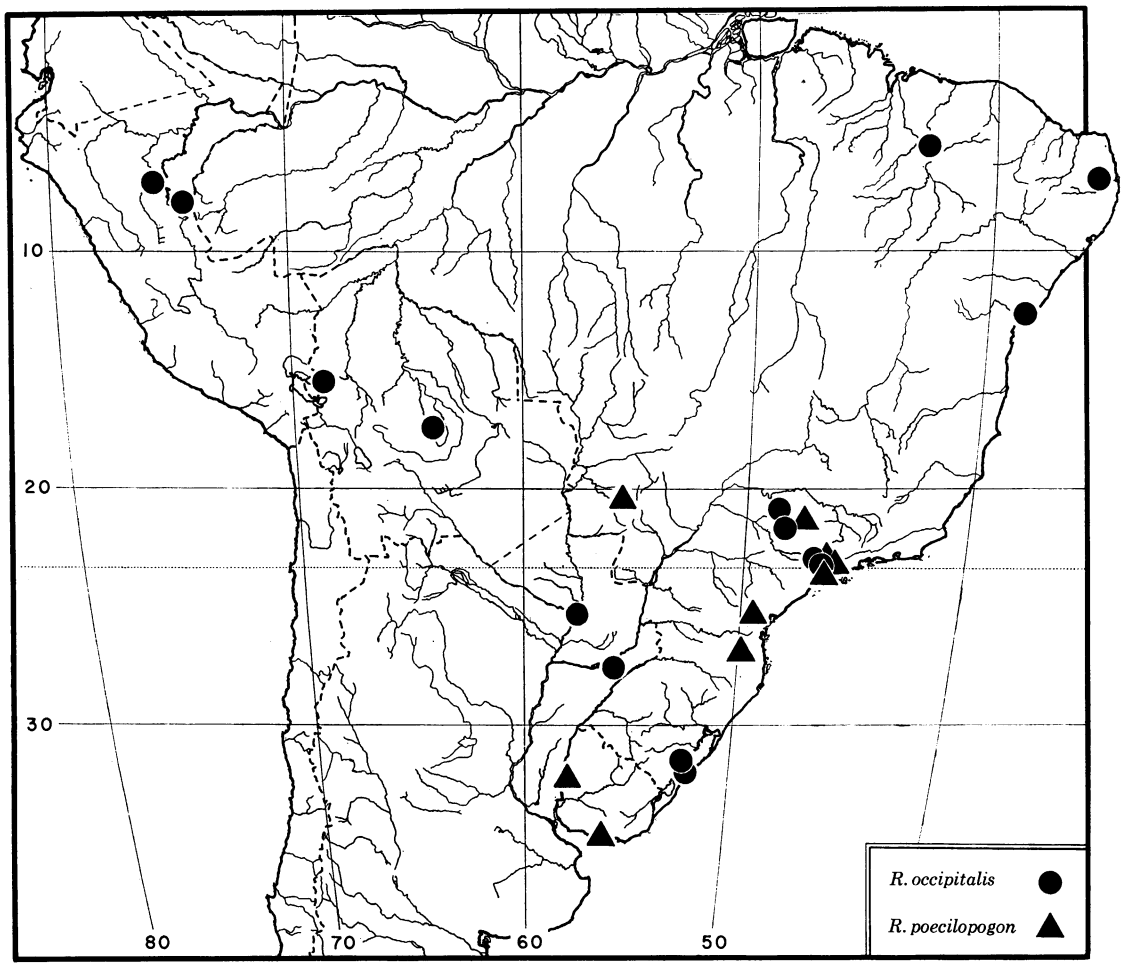
Dromicus melanocephalus PETERS, 1863 ("June 29"), pp. 277, 278 (five syntypes [not seen] in ZMB, from Brazil, probably state of San [São] Paulo; von Sello, collector). *Nomen oblitum.*

Coronella poecilopogon (Cope): BOULENGER, 1885, p. 194; 1886, p. 431.

Liophis poecilopogon (Cope): AMARAL, 1929a, p. 89; 1929b, p. 174; 1936, p. 116 (reference in synonymy to "*Liophis occipitalis*" is a lapsus); 1944, pp. 55, 56 (*Liophis* by implication, but listed as *Rhadinaea poecilopogon*). BERTONI, 1939, p. 47. FREIBERG, 1939, p. 8.

HOLOTYPE: USNM 31278, a male in fair condition, from "Paysondu" [Paysandú], Uruguay; H. W. Kennedy, collector.

DIAGNOSIS: *Rhadinaea poecilopogon* is a handsomely colored species of the *brevirostris* group, in which *poecilopogon* agrees with *R. bilineata* and *R. occipitalis* in having a narrow but conspicuous pale line along the canthus rostralis to the temporal region. *Rhadinaea poecilopogon* differs from *occipitalis* in having 17 dorsal scale rows and a striped pattern (15 rows and spotted in



MAP 20. Locality records for *Rhadinaea occipitalis* and *R. poecilopogon*. Symbols represent specimens examined, and literature records from the following sources: Amaral (1934), Boulenger (1894b), and Prado (1945b) for *R. occipitalis*; Devincenzi (1925) and Prado (1943) for *R. poecilopogon*.

occipitalis); it is distinguished from *bilineata* in having dark sides, a dark vertebral line, more intensely marked labials, and in that the dark head cap extends around and under the corners of the mouth. Additional comparisons are given in the Remarks section under *R. bilineata*, which seems to be the closest relative.

DISTRIBUTION: Southern Brazil (from Minas Gerais), south through adjacent Paraguay and Uruguay, into east-central Argentina along the Río Paraná and Río Uruguay.

DESCRIPTION (FIVE SPECIMENS): The largest specimen is an adult female (containing eggs) 443 mm. total length, 120 mm. tail length; the largest male is 390 mm. total, 112 mm. tail length. The tail is 28.7–29.9 percent of total length in the two males, and 25.6–27.9 percent in the females. Prado (1943, table) gave a maximum size of 558 mm. total, 180 mm. tail length, for a female. Calculations from Prado's (*loc. cit.*) measurements of 15 specimens give a range of 27.4–32.8 percent (mean 30.8) for the tail length of eight males, and 26.7–32.3 percent (mean 30.7) for seven females.

The dorsal scales are in 17–17–17 rows; anal ridges are absent. There are 151–160 ventrals (males, 151, 158; females, 159–160), and 65–79 subcaudals (males, 76, 79; females, 65–71). Prado (*loc. cit.*) gave 141–156 ventrals [males 141–152, mean 146.8; females 141–156, mean 147.3], and 71–91 subcaudals [males 74–90, mean 80.4; females 71–91, mean 81.1]. There is

one preocular, no subpreocular, two postoculars, 1+2 temporals, seven supralabials, and eight infralabials (8/9 in holotype).

The edges of the venter and sides of the body and tail are black or dark brown, to about the middle of row 4 on the body, turning paler gray anteriorly on the sides of the neck. The scales in rows 1–3 are very finely speckled or variegated with whitish, but the dark pigment on the lower part of row 4 is virtually solid, tending to show as a discrete black line that is emphasized at its upper edge by a thin whitish or pale yellow line or series of dashes. The middorsum is brown, with a sharply defined black line on the vertebral scale row, from the head onto the tail (fading on the base or extending to the end); some specimens have a line of dark dashes (inconspicuous on the specimens examined) on the sixth row, on each side of the vertebral dark line. The dorsal scales, especially in the paravertebral regions, are finely speckled with black, and sometimes (ANSP 27344) there are poorly defined whitish dashes.

The top and sides of the head are black or blackish brown, this color extending two or three scales back on the neck and terminating at a half-scale wide, whitish collar, which is interrupted by the dark vertebral line. The blackish head color passes around the angle of the jaws and a wedge extends forward for a short distance along the inner edge of the infralabials. A vivid cream line is continuous around the tip of the snout and extends along the canthus rostralis, through the top of the eye, and terminates behind the eye on the midtemporal region. The dark head is finely speckled with white, and there is a pair of white parietal dots. The dark color extends onto the tops of the supralabials where there is a hint of a darker black line, and, below this, there may be a narrow cream line. The lower parts of the supralabials and the underside of the head are whitish and heavily spotted and speckled with black (except in BMNH 82.10.4.78, which is only modestly spotted). A double line of black spots diverges from the throat, each line then extending across the ends of the ventrals under the neck; posteriorly, these spots tend to fuse into a solid line, which may lose its identity depending on the density of the dark color that encroaches broadly onto the ends of the ventrals and subcaudals. The venter is pale yellow, this color being sometimes restricted to as little as the median third of the ventrals, depending on the degree of encroachment of the ventrolateral dark color.

There are 13–16 subequal maxillary teeth followed by a broad diastema and two enlarged fangs. The ultimate prediastemal socket lies anterior to the front edge of the ectopterygoid process. The last fang is offset laterad.

A retracted hemipenis extended *in situ* to the middle of subcaudal 7, and the retractor muscle originated at subcaudal 26. The hemipenis is single, but there is a short (less than half a subcaudal) division in the insertion of the retractor muscle, on the lateral wall. The hemipenis is noncapitate, except for a distinct overhang in the middle of the asulcate side, slightly below the tip. There are some relatively large calyces on the asulcate side of the tip of the organ, and somewhat smaller calyces on the distal third of the sulcate side; the calyces are papillate, without spines, and the papillae on the asulcate side of the tip are relatively large. The sulcus spermaticus forks more than halfway up the hemipenis and its branches extend to the tip of the organ; the tissue between the branches is calyculate for about the distal two-thirds, leaving only about the basal third as a thick, solid wall (compare with *R. affinis*, *R. persimilis*). There are about 80 small to medium, slightly recurved spines below the calyces. Many of the spines on the asulcate side are arranged in two long, parallel rows below the distal overhang of large papillae. Between the distal halves of these two rows of spines is a low ridge of tissue that bears papillae; this ridge is connected to the rows of spines by a few small "ribs" of tissue, but the ribs do not form such a conspicuous pattern as shown in the illustration for *R. persimilis*. There are scattered spinules near the basalmost spines, and an obvious cluster of spinules near the base of the organ, on the sulcate side. The preceding description is based on the left retracted hemipenis of BMNH 82.10.4.78. This organ is very similar to that of *R. affinis*, except that the calyces between the branches of the sulcus spermaticus extend farther basad in *poecilopogon*.

Remarks: Very little is known about this snake, although Gatti (1955, pp. 96, 97) indicated that it is not uncommon in the vicinity of Asunción, Paraguay, where it is one of several species called *ñuasó*. I have examined Müller's (1968, p. 39) specimen of "*Liophis poecilopogon*" from São Sebastião Island and have reidentified

it as *Rhadinaea affinis*. *Rhadinaea poecilopogon* has a very distinctive pattern, not the least part of which is the heavily dappled labials and chin, thus giving rise to the specific epithet from *poecilos* (variegated) plus *pogon* (beard).

The name *Enicognathus elegans* Jan, 1863, seems to antedate, by a few weeks or more, the name *Rhadinaea poecilopogon* Cope, 1863. But the former name has long been buried in the synonymy of *poecilopogon* (e.g., Boulenger, 1894b, p. 173; Peters and Orejas-Miranda, 1970, p. 267) and it is best suppressed as a *nomen oblitum*. Another old name, *Dromicus melanocephalus* Peters, 1863, seems to have been published somewhat later than *poecilopogon* but, in any case, *melanocephalus* also is a *nomen oblitum*.

ECOLOGY

IT IS SOMETIMES ASSUMED that genera are (or should be) groups in which the contained species are ecologically, as well as morphologically, similar (see especially Inger, 1958). As a generalization this possibly may be true, but in such a diverse and evolutionarily active group as *Rhadinaea* it is unsafe to generalize too broadly on meager data. The following brief remarks are, more than anything, an indication of how little is known about the ecological roles of most species of *Rhadinaea*.

HABITAT: The great majority, if not all, species of *Rhadinaea* are inhabitants of seasonally to continuously humid forests—whether the vegetation type be coniferous or broadleaf, lowland or montane (see pp. 24, 29). The terrestrial microhabitat of nonforaging individuals varies considerably. Many northern species are often found under such cover as rocks and the loose bark of logs and stumps. But, in the lowland tropics small snakes are not so often found under this kind of cover—partly perhaps because of different thermal requirements as well as greater competition from large arachnids—but may be more widely distributed in the leaf litter (Myers and Rand, 1969, p. 9). Several years of field experience in Panama leads me to believe that most tropical species of *Rhadinaea* are active foragers on the forest floor and not so secretive as might be thought, and this probably also applies to many species of the northern *decorata* and *taeniata* groups (see Daily Activity). A few species, especially in the *godmani* group (p. 227), are probably semifossorial. So far as known, there are no species with aquatic or arboreal tendencies.

DAILY ACTIVITY: Observations on times of activity are cited in the Remarks sections of the species accounts, except for *Rhadinaea flavilata* (see below). The following species have been found abroad by day:

R. calligaster
R. decipiens
R. decorata
R. fulviceps
R. fulvivittis
R. hesperia
R. multilineata
R. myersi
R. pulveriventris
R. taeniata aemula

The following few species have been found as they were prowling by night:

R. flavilata
R. fulviceps
R. pilonaorum

It will be noticed that *fulviceps* is the only species falling into both groups; one individual was found by day and two others after dark, in July, at the same locality in eastern Panama. Many species, including *fulviceps*, probably adjust their times of activity according to physiological variables such as hunger and perhaps also to climatic changes. Nonetheless, the available observations indicate that species of *Rhadinaea* are largely diurnal. Those species of *Rhadinaea* that appear most secretive are perhaps the ones most likely to be nocturnal. For example, I have noted that *flavilata* is rarely found away from cover (one was on a road at night) and that captive individuals are mostly nocturnal in their prowling (Myers, 1967, pp. 63, 92).

SEASONAL OCCURRENCE: The only data are for the temperate-zone *Rhadinaea flavilata*, which undergoes cyclic variation in microhabitat selection—seemingly due to seasonal fluctuations in temperature and moisture (Myers, 1967, pp. 63, 64). Other species living in seasonally changeable environments probably have comparable behavior. Also, reproductive state might cause some species to be more "common" at a particular time of year (see Reproduction below).

FOOD: Species of *Rhadinaea* are principally predators of small frogs, salamanders, and lizards—this conclusion being based on the contents of 55 stomachs of 15 species (table 21). Individuals of two species (*decorata* and *lachrymans*) had their stomachs packed with terrestrial egg masses of frogs (*Eleutherodactylus*) or salamanders; Martin (1958) found salamander eggs in the stomach of a third species, *R. gaigeae* ("*crassa*"). A specimen of the small *Rhadinaea hannsteini* contained the collapsed shell of a snake or lizard egg of relatively large size (11 mm. long). Two additional specimens of *hannsteini* contained invertebrate remains that looked like

TABLE 21

FOOD ITEMS FROM STOMACHS OF 15 SPECIES OF *Rhadinaea*

	R. decorata (9)[a]	*R. flavilata* (4)	*R. forbesi* (1)	*R. fulvivittis* (7)	*R. gaigeae* (2)	*R. hannsteini* (3)	*R. hempsteadae* (1)	*R. hesperia* (4)	*R. lachrymans* (9)	*R. laureata* (6)	*R. montana* (1)	*R. montecristi* (2)	*R. omiltemana* (2)	*R. pachyura* (1)	*R. t. taeniata* (1)	*R. t. aemula* (2)
SALAMANDERS																
Thorius	—	—	—	2	—	—	—	—	—	—	—	—	1	—	—	—
Unidentified	2[a]	—	1	5	2	—	—	—	1	1	—	2	—	1	—	—
FROGS AND TOADS																
Acris	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bufo	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Eleutherodactylus	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hyla	—	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—
Tomodactylus	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Unidentified	2	1	—	—	—	—	—	3	3	—	1	—	—	—	—	2
LIZARDS																
Anolis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
Barisia	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Sceloporus	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	—
Scincella	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Unidentified	1	—	—	—	—	—	1	—	—	—	—	—	1	—	—	—
MISCELLANEOUS																
Insect pupae(?)[b]	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—
Amphibian eggs[c]	2	—	—	—	—	—	—	—	5	—	—	—	—	—	—	—
Snake or lizard egg	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—

[a]Numbers in parentheses in column heading are the total numbers of snakes that contained food; numbers in the table are the numbers of snakes that contained a given food item. A few specimens contained more than one kind of food or more than one item of the same kind.

[b]These invertebrate remains were too large to have been secondarily ingested.

[c]Terrestrial eggs of frogs (*Eleutherodactylus*) and/or salamanders.

insect pupae and which were too large to have been secondarily ingested. Excluding a few questionable records (Myers, 1967, pp. 64, 65), the only other evidence of predation on invertebrates is Taylor's (1949) observation that two *Rhadinaea decorata* contained partially digested remains of earthworms.

Conant's (1958 and *in litt.*) inclusion of snakes in the diet of *Rhadinaea flavilata* is based on a captive that ate two small *Storeria dekayi* at the Philadelphia Zoo. Willard (1967) stated that a captive *R. flavilata* ate a "very small mouse . . . late at night," although it is not clear whether this feeding was actually witnessed. Myers (1967, table 2) compiled other records of the food preferences of captive *R. flavilata*. Unfortunately, the behavior of captive snakes does not give an unequivocal indication of the natural diet. Specimens of *Rhadinaea fulvivittis* and *R. taeniata aemula*, from Oaxaca, fed eagerly on goldfish and guppies, although fish are probably not eaten in nature. Not only are fish absent in at least most parts of the montane pine-oak habitat of these snakes (C. M. Bogert, personal commun.), but the captive snakes could feed only when the fish were on a dry substrate; the snakes were unable to seize fish that were covered by even a thin film of water.

REPRODUCTION: All species of *Rhadinaea* are assumed to be oviparous in the absence of data

to the contrary. I have seen eggs, deposited or in the oviducts, from one or more species of each species group except the *brevirostris* group. There are usually several eggs, ranging from an observed minimum of two in various species to a maximum of 13 in *R. taeniata aemula*. The eggs vary in shape from oval in *aemula* to highly elongate in most other species (fig. 49), but there may be considerable variation in egg size and shape even within the same species (fig. 50).

The oviparity of *Rhadinaea* is an exception to the general rule that montane snakes and lizards usually bear living young. Greene's (1970) analysis of reproductive mode of the squamate fauna, in the Gómez Farías region (Tamaulipas, Mexico), shows *Rhadinaea crassa* (=*gaigeae*) to be one of only two oviparous species attaining elevations in excess of 1750 meters. I have verified Greene's assumption (*op. cit.*, p. 566) that *gaigeae* is oviparous; the known elevation of this species in the Gómez Farías region is 1006–1829 meters. The oviparous *Rhadinaea godmani* (fig. 49C) is one of the few high montane animals that have been able to establish themselves throughout Central America, from eastern Oaxaca to western Panama. Many other cases can be cited, as for example *Rhadinaea calligaster*, an unquestionably oviparous (fig. 50) and characteristic species of montane rain forest in lower Central America.

There is evidence of seasonality in the egg laying of a few species for which data are available. Egg deposition of *Rhadinaea flavilata* seems similar to that of sympatric populations of the better known *Diadophis punctatus*, extending from May or June into August (Myers, 1965, 1967). As yet, however, there is no evidence that egg laying of these two species extends over so long a period in any one locality or year. Two hypotheses have been elicited from the same meager data: 1) The egg-laying season is not abnormally long at a given locality, but an unusually severe winter might delay the female reproductive cycle, causing deposition to occur as late as August in some years (Myers, 1965, pp. 77–79) (it was assumed that the long growing season in the southern United States would permit the evolution of such adaptability); 2) Fitch (1970, pp. 128, 146, 211) accepted evidence of long egg-laying seasons at face value, and thought that this was suggestive that *Diadophis punctatus* and *Rhadinaea flavilata* might produce second clutches in the same year.

Several specimens of *Rhadinaea fulviceps* and *R. taeniata aemula*, from Oaxaca, have laid eggs at the American Museum of Natural History in the period from middle November through December. Hatching in captivity occurred in late February for both species, indicating that laying may be timed so that the young can emerge during the winter dry season, in the montane pine-oak habitat of these species.

Even *Rhadinaea calligaster* appears to have a definite egg-laying season, although its primary habitat (montane rain forest) is not subjected to regular seasonal changes in climate. The following data were obtained by William E. Duellman, Linda Trueb, and me in May, 1966, on the northern slopes of Cerro Pando, extreme western Panama (for habitat description, see Myers, 1969c, pp. 33–36). A communal nest of 38 *R. calligaster* eggs was found on May 9 under a pile of rotting thatch—the old remains of a small trail shelter—in a clearing in montane rain forest (fig. 50, top). The eggs were in one bunch, variously adhered to one another, and extraordinarily variable in size (fig. 50, bottom). A representative sample of 13 eggs ranged in size from 20 by 10 mm. to 43 by 8 mm., with a definite inverse relationship between length and width. The eggs were transported to an air-conditioned laboratory in Panama City in early June, and 17 eggs that were not opened or which did not spoil hatched in the period August 5–15.

Seven adult *Rhadinaea calligaster*, only one of which was a male, were found in the rotting thatch at the aforesaid nest site on May 9 (four females), May 12 (one female), and May 30 (one female, one male). One female collected on May 9 when the nest was discovered was recently spent, but the other five females contained 3–5 oviductal eggs (3, 3, 4, 4, 5, mean 3.8); these ova varied in size from 25 by 8 mm. to 32 by 9 mm., well within the size range of eggs already laid. Thus, these five females would have added an additional 19 eggs to the 38 already laid. The average of 3.8 ova per snake suggests that as many as 10 females might have already contributed to the nest. One other specimen was obtained on Cerro Pando on May 31 at a higher elevation (2260 m.) than the nest site (1810 m.); the enlarged, flaccid oviducts indicated that this individual had recently laid.

The intense reproductive activity of *Rhadinaea calligaster* on Cerro Pando, in May, 1966, is

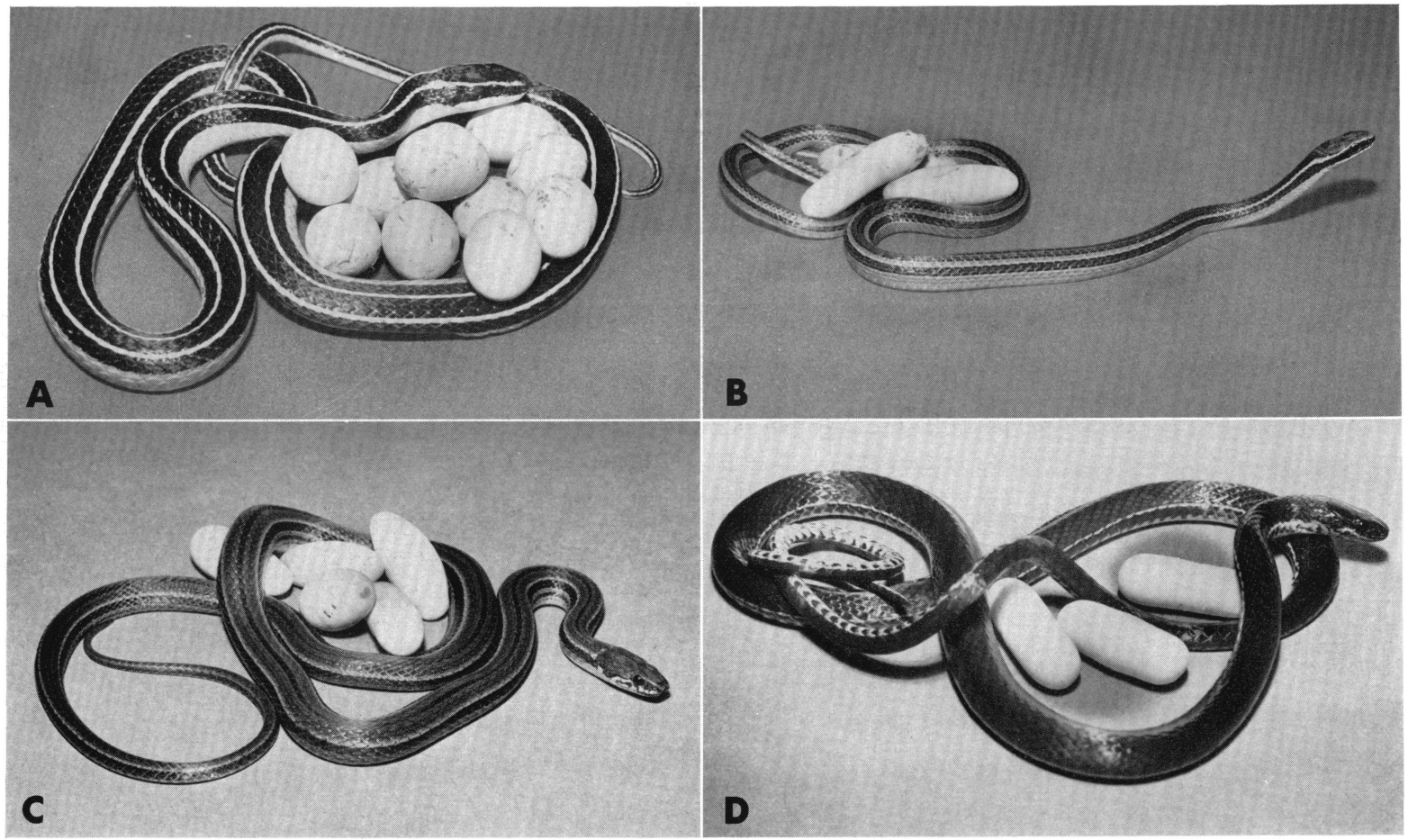


FIG. 49. Specimens of *Rhadinaea* with their eggs. A. *Rhadinaea taeniata aemula*, AMNH 102983, Oaxaca, Mexico. B. *Rhadinaea fulvivittis*, AMNH specimen from vicinity Tejocotes, Oaxaca, Mexico. C. *Rhadinaea godmani*, USC 2983, Cartago Province, Costa Rica. D. *Rhadinaea decipiens*, KU 112439, Bocas del Toro, Panama. Specimens were posed for these pictures, which are not to be taken as evidence of brooding or attendant behavior.

FIG. 50. Communal nest site and eggs of *Rhadinaea calligaster*. *Top*: "La Patona," a small trailside clearing in montane rain forest at 1810 meters, northern slopes Cerro Pando, Bocas del Toro, extreme western Panama. Dark area in grass (foreground) is remnant of overnight shelter similar to the one standing. Eggs were laid in rotting thatch of collapsed shelter, where several adult snakes also were found. *Bottom*: Cluster of 38 eggs, possibly representing efforts of as many as 10 female *Rhadinaea calligaster*. (May, 1966.)

suggestive of a relatively brief and sharply defined egg-laying season in a relatively non-seasonal environment. That the egg-laying season is somewhat longer, or, perhaps more likely, subject to geographic variation, is indicated by two females collected March 29–30, 1966, at 2100 metres elevation on the south fork of Río Las Vueltas, Heredia, Costa Rica. One of these snakes appeared recently spent, judged from the enlarged oviducts, whereas the other contained two eggs (29 by 8 mm., 32.5 by 7 mm.) that seemed about ready to be laid.

PREDATION AND COMPETITION: There must be many kinds of animals with which species of *Rhadinaea* coact, but other snakes, because of similar life styles, possibly comprise the major group of predators and competitors. Circumstantial evidence has caused the ringneck snake, *Diadophis punctatus*, to be nominated as the single most important associate of *Rhadinaea flavilata*, in terms of food and space competition and possibly predation (Myers, 1965, pp. 64–66; 1967, pp. 61–63). Most, probably all, *Rhadinaea* coexist with one or more kinds of ophiophagous snakes, for example *Micrurus*. Charles M. Bogert (personal commun.) found two coral snakes (*Micrurus ephippifer*) that had fed on *Rhadinaea taeniata aemula* in Oaxaca.

DEFENSE: Most *Rhadinaea* seem to rely on concealing coloration and on flight or secretive habits in order to escape detection. I am unaware of any specimen that attempted to defend itself by biting or by a threat display, although the bright red or yellow venters of some species conceivably might have a startling effect on certain predators. Possible traits of protective value include the common snake-habit of discharging contents of the anal sacs, and, especially, the ease of tail breakage in some species. Nearly 30 percent of all specimens of *Rhadinaea flavilata* had stub tails (Myers, 1967, pp. 66, 74), and the percentage is even higher in most long-tailed species of the *lateristriga* group (as can be seen by inspection of table 16).

MIMICRY: Close resemblances in color and pattern of unrelated species of snakes, living in the same region, are suggestive either of parallel environmental adaptations or of subtle interactions between species. Examples in *Rhadinaea* include resemblances between *Rhadinaea schistosa* and sympatric *Tantilla schistosa* (p. 150), and between nearly sympatric populations of *Rhadinaea calligaster* and *R. decipiens* (p. 175). I offer no solution in the aforesaid cases, but I suggest that *Rhadinaea taeniata aemula*, with its unusual coloration and innocuous nature, is a mimic of the presumably pugnacious and poisonous *Coniophanes piceivittis* (see p. 117).

EVOLUTION

THE DETECTION of evolutionary trends within a group of organisms implies the determination of character-states that are "primitive," or present earlier in time, and those that are "advanced," or derived later in a given lineage. This is not a simple matter in a group such as *Rhadinaea*, which is virtually devoid of a fossil record and the members of which are generalized both in habits[1] and in the sense of being similar to many other colubrid snakes in a majority of characters. But, consideration of intrageneric variation caused me to conclude that the *godmani* group has important features of dentition and hemipenis that were present in the ancestral stock of the genus and later modified in most lineages; I additionally decided that the high number of dorsal scale rows in some members of the *godmani* group also is probably a primitive condition. A theory of geographic origin and dispersal of the *godmani* group, and of the genus, naturally followed. Although I hereafter refer to the *godmani* assemblage as being a primitive group, I do not mean to insinuate that any of its species are geologically older or less well adapted than species in other groups. Except for a few Pleistocene fossils of a member of the *flavilata* group, there is no direct evidence on the age of any species of *Rhadinaea*.

The major aspects (fig. 51) of the proposed evolutionary scheme hinge importantly on my interpretations of variation in the hemipenis and in the maxillary dentition, which appear to be completely independent characters. Should I prove to be wrong on one count the scheme would be weakened although not necessarily

[1]Although some species probably live mainly under cover, most seem to be diurnal foragers on the forest floor during their times of activity. There are no apparent specializations for arboreal, aquatic, or nocturnal habits, or for xeric environments.

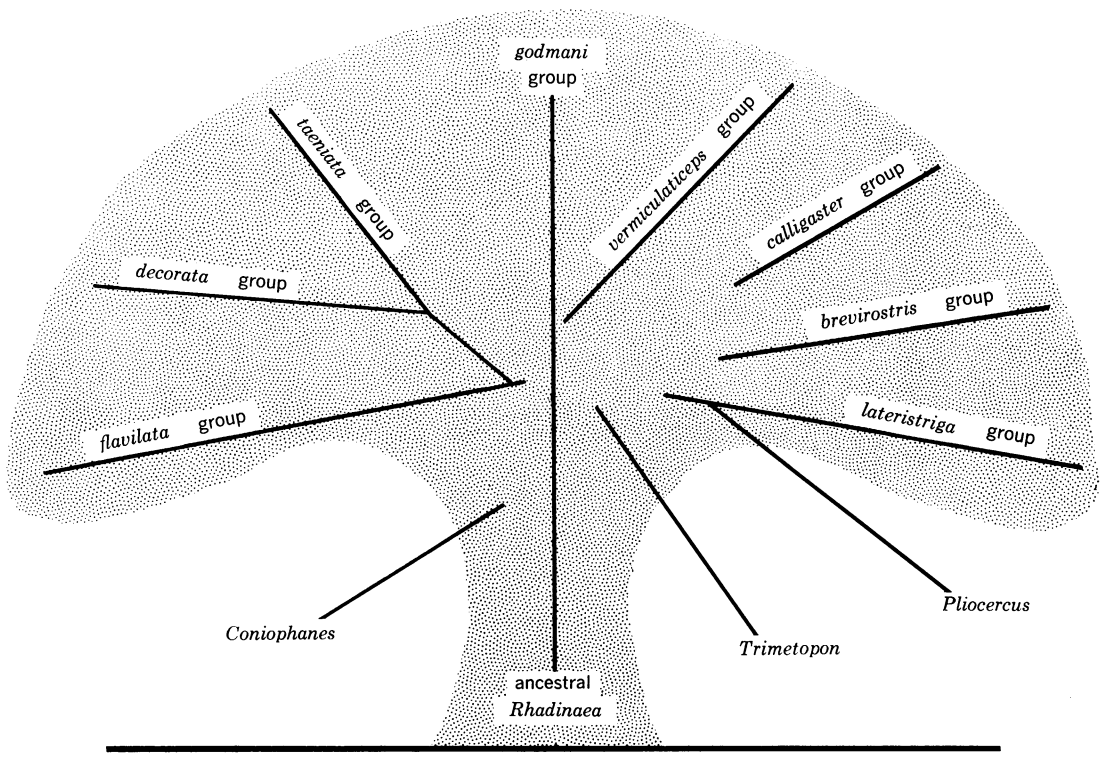


FIG. 51. Radiation of modern species groups of *Rhadinaea*, and probable origin of some derived genera.

invalidated, as would probably be the case if both interpretations were false. Some important aspects of the hemipenis and dentition are reemphasized below.

HEMIPENIS: The copulatory organ is slightly bilobated and associated with a divided retractor muscle in most species of the *godmani* group, and in the one species comprising the *calligaster* group, and in some individuals of two species of the *brevirostris* group (table 2). The reason for the presence of two slips of retractor muscle is obvious in the case of a divided or bilobated hemipenis, but I can think of no functional advantage in there being a split insertion on a hemipenis with a single head. Therefore, it follows that a divided retractor insertion on a nonbilobated organ would be evidence of a derived condition, and this actually occurs in the *brevirostris* group and in one species of the *godmani* group (table 2). It seems a reasonable conclusion that the bilobated hemipenis is primitive in *Rhadinaea*, that the single hemipenis with divided retractor insertion is intermediate, and that the single hemipenis with undivided retractor muscle is the most advanced condition.

A basal pocket, or naked groove, is characteristic of the hemipenis in the *godmani* group, but occurs elsewhere in the genus only in the geographically distant *flavilata* and *vermiculaticeps* groups. Probably this is a primitive feature that has been lost in other lineages.

The *godmani* and *brevirostris* groups have the greatest concentrations of special hemipenial features (table 2). The absence of most of these features (capitation, or spinules on the basalmost calyces for example) is probably a derived state, as the general trend seems to have been simplification of the hemipenis. The tendency for retention of specialized features has been greater in the *godmani* group than in the *brevirostris* group, suggesting that hemipenes of the most primitive structure are to be found among species in the former assemblage. A few specialized features of the capitulum (distal asulcate pockets and enlarged asulcate papillae) are not known in the *godmani* group, and might be either derived modifications or else primitive conditions that have been lost in the modern species of that group.

MAXILLARY DENTITION: The two basic types of maxillary dentition are illustrated in figures 1 and 2, and are discussed in the section on Taxonomic Characters and Methodology. It is thought that the arrangement and size of the posterior maxillary teeth are under the control of selection pressure associated with the efficiency of venom flow from the parotid (Duvernoy's) gland. The isolation of enlarged, offset teeth by a distinct diastema (figs. 1B, 2B–C) seems to be a reasonably efficient apparatus for getting venom into prey items. This is a widespread pattern among rear-fanged snakes and doubtlessly was independently derived (as were grooved teeth in some genera) in several stocks, and is here considered to be the advanced condition in *Rhadinaea*. The tendency for all maxillary teeth to lie along the same plane, as in the *godmani* group (fig. 1A), is considered primitive. The tendency in all groups for enlargement of the posterior teeth is a specialization that may or may not have been present in the ancestral stock of *Rhadinaea*.

EVOLUTIONARY TRENDS AND INTRAGENERIC RELATIONSHIPS

THE *godmani* GROUP: As shown above, the *godmani* group seems to contain the most primitive hemipenes and dentitional pattern to be found among living species of *Rhadinaea*. Primitiveness in unrelated characters that are intimately associated with vital functions (feeding and reproduction) seems particularly significant, and suggests that other important features also might have been carried over from the ancestral stock of the genus. In this connection, I am impressed by the fact that *Rhadinaea godmani* has the highest number of dorsal scale rows in the genus. This widely distributed snake is characterized by 21 rows, but near each end of its geographic range there is a close relative having 19 scale rows. The simplest explanation is that isolated populations of *R. godmani* gave rise to *hempsteadae* north of the Chiapas-Guatemalan depression and to *serperaster* in the Cordillera Central of Costa Rica; subsequent and partial breakdown of geographical or ecological barriers has allowed the terminal offshoots to reapproach the parental species, and perhaps even to hybridize in the case of *hempsteadae*. Therefore, it seems most likely that there has been a trend toward reduction in number of scale rows rather than an increase, and that the 19 and 21 rows in some members of the *godmani* group are more primitive than the generic norm of 17 rows. The only other *Rhadinaea* having

more than 17 scale rows is *montecristi*, which has 19 rows and is probably a remnant of the same stock that gave rise to the 17-row *lachrymans*; these two snakes are quite similar, but *montecristi* seemingly has a smaller range and possibly a more restricted habitat than *lachrymans*, so *montecristi* fits the picture of a peripheral relict that has been largely replaced by a more modern derivative. Three species having 17 scale rows form a closely related series: *Rhadinaea kinkelini*, *R. pinicola*, and *R. hannsteini* are small in size (to 350 mm. total length) and generalized in scutellation, except that *hannsteini* has lost a postocular; the color patterns indicate that these three snakes are more closely related to the larger *godmani* and *serperaster* than to other 17-row species. The remaining three species of the *godmani* group are diminutive snakes and all have 17 scale rows; although there is no direct evidence that the ancestors of these species had more than 17 scale rows, such a theory is not inconsistent with the morphological evidence of an evolutionary trend toward semifossorial habits: *Rhadinaea pilonaorum* and *R. posadasi* seem to have had common ancestry and probably are semifossorial as indicated by the sum of their characters, including their slender bodies (especially in *pilonaorum*), their small size, the single postocular, the reduced number of supralabials in *posadasi*, and the white head of *pilonaorum*. *Rhadinaea schistosa* is a tiny *Tantilla*-like snake with a reduced number of temporals and postoculars, and with the shortest tail and lowest number of subcaudals in the genus; the color pattern of the body is suggestive of relationship with *posadasi* and *pilonaorum*, but *schistosa* has a much shorter tail and a very different hemipenis, about which more will be said in connection with the *vermiculaticeps* group.

The center of dispersal and probable place of origin of the *godmani* group is the old highland region of upper, or "Nuclear," Central America, where it is the only group of *Rhadinaea* present (except for *R. decorata* in the Caribbean lowlands). There was dispersal out of this region in times past, as proved by the relict distribution of *schistosa* in central Veracruz, *serperaster* in Costa Rica, and the disjunct, southern populations of *kinkelini* in northern Nicaragua and *godmani* in Costa Rica and Panama. Specimens from the northernmost (Mexico) and southernmost (Costa Rica–Panama) populations of *R. godmani* are remarkably similar in color pattern of the body, suggesting that they represent the primitive condition from which intervening populations in Guatemala and El Salvador have been derived. Another indication of the primitiveness of this color pattern is its presence in *R. serperaster*, which probably evolved from southern *R. godmani* in some segment of the Costa Rican highlands (see above).

The origin of several modern species groups of *Rhadinaea* can be attributed to dispersals of the ancient *godmani* group from its ancestral homeland in Nuclear Central America, and the same phenomenon also accounts for the origin of the genus *Trimetopon* and possibly of *Coniophanes* (see Intergeneric Relationships). Geographic isolation and subsequent evolution of terminal populations occurred, probably after unfavorable climatic changes (or even flooding) made barriers of such lowland regions as the Isthmus of Tehuantepec and the Nicaraguan Depression. First, I shall hypothesize what happened in North America above the Isthmus of Tehuantepec, where there are three species assemblages of *Rhadinaea*—the *decorata*, *flavilata*, and *taeniata* groups—not counting the relict *R. schistosa*, which belongs to the *godmani* group.

THE *flavilata* Group: This group is comprised of two isolated species, the lowland *Rhadinaea flavilata* of the southeastern United States and the montane *R. laureata* of western Mexico. *Rhadinaea flavilata* was isolated in a Floridian refuge during the late Pleistocene, and spread into its present range in postglacial times; there is some evidence that southern populations of this snake, being most influenced by a warming postglacial climate, are evolving faster than northern populations, which retain a primitive color pattern and show less variability in scutellation (Myers, 1967). *Rhadinaea laureata* has a small number of rather stout teeth, probably a specialization that allows it to more effectively hold onto such prey as the lizards *Sceloporus* and *Barisia*, which probably struggle vigorously before being eaten. The hemipenes of *flavilata* and *laureata* have a basal naked pocket, a primitive character that I regard as indicating probable relationship to an ancestral *godmani* group; the hemipenes otherwise have been greatly modified through loss of bilobation and by a shortening of one of the branches of the sulcus spermaticus. Although the basal pocket on the hemipenes seems to be an important clue to the derivation of the *flavilata* from the *godmani*

group, few other signs of relationship have been retained, unless the presence or absence of a subpreocular scale be so construed. The subpreocular is absent in the *godmani* group and appears only as a rare aberration in the *flavilata* group, although it is normally present in other northern *Rhadinaea* (*decorata* and *taeniata* groups). The two species of the *flavilata* group are widely separated geographically, and in between there is a segment of the *decorata* group in eastern Mexico. Thus, *R. flavilata* and *R. laureata* are peripheral relicts of a once widespread group that probably originated in Mexico, from a *godmani*-group ancestor, and which has been largely replaced by the modern *decorata* and *taeniata* groups.

THE *taeniata* AND *decorata* GROUPS: These are strictly Mexican in their distribution, except for one species (*R. decorata*) that ranges from Mexico to South America. The two groups are sufficiently similar (table 3) to suppose that they came from common stock. The hemipenis lacks a basal naked pocket and so has been simplified even more than in the *flavilata* group (table 2). Although no conclusive evidence remains of the ancestry of the *decorata* and *taeniata* groups, I am inclined to believe that their genetic predecessor was in the *flavilata* group, which has now been largely replaced by the more modern derivatives. Individuals of both the *decorata* and *taeniata* groups invariably have a pale postocular marking in the upper temporal region, in most cases in the form of a continuous stripe from the eye to the body. This characteristic would likely have been inherited from the *flavilata*-group ancestor, in which such a marking was a major departure from the condition in the primitive *godmani* group.

The *taeniata* group contains three species. *Rhadinaea fulvivittis* and the geographically restricted *R. omiltemana* are closely related, with the latter probably being a remnant of a once broadly distributed snake that gave rise to *fulvivittis*, which is the derived form as indicated by a reduced number of temporal plates and its peculiarly dark-edged stripes. *Rhadinaea fulvivittis* also is the smallest species in the *taeniata* group, in which large size is perhaps a primitive feature. *Rhadinaea taeniata* attains a larger size than any other species in the genus and consists of two strikingly different subspecies, which evolved in isolation and nearly attained the status of separate species before reapproaching one another in limited zones of secondary hybridization (map 9). There is no question but that the brown-striped *R. t. taeniata* is the most primitive of the two forms; it occurs entirely north of the arid basin of the Río Balsas drainage. The black and white *R. t. aemula*, which occurs mainly south of the Balsas, looks like no other *Rhadinaea* and possibly evolved as a mimic of *Coniophanes piceivittis* (see taxonomic account).

There are 11 species in the *decorata* group, whose center of evolution has been in the mountains of eastern and southern Mexico, although there is one widespread species in western Mexico and another ranges from Mexico to Ecuador. One series of four species (*Rhadinaea montana*, *gaigeae*, *quinquelineata*, and *forbesi*) forms an obviously natural subgroup that is defined by a tendency for a relatively high number of ventrals and especially by aspects of color pattern, including tendencies for a pale streak on each side of a distinct vertebral dark line and for a short white line on the nape of the neck. The species in this subgroup form a linear series (map 7) and presumably originated by fragmentation of a single stock that had dispersed northward along the Sierra Madre Oriental. *Rhadinaea forbesi* is the southernmost member of this series of snakes, and seemingly the most primitive one; it has a white line on the nape followed by a usually distinct vertebral dark line, but in other aspects of pattern (see below), and in numbers of ventrals, *forbesi* resembles the remaining species of the *decorata* group.

The seven remaining species form a complex in which relationships are difficult to seek, although there seems to be a general tendency toward darkening of the sides (as in *forbesi*) and toward interruption and loss of the vertebral dark line (as also occurs in occasional specimens of *forbesi*). Four highland members of the *decorata* group seem interrelated, but in a puzzling way: One species, *Rhadinaea macdougalli*, shows an approach to the *montana–forbesi* series in that some individuals have a barely discernible white line on the nape, but in general color pattern *macdougalli* also approaches the geographically adjacent *bogertorum*. *Rhadinaea bogertorum* and *R. macdougalli* differ significantly in number of maxillary teeth (see discussion under Taxonomic Characters and Methodology), number of ventrals, and in habitus and size. In the characters just mentioned, *macdougalli* seems to show closest affinity to the geographically distant *marcellae*, but the latter differs in color

pattern of head and neck and stands alone in the group by virtue of the large number of spines on the hemipenis. In a similar manner, *bogertorum* greatly resembles *myersi* in color pattern and habitus, but, in addition to having fewer ventrals, *myersi* differs significantly in hemipenial morphology. The four species just discussed are known from only nine specimens, and it is hoped that additional material and discovery of new populations will clarify their relationships. *Rhadinaea marcellae* occurs in the Sierra Madre Oriental, but the others live in the highlands of Oaxaca. Some or all are probably cloud-forest relicts and it seems unlikely that any has a large range, although *macdougalli* occurs on both sides of the plains of Tehuantepec. *Rhadinaea bogertorum* was possibly isolated at the same time as two recently discovered, monotypic genera of snakes that occur in the same region—*Exiloboa* Bogert and *Cryophis* Bogert and Duellman.

Three remaining species of the *decorata* group are each distinct and apparently without close living relatives. *Rhadinaea cuneata* has a distinctive head and neck pattern, the wedge-shaped postocular marking being reminiscent of the head pattern of an unrelated Brazilian species (compare figs. 10F and 45F). The probable method of evolution of the *cuneata* pattern may be visualized by comparing it (fig. 10F) with one of the pattern types of *hesperia* (fig. 10G, upper). The *cuneata* pattern would be produced simply by expansion of part of the postocular line of *hesperia* and expansion of the ocellus on the side of the neck of *hesperia*. In fact, the pale neck markings of *cuneata* are nearly matched in an aberrant specimen of *hesperia* that has an expanded, broken collar rather than ocelli (KU 73619, a juvenile). These similarities are only mentioned to illustrate a point, not to suggest derivation of *cuneata* from *hesperia*. *Rhadinaea hesperia* and *R. decorata* share the feature of having the lateral dark line primarily on the fifth row of scales, rather than on the fourth as in other species of the *decorata* group, but I am uncertain whether to give much weight to this similarity. *Rhadinaea hesperia* is the only member of the *decorata* group in western Mexico, and lack of competition with other small congeners might explain its broad distribution. *Rhadinaea decorata* is the most successful member of the genus if range size and relative abundance are used as criteria of success. It is found from San Luis Potosí to northwestern Ecuador, a distribution made possible by its adaptability to lowland and foothill situations; no other member of the *decorata* group, except possibly the sympatric *cuneata*, is a primarily lowland snake. *Rhadinaea decorata* dispersed from the north to the south, evolving a distinctive head pattern of ocelli from a primitive temporal stripe that is still retained in the variational repertory of southern populations. Response of this species to unknown selective forces also added a new character to the genus, namely keeled scales, which are possibly homologous with the anal ridges that occur in most species of *Rhadinaea*. Another measure of the adaptability of *decorata* is the extraordinary geographic variation shown by the hemipenis (fig. 16), one of the most extreme cases of intraspecific variation yet documented for this usually conservative organ. I presume that the long slender hemipenis represents the derived state in *decorata*, because the organ is relatively short and bulbous in other members of the species group.

Perusal of range maps 4–9 indicates that montane pine-oak forest has provided the primary dispersal route of most species of Mexican *Rhadinaea*. Although not shown on range maps 10 and 11, this habitat also appears to have been crucial to dispersal of the primitive *godmani* group in Nuclear Central America. But, extension of the genus into lower Central America and South America has necessitated complete adaptation to tropical broadleaf forests. Therefore it is scarcely surprising to find southern assemblages of species that differ greatly from the northern groups, even though it seems impossible to judge the relative importance of environmental selection versus the element of chance in the evolution of genotypes. I shall now attempt to decipher clues to the relationships of the *calligaster* and *vermiculaticeps* groups of lower Central America, the *lateristriga* group of lower Central America and northern South America, and the strictly South American *brevirostris* group.

THE *calligaster* GROUP: *Rhadinaea calligaster* is one of the most divergent members of the genus and forms a "group" by itself. It is endemic to the montane rain forests of Costa Rica and western Panama, and exhibits remarkable intrapopulational variation in color pattern. The hemipenis is primitively bilobed, but spinules on the calyces, and capitation, have been lost. I am

not wholly convinced that the affinities of *calligaster* do not lie elsewhere (see p. 237), but the species conceivably might have been derived from some element of the ancestral *godmani* group and subsequently evolved nearly beyond recognition as a *Rhadinaea*. Aside from the bifurcated hemipenis, *calligaster* lacks a subpreocular and some individuals have a pale bar from the lower edge of the eye to the corner of the mouth, such as occurs in most modern species of the *godmani* group. I have nothing to add to my remarks in the taxonomic section about the curious resemblance of *calligaster* and some specimens of the unrelated *Rhadinaea decipiens* (*lateristriga* group), which occur in the same region; but, it seems a possibility that one or both species is affecting the evolution of the other in some way yet to be ascertained.

THE *vermiculaticeps* GROUP: There are three allopatric species, which occur from northern Costa Rica to central Panama. *Rhadinaea vermiculaticeps* is found west of the present-day Panama Canal, and *R. sargenti* lives in the hills to the east. These two species are closely related, and *sargenti* probably evolved from a *vermiculaticeps* ancestor whose east-west distribution had been broken at the structural depression in central Panama. They are nearly identical in all features except color pattern of the trunk; *sargenti* has evolved uniformly dark sides, but the characteristic dorsal pattern of *vermiculaticeps* remains faintly discernible. *Rhadinaea pulveriventris* differs little from *vermiculaticeps* and *sargenti* except in color pattern, which gives it a totally different appearance. But close attention to the pattern on the head and nape of *pulveriventris* reveals derivation from a *vermiculaticeps*-type ancestor through simple loss of pattern; especially instructive is a feature not present on all specimens of *pulveriventris*, namely a pale vertebral streak in the remnant of the middorsal black stripe on the neck. Although color pattern demonstrates interspecific relationships within the *vermiculaticeps* group, it seems to provide no clues to the ancestry of the group. These snakes resemble members of the *decorata* group in color pattern and habitus, but the hemipenis (unknown for *pulveriventris*) indicates almost certain relationship with the *godmani* group. Not only has there been retention of the primitive basal pocket, but the hemipenes of *vermiculaticeps* and *sargenti* bear remarkable resemblance to the tiny organ of *Rhadinaea schistosa* (compare figs. 30G and 39), the most northern representative of the *godmani* group and the smallest snake in the genus. The basic structure of the hemipenis is identical in these divergent snakes, even to the presence of virtually straight spines that were once thought to characterize the monotypic genus *Rhadinella* (=*Rhadinaea*) in which *schistosa* was first placed. Bilobation of the hemipenis has been lost in *schistosa* as well as in the *vermiculaticeps* group, but *schistosa* still retains the split insertion of the retractor muscle. In the *vermiculaticeps* group, the spinules on the capitulum of the hemipenis have been replaced by soft papillae, but this seems a minor change, involving only loss of a regional ossification process during ontogeny, and does not alter the appearance of the organ. Despite differences in all other features, I cannot believe that the hemipenial correspondence seen here is fortuitous. The hemipenis of *schistosa* is a bit more primitive in retaining a split retractor insertion, and spinules on the capitulum, but this diminutive snake is too specialized to represent an ancestral form. I think that the northern *Rhadinaea schistosa* and the species of the southern *vermiculaticeps* group are of common descent from a section of the old *godmani* group once widely distributed in Middle America, but now extinct or modified beyond recognition.

THE *lateristriga* GROUP: In this group we find seven species, or possibly eight including one puzzling Costa Rican specimen assigned as *species inquirenda*. There are five central American species, two of which extend also into South America, and three additional species are confined to South America. This is a taxonomically difficult assemblage, and I might as well state at the outset that I have only the most tentative idea as to its origin; indeed, it might be easier to show an ancestral-descendent relationship with the specialized genus *Pliocercus* (see Intergeneric Relationships) than to convincingly demonstrate the nature of the relationship of the *lateristriga* group with the other species groups of *Rhadinaea*. A distal asulcate pocket on the hemipenis is characteristic of the group; a similar pocket occurs at least in one other species of the genus (table 2), but could have arisen independently by simple enlargement of one of the calyces. The pocket in the *lateristriga* group is formed either by an enlarged calyx or as a space within a double fusion of the edge of the capitulum and underlying stalk, with the latter condition probably being derived from the former. A tendency

for enlargement of specific calyces also occurs in certain species of the *godmani* group (see fig. 30B for example), and might well be an indication of relationship. But I hesitate to consider this feature as a definite sign of relationship between groups without additional, supporting data.

The lateral white lines in the *lateristriga* group are a new feature, and the absence of the lines in a few species is probably due to secondary loss rather than to primitiveness of pattern. The most primitive color pattern in the group is probably displayed by *Rhadinaea multilineata*, a species endemic to the Cordillera de la Costa of Venezuela. The body pattern of *multilineata* (fig. 41C) is not greatly different from that of some species in other groups, except for the discrete white line on the first scale row, and there is a continuous pale stripe from the eye to the body. The closest relatives of *multilineata* are *R. lateristriga*, a widespread Andean species that shows considerable variation in color pattern, and *R. guentheri*, a species confined to the highlands and certain wet lowlands of Costa Rica and western Panama. I have no doubt that all three species are descended from a single progenitor, as there are many points of similarity, such as the vague pattern atop the snouts, the short white line or ocellus on the napes of at least some individuals in each species, the overall similarity of the hemipenes, and the low number of maxillary teeth. The ancestral species probably had a color pattern similar to that of *multilineata*, with the patterns of *guentheri* and *lateristriga* being derived by fragmentation or restriction of the temporal stripe, narrowing or loss of the dorsolateral stripe, and a general intensification of the dorsal ground color. All three species have tended to retain a vague but distinctive pattern of interconnecting tan markings on top of the snout; a distinctive, narrow collar has been developed in southern populations of *lateristriga*. The hemipenes are similar, but dissection of the retracted organs shows that the asulcate fold is doubled in *lateristriga* and *multilineata*, but single in *guentheri* (compare fig. 42B and 42C).

The maxillary shape (fig. 44) and dental pattern, including a low number of prediastemal teeth, are similar and indicative of relationship in the *guentheri–lateristriga–multilineata* series, but there are a few significant points of divergence to consider. There has evidently been stronger selection for a low number of prediastemal teeth in *lateristriga* and *multilineata* than in *guentheri*; no variation at all has been noted in the first two species, whereas the small sample of *guentheri* exhibits normal variation (table 17). But *R. guentheri* is unique in the genus in that there are shallow grooves on the posterior fangs of most, although not all, individuals. I suggest that this species represents an initial stage in the evolution of opisthoglyphy, and that the grooves are a new and advanced feature within the genus *Rhadinaea*. Underwood (1967a, pp. 127, 128) correctly recognized that the aglyphous *Rhadinaea* is related to the opisthoglyphous *Coniophanes* (which I believe evolved from a stock of *Rhadinaea*). Consequently, notice should be taken of Underwood's view (*op. cit.*, p. 22) that, "The majority of the Dipsadidae, Natricidae and Colubridae are aglyphous *and, I believe, secondarily so*." (Italics mine.) Underwood is evidently suggesting that in a large number of snakes, possibly including *Rhadinaea*, the ungrooved teeth are an advanced condition derived from primitively grooved fangs—which, presumably, must have been once derived from even more primitively ungrooved teeth—thus bringing us full circle. Such large-scale reversal of evolution would indeed be extraordinary and I do not believe that it occurred. I can readily conceive that selection for the venom apparatus might be relaxed in isolated cases, in correlation with a more or less complete shift to food for which venom is not needed or is useless (see Bailey, 1966, p. 68, for an example), but it is hard to believe that there could have been such drastic change in the food habits of a "majority" of the groups mentioned by Underwood.[1] Venom is used by some (all?) species of *Rhadinaea* in order to subdue at least some types of prey, and grooves in which to more efficiently channel the venom would not seem likely to be lost once present. I do not concur with Underwood (*op. cit.*, p. 23) that presence and absence of grooves within a single species is necessarily indicative of relaxation of selection pressure. There must also be times when such variation is the result of positive selection increasing the number of grooved-fang variants within populations, and I suggest

[1]The possibility does exist, however, that colubrids might be primitively venomous and that adaptive radiation might have led to loss of venom in ancestors of a few now flourishing groups. But this possibility does not affect my belief that grooved fangs are a derived feature and have been independently evolved in various stocks. The presence of venom would not, and does not, automatically dictate the presence of grooved fangs.

this as an explanation for the intraspecific variation in *Rhadinaea guentheri*.

Rhadinaea decipiens has a disjunct distribution from northern Costa Rica to northern Colombia. Individuals of some populations are remarkably similar to *R. guentheri* in body coloration, and some specimens even resemble the unrelated *R. calligaster* in having midventral dark spots and a dorsal green coloration, as already commented on. But details of the color pattern in some populations, and the hemipenial morphology, reveal that *decipiens* is most closely related to *R. pachyura*. The latter species occurs from Atlantic-side Costa Rica into western Panama, where it is replaced by *R. fulviceps*, a similar species that ranges into the Magdalena Valley of northern Colombia and along the Pacific coast to northwestern Ecuador. A trend toward secondary loss of the white line (on scale row 1) can be traced from the vivid condition in *decipiens*, through an intermediate condition in *pachyura*, to near absence of the line in *fulviceps*. The Costa Rican specimen assigned to *species inquirenda* completely lacks a body pattern, but its relationship seems closer to *decipiens* or *pachyura* than to *fulviceps*. There has been significant hemipenial modification in the *decipiens–pachyura–fulviceps* series. The hemipenes of *decipiens* and *pachyura* are slender and have a relatively small capitulum, whereas *fulviceps* has a stout organ with a relatively large capitulum (compare fig. 42E and 42F), but it is difficult to say which condition is most primitive. The asulcate fold is single in the retracted hemipenis of *fulviceps*, and doubled in the other two species; the condition in *fulviceps* is probably the derived one, because the distal asulcate pocket lies to one side of the single fold, which is an asymmetry that would be expected if half of a double fold were lost without any other change occurring. The double fold characterizes all species except *fulviceps* and *guentheri*, and presumably is the primitive condition for the entire *lateristriga* group. The primitive formula of 1+2 temporal plates characterizes *fulviceps* and *dumerilii*, but other species of the *lateristriga* group normally have 1+1, a derived condition in the genus.

Rhadinaea dumerilii is the only member of the genus known to inhabit the extensive rain forests of the Río San Juan drainage on the Pacific coast of Colombia, although two other primarily lowland species (*R. fulviceps* and *R. decorata*) occur on both sides of that region. *Rhadinaea dumerilii* thus inhabits one of the wettest regions on earth (map 15; a record shown for the Cordillera Central needs to be verified). This little-known snake has the primitive temporal formula of *fulviceps* (see above), with which it shares the tendency for loss of color pattern. Nonetheless, *dumerilii* does not seem close to any other living species of the *lateristriga* group. The muzzle is peculiarly shortened and truncated, and capitation of the hemipenis seems to be lacking; these features suggest that *dumerilii* has embarked on an evolutionary course quite different from other species of its group.

THE *brevirostris* GROUP: This is the most diverse of the species groups of *Rhadinaea*, probably a reflection both of its large range and the absence of sympatric congeners. It is the only group confined to South America; one species is widespread in the Amazon Basin and five others occur south of the Amazonian lowlands. That the group is not larger and even more diverse is likely due to competition from a host of other small South American snakes. It is hard to speak with assurance on the origin of the *brevirostris* group, but hemipenial morphology and the absence of a subpreocular scale are not inconsistent with a possible derivation from the old *godmani* group. There has been a definite tendency toward loss of bilobation of the hemipenis; and one species has an enlarged asulcate calyx on the organ, a condition possibly homologous with the one sometimes occurring in the *godmani* group (table 2). Nevertheless, the present taxonomic position of the *brevirostris* group should be re-evaluated as data become available on the systematics of other groups of South American colubrids, especially those in the alsophiine series (see discussion under Intergeneric Relationships).

The Amazonian *R. brevirostris* is the only *Rhadinaea* in which posterior scale-row reduction (17–17–15) is the rule rather than the exception. There is intraspecific variation in whether the hemipenis is bilobed or single, and some specimens have peculiar, stubby spinules on the asulcate calyces of the capitulum; these features and other similarities of the hemipenes demonstrate the relationship of *R. brevirostris* with *R. occipitalis*, a wide-ranging snake south of the Amazon Basin. *Rhadinaea occipitalis* has acquired a partly blotched pattern, the only *Rhadinaea* so marked, and scale-row reduction has been carried to the generic low of 15–15–15 or 15–15–13.

The head pattern of *occipitalis* is similar to that of some other southern species, whose center of evolution seems to have been in the coastal *serras* of Brazil (the Serra do Mar Refuge, see Müller, 1971). I have seen few specimens of these southern *Rhadinaea*, but *poecilopogon* and *bilineata* obviously form one pair of closely related species, and *affinis* and *persimilis* form another pair. The color patterns of these southernmost *Rhadinaea* are not very different from the patterns of certain northern species of the genus. The head pattern of *poecilopogon*, for example, is similar to the Mexican *laureata*, and the wedge-shaped postocular mark of *affinis* (and occasional *occipitalis*) corresponds to the Mexican *cuneata*; the body patterns are reminiscent of some of those in the northern *decorata* group. Although not precise, these convergences are close enough to be impressive; the hemipenes are different, however, and any direct relationship is extremely unlikely.

INTERGENERIC RELATIONSHIPS

The closest relatives of *Rhadinaea* are doubtless to be found among the New World "xenodontine" snakes. Within this mass of genera which, for the most part, are poorly understood, it seems reasonable that the search be started with those genera that fall in Dowling's (1969, p. 5) group 2, namely those in which there is "a single, capitate, spinose, and calyculate hemipenis with a simple or apically bifurcate sulcus ('dipsadines')." There is considerable diversity among the snakes having this sort of hemipenis. Several genera are highly specialized arboreal snakes modified for a diet of slugs and snails, and are currently placed in their own subfamily (Dipsadinae). Most other genera also seem relatively distant from *Rhadinaea*, but it is probable that in some cases this is an illusion caused by divergence in relatively few features. The long-tailed, terrestrial snakes of the genus *Pliocercus*, for example, show most of the same structural features as *Rhadinaea*, but they are vividly ringed snakes that have evidently adapted to the specialized role of Batesian (or Müllerian?) mimics of *Micrurus* or other poisonous snakes. Despite the different adaptive facies of *Rhadinaea* and *Pliocercus*, I suspect that the latter is a direct offshoot from ancestral stock of the *lateristriga* group of *Rhadinaea* (fig. 51). Boulenger (1894b) was close to this idea when he placed *lateristriga* and *dumerilii* in the same genus (*Urotheca*) with species now referred to *Pliocercus*. The resemblance that probably impressed Boulenger, in addition to scutellation, is the extremely long and disproportionately thick tail. As confirmation that the aforesaid is indeed a character of relationship, I would note that the everted hemipenis of *Pliocercus euryzonus* has a well-defined "pocket" at the asulcate edge of the capitulum. Such a pocket characterizes the *lateristriga* group of *Rhadinaea*, and the hemipenis of *Pliocercus euryzonus* is in fact very similar in appearance to that of *lateristriga* itself. More detailed studies must be made of *Pliocercus* before this relationship can be elaborated. I should not be surprised if other genera as distinct as *Pliocercus* are similarly linked to the rather generalized *Rhadinaea*, but at this time I can point to only two others—*Coniophanes* and *Trimetopon*—that I think are closely related to *Rhadinaea* (fig. 51).

Coniophanes is a genus of small, striped snakes that are frequently confused with rhadinaeas. *Coniophanes* seems to differ from *Rhadinaea* in only two consistent features. All species of *Coniophanes* are characterized by deeply grooved fangs and by posterior reduction in number of dorsal scale rows. Some individuals of *Rhadinaea guentheri* have shallow grooves on the enlarged maxillary teeth, and scale-row reduction occurs in several species of *Rhadinaea*, although consistently only in *R. brevirostris*. These features seem to be independent developments unrelated to the situation in *Coniophanes*. I discussed in the previous section my reason for believing the grooved fangs of *R. guentheri* to be a new development. Concerning scale-row reduction, it probably is significant that reduction in *Coniophanes* normally involves the paravertebral rows, rarely the third lateral rows (*fide* Bailey, 1939), whereas in the *brevirostris* group of *Rhadinaea* the reduction involves only lateral rows. Paravertebral reduction even holds true for the recently described *Coniophanes joanae* (see Myers, 1969a), which otherwise resembles *Rhadinaea brevirostris* in having 17–17–15 scale rows and a similar habitus and color pattern. Changes involving the paravertebrals have been noted in occasional specimens of *R. godmani*, but reduction in that species is decidedly aberrant and inconsistent, and also occurs by changes in lateral rows. Reduction also occurs in occasional specimens of *R. hempsteadae*, a close relative of *godmani*, but only changes involving the lateral rows have been noted.

Coniophanes is an ecological replacement of *Rhadinaea*, occurring generally at lower elevations and in less humid, even semiarid, environments.[1] For example, *Rhadinaea* is replaced completely in such areas as the coastal plain of northeastern Mexico (*C. imperialis*), the Yucatan Peninsula (several spp., see McCoy, 1969), and in the Pacific lowlands from southern Guerrero to the Guanacaste region of northwestern Costa Rica (*C. piceivittis*). Relatively few *Rhadinaea* occur at low elevations, and none seems adapted to habitats in regions of dry climates. On the other hand, some *Coniophanes* (*bipunctatus*, *quinquevittatus*) live in marsh and swamp-forest situations, another class of habitats avoided by *Rhadinaea*. One species, *Coniophanes fissidens*, is a wide-ranging forest snake and occurs at some of the same places (in mesic forest) as *Rhadinaea decorata*, *R. fulviceps*, and probably *R. pachyura*. *Coniophanes joanae* is another inhabitant of mesic forest and possibly occurs sympatrically with one or more species of *Rhadinaea* (*sargenti*, *decorata*), but *C. joanae* has a limited distribution in the low mountains of eastern Panama. Bailey (1939, p. 6) considered *fissidens* as the most generalized species of *Coniophanes* and suggested that it was also closest to the ancestral members (but see below).

It seems probable that *Coniophanes* is a direct offshoot of some early stock of *Rhadinaea*. *Coniophanes* became the more specialized group in its invasion of subhumid or semiaquatic environments, and more advanced in its acquisition of grooves on the enlarged maxillary teeth. The reduction in posterior scale rows was perhaps an adaptation or preadaptation which caused slight alteration in body shape that was somehow advantageous in the new environments; but it may be that *Coniophanes* is less departed from the ancestral condition in this regard than *Rhadinaea*, which might have become specialized through loss of reduction. *Coniophanes* presumably arose in Nuclear Central America or in Mexico, where most species are found today. The two southernmost species of *Coniophanes*, *C. joanae* in Panama and *C. dromiciformis* in Ecuador, are related to each other and are regarded as relicts of an ancestral stock that at one time was more widespread (Myers, 1969a, p. 26). Three other species occur in lower Central America, but they are widely distributed forms which are also found in Mexico, and it seems more likely that they have dispersed southward than vice versa. In other words, the present geographical distribution of the greatest number of species favors a northern origin of *Coniophanes*. It also is suggestive that the most primitive species of *Rhadinaea* are clustered in Nuclear Central America.

Coniophanes is a diverse assemblage and as such cannot be directly related to any single group of *Rhadinaea* species now extant. It seems a reasonable assumption that the ancestral form had at least 19 rows of scales and possibly as many as 25. The range in number of anterior (i.e., before reduction) dorsal scales is 17 to 25 in *Coniophanes*, with all but two species having 19 or more. The two exceptions are *C. joanae* and *C. meridanus*, which seem to be reduced derivatives; *joanae* and *meridanus* are not closely related to each other, and each has a relative that is characterized by 19 rows of scales. In *Rhadinaea*, on the other hand, 17 scale rows is the common number, and is consistent in 89 percent of all species; a higher number is found only in the primitive *godmani* group, in which three species have 19 rows and one species has 21 rows. Differences in color pattern and, especially, the primitive dentition removes the *godmani* group from any consideration of direct-line ancestry with *Coniophanes*, but it is tempting to speculate that both are derived from the same or a similar stock. In addition to presumably primitive features of dentition and (in some species) high number of scale rows, the *godmani* group also is characterized by a primitively bilobed hemipenis. At least weak bilobation of the hemipenis occurs in members of all except the *fissidens* and *lateritius* groups of *Coniophanes* (Bailey, 1939, p. 7; Myers, 1969a). In searching for the most nearly primitive group of existing species of *Coniophanes*, we can safely discard the *imperialis* assemblage, whose members obviously are highly specialized in having lost the spines and capitation of the hemipenis. Bilobation has been nearly lost in the *bipunctatus* group but is still weakly indicated in at least some specimens of *C. bipunctatus* (*fide* Myers, 1969a); the bold ventral spotting and semiaquatic habits of the two species of the *bipunctatus* group indicate specialization rather than retention of primitive features. The *dromiciformis* group is perhaps related to the *bipunctatus* group (Myers, 1969a); the southern, relict distribution

[1] I refer to major vegetational zones in the drier climatic regions, and make no inference regarding degree of moisture in the microhabitats of *Coniophanes*.

of the two species comprising the *dromiciformis* group indicates that they could be remnants of an ancient stock that gave rise to other modern forms (e.g., species of the *bipunctatus* group). A case could be made that the white postocular bar (extending obliquely from eye to mouth) of *dromiciformis* and *joanae* is a primitive feature that today is retained also in the *godmani* group of *Rhadinaea*. But such markings probably have adaptive value as disruptive coloration and might be independently derived in these genera, and, in any case, the reduced number of dorsal scale rows in *joanae* almost certainly is a new development. The *piceivittis* group of *Coniophanes* is characterized by what may be a modern and specialized color pattern. But, in addition to a primitively bilobed hemipenis, the species of the *piceivittis* group also have the highest number of scale rows (23, 25) in the genus. Might this not be the most primitive group of *Coniophanes* still extant, at least in number of dorsal scale rows? If so, it implies that the ancestors of *Rhadinaea* had more scale rows than now found in the genus, in which *R. godmani* has the highest number (21).

Bailey (1939, pp. 6–11) came to a different conclusion from the one suggested above. He thought that the *piceivittis* group was morphologically the furthest removed from the ancestral stock of *Coniophanes*, and that the *fissidens* group was closest in being most generalized and in having the most primitive hemipenis. But I believe that the bilobed hemipenis is primitive and the single organ derived, for reasons given at the beginning of the evolutionary discussion. The nonbilobate hemipenis of *C. fissidens* is somewhat like those seen in the *decorata* group of *Rhadinaea*, in that the organ is relatively short and the capitulum comprises about half of the total length.[1] Furthermore, the hemipenis of *C. fissidens* has an especial resemblance to that of *R. decorata* in that the free edge of the capitulum is virtually fused to the stalk in the middle of the asulcate side (compare fig. 12A [*R. decorata*] with Myers, 1969a, fig. 4B [*C. fissidens*]; see Bailey, 1939, fig. 1, for a view of the sulcate side of the hemipenis of *C. fissidens*). I agree with Bailey that *Coniophanes fissidens* is a "generalized" species, but in the sense of being simplified rather than primitive. Both it and *Rhadinaea decorata* strike me as modern snakes that have undergone parallel evolution of the hemipenis. Loss of bilobation and/or a tendency for partial or even complete fusion of the capitulum to the stalk has occurred in the hemipenis in several groups of *Rhadinaea*, and I see no reason why a similar event should not occur independently in the derived *Coniophanes*. There is geographic variation in the dorsal-scale formula of *C. fissidens*. Because I think that the evolutionary trend has been toward reduction in number of scale rows, it seems likely that the *fissidens* populations characterized by 21 rows are most primitive in at least this one respect. Bailey (1939, p. 9) believed populations of 19 scale-row snakes to be most primitive, but, as noted elsewhere (Myers, 1969a, p. 25), Bailey's views were influenced by an erroneous locality datum and the mistaken impression that phylogenetic significance should be accorded to high numbers of ventrals in an insular population. It may be noted in passing that *Rhadinaea decorata* and *Coniophanes fissidens* are among the most successful members of their respective genera, if abundance and large geographic range are used as criteria of success. Each species occupies the largest range in its genus, and, in fact, their distributions are nearly identical, except that *C. fissidens* occurs in some areas (especially parts of the Pacific lowlands) that are unoccupied by *R. decorata*.

Trimetopon (*sensu stricto*) is comprised of six species of diminutive snakes that are found only in Costa Rica and Panama. They form a natural unit which I think was derived from an ancestor close to the *godmani* group of *Rhadinaea*. Evidence of that ancestry is seen in the color pattern of the head and in the maxillary dentition. Some species have the hemipenis primitively bilobed, but in others the organ is single. *Trimetopon* exhibits trends toward small size and *Tantilla*-like habitus, fusion of certain head plates, and, on the hemipenis, loss of calyces, loss of bilobation, and loss of capitation. Some of these trends are seen also in other diminutive species herein placed in the *godmani* group of *Rhadinaea* but formerly in *Trimetopon* or *Rhadinella* (see discussion in the taxonomic section, under The *godmani* Group). Thus, bilobation of the hemipenis has been lost in *veraepacis* (=*kinkelini*) and *schistosa*, and capitation of the hemipenis has been reduced in *pilonaorum*. Despite somewhat similar

[1]*Rhadinaea decorata* shows considerable geographic variation, and in some populations the capitulum comprises only a small part of the total length of the organ on account of a greatly elongated base (fig. 16). *Rhadinaea myersi*, also of the *decorata* group, has a shortened capitulum.

evolutionary trends, these small snakes seem to represent phylogenetic lines separate from the more southern *Trimetopon*, albeit the latter is also allied with the *godmani* group. The genus *Trimetopon* as here restricted is treated more fully elsewhere (Myers, MS).

No relationship is seen between *Rhadinaea* and members of the South American *Liophis–Leimadophis–Lygophis* complex, although these groups have been confused in the past.[1] The *Liophis* hemipenis is entirely different (disked, distally spinose and acalyculate; e.g., see Gans, 1964, figs. 2, 3). Also, completely different color patterns occur in many species of the *Liophis* complex, namely dorsal crossbands, anterior blotching-posterior striping, and dark-checkered venters. *Rhadinaea occipitalis* is somewhat convergent with *Leimadophis* in having dark blotches anteriorly and an indication of posterior stripes, but the overall aspect of *R. occipitalis* is different, as it is a more slender snake with a relatively light ground color and a pale canthal-temporal line. Also, *R. occipitalis* lacks the loose skin ("hood") of the neck, which species of *Leimadophis* spread in a defense display.

No firm relationship presently can be traced between *Rhadinaea* and other groups of Neotropical colubrids. Such genera as *Alsophis* and *Philodryas*, however, may be distantly related: They have a usually bilobed hemipenis, with the lobes partly calyculate but not contained within a single capitulum. Capitation, if present, is separately confined to the tip of each lobe on the asulcate side. Most of the asulcate side of each lobe is either nude or sparsely spinose, and the calyculate region is confined mainly to the sulcate side. A good idea of the shape of such a hemipenis when everted may be gained from Vellard's (1946, figs. 6–8) illustrations for *Cyclagras gigas*; an idea of the appearance of this kind of hemipenis when retracted may be had from illustrations given by Myers (1969b, 1973) for *Saphenophis boursieri* and *S. tristriatus*. This kind of hemipenis conveniently can be referred to as the alsophiine type.[2] I have suggested elsewhere (Myers, 1973) that the alsophiine hemipenis is more primitive than the single-head type of organ found in *Rhadinaea*. A gradual shortening of the lobes of the alsophiine hemipenis, with a basad retreat and gradual union of the two calyculate areas, could have resulted in the primitive *Rhadinaea* type of hemipenis, which, although slightly bilobed, has the calyces contained in a single head. Continuation of this trend would have resulted in the more derived hemipenes of *Rhadinaea*, in which all traces of bilobation have disappeared from the organ, even including loss of the split insertion of the major retractor muscle. Capitation was elaborated in some stocks of *Rhadinaea* (e.g., the *decorata* group) and lost or but weakly developed in others (e.g., the *calligaster* and *brevirostris* groups). Therefore, the ultimate ancestry of *Rhadinaea* is possibly to be sought within some former alsophiine stock. The possibility should also be kept in mind that the *brevirostris* group might have been independently evolved from alsophiine ancestry—although reasonably conclusive evidence should be presented by anyone wishing to remove that group from *Rhadinaea*. In the *affinis–persimilis–poecilopogon* series of the *brevirostris* group, calyces have been lost (if ever present) on the asulcate side of the retracted hemipenis, and capitation is indicated by no more than a slight distal overhang. The hemipenis of these species is single, but a slight division in the retractor insertion is evidence of derivation from the bilobed condition. Although I have not seen an everted hemipenis from the *affinis–persimilis–poecilopogon* series, I suspect that it would resemble a single lobe of an alsophiine hemipenis. And, it should be noted that hemipenial bilobation may be essentially lost even within a single alsophiine genus, as shown by Vellard's (1946, fig. 14) illustration for *Philodryas psammophideus*. However, I am presently inclined

[1]Nonetheless, there presently are species erroneously assigned to *Liophis*, and at least some may prove related to *Rhadinaea*. My knowledge of these undefined groups is sketchy at present, and further discussion must wait another time.

[2]Herndon G. Dowling suggested this term to me. Dowling (1969, p. 5) previously had referred to this as the "dromicine" type, but, as shown by Maglio (1970, p. 30), the hemipenis of *Coluber cursor* (type species of *Dromicus*, designated by Smith and Grant, 1958b, p. 216) is of the *Liophis* type. *Dromicus cursor* is, according to Maglio, congeneric with the group usually called *Leimadophis*. Smith and Grant's (*loc. cit*) preoccupation with details of nomenclature, to the exclusion of biological considerations, seems to have insured that (according to the Law of Priority) the well-known name *Leimadophis* must be replaced by *Dromicus*. To be sure, the latter name is equally well known, but usually it is applied to small West Indian colubrids that are unrelated to *Leimadophis*, which is a distinctive South American group that barely enters the West Indies. Conservation of the name *Leimadophis* is desirable.

to think that any such resemblances between alsophiine and *brevirostris*-group hemipenes are the result of convergence rather than direct relationship. One important difference that is useful (but not infallible) in identifying phyletic lines is the site of bifurcation of the sulcus spermaticus. In *Rhadinaea* and its relatives the sulcus usually branches at least halfway toward the apex of the hemipenis, close to or actually in the calyculate area, whereas in the alsophiine type the sulcus forks usually well below the halfway point, in some cases quite close to the base (as in Vellard's illustration, *loc. cit.*).

Maglio (1970) recently suggested *Rhadinaea* as a close relative of the West Indian *Arrhyton* and postulated a common ancestry for the two genera. I have given the West Indian species cursory attention but have not arrived at a definite opinion on the matter, although Maglio (*op. cit.*, p. 43) has possibly provided a real clue to the affinities of the enigmatic *Rhadinaea calligaster* (see p. 230). A thorough review of *Arrhyton* (*sensu* Maglio) is in order, particularly in respect to the remarkable hemipenial variation of that group. A study of osteological variation among the species groups of *Rhadinaea* would also help in evaluating Maglio's conclusions.

THE TIME FACTOR

The foregoing conclusions about intrageneric and intergeneric relationships and evolution are based on inferences from study of Recent genera and species. Can the supposed evolutionary events be placed with any confidence within the framework of the geological time scale? No.

In discussing the evolution of modern Neotropical colubrids, there has been some tendency to start events as far back in time as possible—in the Miocene for example (Duellman, 1958; Wilson and Meyer, 1971)—thus ignoring the largely archaic nature of the pre-Pliocene snake fauna in North America and elsewhere (Gilmore, 1938; Auffenberg, 1963; Hoffstetter, 1962). Although extinct species of a few modern colubrid genera were present in North America during the Miocene–Pliocene transition (Holman, 1964), if not before, the colubrid genera take on a recognizable aspect mainly in the Pliocene (some extinct genera, but also still-living species of modern groups) and Pleistocene (many living species), as indicated in Gilmore (1938), and shown more conclusively by Auffenberg (1963) and Gehlbach (1965). It seems unnecessary to go back farther than the Pliocene to account for the origin of most living species of colubrids. Some modern colubrid genera of the New World doubtlessly had their origin in pre-Pliocene time, and it might reasonably be supposed that certain ancestral stocks were even present in Middle America by early Miocene (Tihen, 1964, pp. 272, 273). Savage (1966, p. 744), however, carried antiquarianism to an extreme in pushing the ancestry of certain modern snakes (including *Rhadinaea*) back to the Eocene—long before the first known fossil occurrence of the family anywhere. In a major survey of the history of the Central American herpetofauna, Savage (*loc. cit.*) theorized that: "During Eocene . . . the [Nuclear Central American] peninsula was dominated by the evolving groups of the Middle American Element, including all of the modern genera of this unit or their ancestors (Table 6 [which includes 28 genera of living colubrids])." So far as colubrids are concerned, I do not accept the idea that modern genera or their immediate ancestors were present in the Central American Eocene. In fact, given the known albeit fragmentary history of the higher snakes, the existence of *any* kind of colubrid in Central America during the Eocene can be questioned. Also, the classic idea of a long tertiary evolution of colubrids isolated in South America (Dunn, 1931b; Savage, 1966) must be re-examined carefully in view of the suggestion that colubrids might be late arrivals in the southern continent (Hoffstetter, 1967). One is always admonished not to build zoogeographical theories on negative fossil evidence, but neither can such "evidence" always be ignored.

There is no direct evidence concerning the time of origin of *Rhadinaea*, but (for what it is worth) I doubt that the genus appeared before the Pliocene, or late Miocene at the very earliest. Auffenberg (1958, p. 12) saw a few resemblances between vertebrae of *Rhadinaea* and the Upper Miocene (Montana) *Dryinoides*, but there were no indications of particularly close relationship. Genera that I believe to be derived from rhadinoid stock probably originated later, rather than at the same time as *Rhadinaea*; this is suggested by still existing overlap in generic characteristics.

The *godmani* group is possibly a direct lineage from the ancestral stock of *Rhadinaea*, but other groups may not have originated until well into

the Pliocene or later. Some of the living species of *Rhadinaea* may date from the Pliocene, but I think that many species, especially those that are but weakly differentiated, did not come into being until the Pleistocene. The present distributions of the species are principally the result of climatic-related events in the Quaternary. Humid, subtropical forest was of greater horizontal extent during cool glacial maxima, and occurred even on low mountains that now have a largely tropical aspect. Montane species of *Rhadinaea* thus had potentially larger ranges than is possible today, and a few (especially *Rhadinaea godmani*) even crossed such barriers as the plains of Tehuantepec and the Nicaraguan Depression. Such barriers were less formidable then because of the closer proximity of patches of humid montane forest and the presence of intervening humid lowland forest. Interglacial and postglacial contractions of montane forest provided ample opportunity for isolation and speciation, thus leading to disjunct distributions of individual species (as seen today in *R. decipiens* and *R. godmani* for example) and ultimately to the diversity of species in the various groups, especially the *decorata*, *godmani*, and *lateristriga* groups. Lowland species of *Rhadinaea*, although fewer in number, were affected by lowered sea levels and spread of lowland humid forest during glacial maxima, and by subsequent restriction and fragmentation of this habitat at the end of glacial episodes. Tropical montane and lowland species of *Rhadinaea* were isolated in suitable refuges during arid periods of interglacial times, and one extratropical species (*R. flavilata*, Myers, 1967) was probably similarly isolated in a Floridian refuge during the height of northern continental glaciation.

In closing, I wish to reiterate my belief that many evolutionary events in the genus are fairly recent. The profound climatic vicissitudes and consequent biotic changes in the South American Quaternary are becoming known (Haffer, 1967a, 1967b, 1969, 1970; van der Hammen, 1961; Vuilleumier, 1971), and it is increasingly clear that we must finally reject the speculative notion of historically stable ecosystems in the New World tropics.

SUMMARY OF TAXONOMIC CHANGES

THERE ARE ONLY A FEW generic names that are strictly synonymous with *Rhadinaea*. The reason for this is that the species of *Rhadinaea* are sufficiently generalized to have permitted their misassignment to a wide variety of named genera, as is obvious from a glance at the generic synonymy on pages 16–17. The rediscovery of *Calamaria dumerilii* is reported; it was originally thought to be a Cuban species and is the type of the name *Urotheca*. The species is a distinct South American member of the *lateristriga* group, thus confirming Dunn's suggestion that the name *Rhadinaea* Cope, 1863, is a junior synonym of *Urotheca* Bibron, "1843" [184–?]. However, the name *Rhadinaea* is retained in the interest of nomenclatural stability, pending application for conservation by the International Commission on Zoological Nomenclature.[1] The names *Taeniophallus* Cope, 1895, and *Rhadinella* Smith, 1941, are considered to be junior subjective synonyms of *Rhadinaea*, and the emendation *Rhadinea* Garman, 1883, is a junior objective synonym. *Taeniophallus*, however, is a complex case and its validation as a synonym of *Rhadinaea* will require designation of a type species (*Rhadinaea brevirostris*) by the International Commission.

Lectotype designations are made for the following species: *Rhadinaea affinis* (Günther), *R. calligaster* (Cope), *R. decorata* (Günther), *R. godmani* (Günther), *R. guentheri* Dunn, *R. multilineata* (Peters), *R. taeniata* (Peters), and *R. vermiculaticeps* (Cope).

The following innovations or taxonomic changes are proposed herein:

Enicognathus bilineatus Fischer, 1885	=*Rhadinaea bilineata*, new combination
E[*nicognathus*]. *elegans* Jan, March 31, 1863	=*nomen oblitum* [=*Rhadinaea poecilopogon* Cope, April, 1863]
E[*nicognathus*]. *taeniolatus* Jan, March 31, 1863	=*nomen oblitum* [=*Rhadinaea brevirostris* (Peters, June 29, 1863)]
Liophis insignissimus Amaral, 1926b	=*Rhadinaea persimilis* (Cope, "1868" [1869])
Liophis persimilis Cope, "1868" [1869]	=*Rhadinaea persimilis*, new combination
Rhadinaea aemula Bailey, 1940	=*Rhadinaea taeniata aemula*, new combination
Rhadinaea albiceps Amaral, 1924	=*Rhadinaea decipiens* (Günther, 1893 [1885–1902])
Rhadinaea altamontana Taylor, 1954	=*Rhadinaea godmani* (Günther, 1865)
Rhadinaea beui Prado, 1943	=*Rhadinaea persimilis* (Cope, "1868" [1869])
Rhadinaea binfordi Rossman, 1965	=*Rhadinaea godmani* (Günther, 1865)
Rhadinaea bogertorum Myers	=new species
Rhadinaea crassa Smith, 1942	=*Rhadinaea gaigeae* Bailey, 1937
Rhadinaea cuneata Myers	=new species
Rhadinaea decipiens rubricollis Taylor, 1954	=*Rhadinaea pachyura* (Cope, 1875a)
Rhadinaea hesperia baileyi Smith, 1942	=*Rhadinaea hesperia* Bailey, 1940
Rhadinaea hesperia hesperia Bailey (Smith, 1942)	=*Rhadinaea hesperia* Bailey, 1940
Rhadinaea hesperia hesperioides Smith, 1942	=*Rhadinaea hesperia* Bailey, 1940
Rhadinaea persimilis Dunn, 1938	=secondary homonym=*Rhadinaea guentheri* Dunn, 1938
Rhadinaea stadelmani Stuart and Bailey, 1941	=*Rhadinaea hempsteadae* Stuart and Bailey, 1941
Rhadinaea taeniata taeniata (Peters, 1863)	=new combination
Rhadinaea veraepacis Stuart and Bailey, 1941	=*Rhadinaea kinkelini* Boettger, 1898
Rhadinaea zilchi Mertens, 1952a	=*Rhadinaea godmani* (Günther, 1865)
Rhadinella schistosa Smith, 1941	=*Rhadinaea schistosa*, new combination
Trimetopon hannsteini Stuart, 1949	=*Rhadinaea hannsteini*, new combination
Trimetopon piloñaorum Stuart, 1954a	=*Rhadinaea pilonaorum*, new combination
Trimetopon posadasi Slevin, 1936	=*Rhadinaea posadasi*, new combination

[1]Maglio (1970, p. 43) anticipated my actions in regard to *Urotheca*, and, in a footnote, created the first combination of the generic name *Rhadinaea* with the epithet *dumerillii* (*sic*). But, despite the antiquity of its name, *dumerilii* does not become the type species of *Rhadinaea* as inferred by Maglio. The type of *Rhadinaea* Cope is *Taeniophis vermiculaticeps* Cope (=*Rhadinaea vermiculaticeps*), by original designation. Brown (1908, p. 123) also erred somewhat in stating that Cope had, at various times, claimed two type species for *Rhadinaea* in addition to the one originally designated. However, Brown misread Cope's remarks on "*R. melanocephala*"; Cope (1900, p. 754) did mistakenly give "*R. obtusa*" as the type species, but only because he evidently had forgotten in which paper he originally had described the genus (the original description is not listed in Cope's 1900 synonymy).

APPENDIX

SPECIMENS EXAMINED

THE FOLLOWING MATERIAL is arranged alphabetically, except that names of countries are given from north to south under a species, and specimens lacking data are listed first. Most locality listings are taken relatively unaltered from museum catalogues or loan invoices, although I have corrected some obvious misspellings and have attempted to place localities in the proper political unit (province, state, department, or territory) when this had not been recorded.

Some specimens were examined after the manuscript had been completed, as indicated by a parenthetical statement that data are not included in text.[1] The localities of a few such specimens, however, have been plotted on the distribution maps.

Rhadinaea affinis

No locality data, MNHN 7863.

BRAZIL: *Rio de Janeiro*: Rio de Janeiro, BMNH 1946.1.5.80. [*Santa Catarina*]: Theresopolis, BMNH 89.12.16.117. *São Paulo*: Ilha São Sebastião, MCZ 17930, ZIUS 3966; Taubate, USNM 76339.

Rhadinaea bilineata

BRAZIL: *Santa Catarina*: Theresopolis, SMF 19052. *São Paulo*: No specific locality, ZMB 2100 (data not included in text); Alto da Serra, Estação Biologica, UMMZ 109072 (data not included in text).

Rhadinaea bogertorum, new species

MEXICO: *Oaxaca*: 10 mi. NE Cerro Pelón, nr. km. 120 on Tuxtepec Rd., 6800 ft., AMNH 100906; 10.5 mi. N Cerro Pelón, nr. km. 123, 6650 ft., AMNH 100907.

Rhadinaea brevirostris

FRENCH GUIANA: Cayenne, NMB 1485 (data not in tables but see Remarks under species account).

BRAZIL: *Amapá*: Serra do Navio, KU 97877. *Amazonas*: Caruru, upper Río Vaupes [Rio Uaupés] nr. Colombian border, AMNH 4462; Rio Manjura, 4°S, 57°W, AMNH 101972, 101973; Rio Purús, ANSP 14705.

COLOMBIA: *Putumayo*: Puerto Asis, AMNH 53454.

ECUADOR: No specific locality ("Ecuador?"), MCZ 6768. Río Chambrio, region of Río Pastaza, AMNH 49138. Río Pastaza between Canelos and Río Marañon [Río Marañon is in Peru], MCZ 36947. Santa Rosa, Río Tigre, AMNH 49171. *Chimborazo*: Riobamba, AMNH 15207, 15208, 23289. *Napo-Pastaza*: Canelos "and" Baños, AMNH 35871; Limón Cocha, KU 105427, UIMNH 61272; nr. Mera, Alpa-yacu, 300 m., UMMZ 92018; 20 km. NE Mera, 1500 m., KU 119391; Montalbo, Río Bobonaza, AMNH 49066; Santa Cecelia, 300 m., KU 119389, 119390; Sara-yacu, [Río Bobonaza], AMNH 28792, 28798 (2 spec.), 28799. *Santiago-Zamora*: No specific locality, UMMZ 82880, 82881.

PERU: No specific locality, ANSP 3339. *Amazonas*: mouth Río Santiago, Río Marañón, AMNH 52394, 53458. *Cuzco*: Cordillera Vilcabamba, 1410 m., AMNH 101397. *Huánuco*: Monte Alegre, Río Pachitea, AMNH 52776. *Loreto*: Alto Cushabatay, AMNH 52797; Cashiboya, Río Ucayali, AMNH 52308, 52836, 52839, 52842, 52913; Monte Carmelo, Requena, AMNH 55652, 55647; Ollanta, AMNH 53016; Pampa Hermosa, Río Cushabatay, AMNH 52350, 53388, 55758, 55781, 55967, 56020; Pebas, BMNH 1946.1.1.9, 1946.1.1.10; Pte. Balsa, Río Cushabatay, AMNH 52689; Río Apaga, AMNH 52504; Río Tapiche nr. Brazilian frontier, AMNH 53598. *San Martín*: Ampi Urca (Lamas Region), 3000 ft., AMNH 52549; La Pina, Río Mixiolla, AMNH 53591.

Rhadinaea calligaster

COSTA RICA: *Cartago*: Navarro, 4000 ft., UMMZ 74300; Río Playas, 5 km. NE Capellades, USC 7055; Volcán Turrialba, 5 mi. SE Lecheria Central, USC 41; Volcán Turrialba, *ca.* 20 km. NW Turrialba, USC 2923. *Heredia*: Cerro Chompipe, 6.4 rd. mi. N San Raphael, 2100 m., LSU 9630; Cerro Chompipe, south fork Río Las Vueltas, USC 3048 (3 spec.); south fork Río Las Vueltas, 2100 m., KU 103889–103891; between north and south forks Río Las Vueltas, USC 2130–2133 (data not included in text). *Limón*: Cerro Utyum [not "Pico Blanco" *fide* Savage, 1970], 5000–7000 ft., USNM 30607, 30679. *San José*: 15.4 mi. N San Isidro del General, 8000 ft., UMMZ 117650; Santa Maria, USNM 38335.

PANAMA: No specific locality, MCZ 50195. *Bocas del Toro*: nr. summit Cerro Pando, 2260 m., KU 107814; north slope Cerro Pando, 1810 m., KU 107815–107838. *Chiriquí*: above Cerro Punta [town] on trail to Boquete, FMNH 68101.

[1]This new material does not alter present species concepts in any significant way. The more noteworthy specimens will be discussed in a future publication.

Rhadinaea cuneata, new species

MEXICO: *Veracruz*: vicinity km. 324, *ca.* 9 km. SW Fortín, UMMZ 128998; Ojo del Agua, Nacimiento del Río Atoyac, *ca.* 10 km. (air line) NNE Córdoba, UAZ 26580.

Rhadinaea decipiens

No exact locality data ("probably from Ecuador" [see text]), USNM 22446.

COSTA RICA: San José [town or province?], MCZ 28071. *Alajuela*: Cinchona, KU 35637; Cinchona, 1600 m., KU 103892. *Cartago*: Moravia, 1200 m., USC 94; Navarro, MCZ 15300. *Cartago* or *San José*: Irazú, BMNH 1946.1.3.96. *Limón*: La Lola, KU 84677, USC 141; Los Diamantes nr. Guapiles, USC 8282. *Puntarenas*: Gromaco, UMMZ 123659; 6 km. SE Villa Neily, 15 m., KU 103893.

PANAMA: *Darién*: northeast slope Cerro Sapo, 1050 m., KU 112441. *Bocas del Toro*: north slope Cerro Pando, 1620 m. and 1450 m., KU 112439, 112440.

COLOMBIA: *Antioquia*: Santa Rita N Medellin, 9000 ft., BMNH 98.10.27.2.

Rhadinaea decorata

No locality data, ANSP 3474.

MEXICO: No specific locality, BMNH 1946.1.9.3., 1946.1.9.4, FMNH 25411, USNM 12096, 30409. Atoyac, BMNH 94.5.17.1–94.5.17.3. Ojo de Agua, Paraje Nuevo, UMMZ 85311. *Chiapas*: between El Censo and Monte Libano, MCZ 53899; Ibarra, 64 km. ESE Altimirano, 970 m., TCWC 19550; Jetja, AMNH 66465; Ocuiltapa, USNM 46527; Palenque Ruins, UIMNH 11345. *Oaxaca*: nr. Camotlan, USNM 120955; Cosolapa, CAS 74328, 74329, 74347; La Gloria, UIMNH 37160–37162, 40893, 40894; between La Gloria and Cerro Azul, UIMNH 37159; between La Gloria and Río Grande, UIMNH 37158; Rancho Vicente, *ca.* 25 km. N Tapanatepec, UAZ 26099; mts. nr. Santo Domingo, USNM 46361–46363; 2 mi. E Tollocito, KU 39683. *Puebla*: vicinity La Mesa and Mexaca, MCZ 56216; Necarxa, UMMZ 85969. *San Luis Potosí*: Xilitla region, LSU 265, KU 24015; Xilitla region, 2400 ft., LSU 267. *Veracruz*: No specific locality, USNM 12308 (2 spec.). Colonia Bastonal, 7 mi. E Tebauca, TCWC 21982; Coyame, 1200 ft., UMMZ 111446, 111447; Coyame, 7 mi. E Catemaco, UIMNH 36882; Coyame, 9 rd. mi. SE Catemaco, UAZ 26579; Cuautlapan, FMNH 113718, 113720, 113721, 113724–113734, UIMNH 30339–30344, 60786, USNM 110354–110359, 110361; Cuichapa Culiacan, UIMNH 52976; 2 mi. N Fortín, UIMNH 25959; *ca.* 9 km. SW Fortín, vicinity km. 324, UMMZ 95074 (6 spec.); 4 km. WNW Fortín, KU 23244; Hacienda El Potnera nr. Córdoba, MCZ 45681; 20–30 km. ENE Jesus Carranza, KU 27562, 27563; Jicaltepec, ANSP 11709; between Laguna Catemaco and Volcán Santa Marta, UMMZ 121144; nr. Las Vigas, FMNH 113722, 113723, UIMNH 30345; Penuela, USNM 110362, 110363; Portrero Viejo, UIMNH 30338, 48762, USNM 110348–110353; Presidio, BMNH 1903.9.30.199; Río Quezalapam, 1 and 2 mi. E Lago Catemaco, TCWC 21389–21391; Río Tecolapan, 2.4 mi. NNW Tapalapan, 900 ft., UMMZ 114657; San José de Gracia, FMNH 113719; San Martín Mt., El Tular Sta., UIMNH 35471; 1 mi. S Sontecomapan, TCWC 21392; 1.5 mi. NE Vigia, 700 ft., LSU 11759.

GUATEMALA: *Alta Verapaz*: Finca Volcán, UMMZ 91046; Trece Aguas, USNM 38133.

NICARAGUA: No specific locality, USNM 14217. *Río San Juan*: vicinity El Castillo, JV 857; San Juan de Norte (Greytown), USNM 15641, 102274. *Zelaya*: Cupitna Camp, 2000 ft., AMNH 12717; Río Huahuashan, Camp Corozo, AMNH 70243.

COSTA RICA: No specific locality, USNM 9788, 30609–30613. Guayapilas, UMMZ 83180. Sta. Cecilia, MCZ 15304. *Alajuela*: 5 mi. N Ciudad Quesada, USC 7156. *Cartago*: No specific locality ("probably Turrialba"), USC 2796; El Silencio de Sitio Mata, above La Suiza, 1200 m., USC 232; IICA campus nr. Turrialba, USC 257; La Suiza, KU 25733; Turrialba, KU 30960, 31942, 35514, 35515, MCZ 56098, 56099. *Guanacaste*: Laguna de Arenal, USC 2911 (data not included in text); Tenorio, KU 31941; Tilaran, ANSP 22266. *Heredia*: Finca La Selva nr. junc. Río Sarapiquí and Río Puerto Viejo, UMMZ 123658, USC 2163, 3128. *Limón*: Alto Guayacán, UCR 2526 (data not included in text); Baja Talamanca, Bambu, USC 7183; Coen Dispensary, MCZ 19335; Guapiles, MCZ 15310; La Castilla, lower Río Reventazón, ANSP 22364; La Lola, USC 131, 199, 2635, 8068; Limón, KU 31940, MCZ 19739; Pandora, USC 7192; Suretka, USNM 120832; Tortuguero, UF 10190. *Puntarenas*: Boruca, AMNH 17303; Los Helechales, 15 km. NE Portrero Grande, USC 8269.

PANAMA: No specific locality, MCZ 50196. Isthmus of Darién, Atlantic side, USNM 24501, 24502. *Bocas del Toro*: nr. Almirante, KU 80238, 80239, 112449; Isla Bastimentos, 10 m., AMNH 107586–107588 (data not included in text); Isla Colón, vicinity Punta Rocosa, 5–10 m., KU 112450. *Canal Zone:* No specific locality, FMNH 6115. Barro Colorado Island, FMNH 22851, KU 75746, 80601, UMMZ 63744; nr. Fort Clayton, UIMNH 41724; Fort Sherman nr. Colón, MCZ 18931; Frijoles, MCZ 23885, 43949. *Chiriquí*: Progreso, UMMZ 57972. *Coclé*: El Valle, AMNH 90070, 90071. *Colón*: Agua Clara, nr. Río Chagras, ANSP 22568, MCZ 45380; 3.5 km. SE Puerto Pilón, KU 112452. [*Colón or Panamá*]: Bruja Mts. inland from Nombre de Dios, MCZ 24930. *Darién*: Cana, MCZ 43948; southeast slope Cerro Cituro, Serranía de Pirre, 1000–1100 m., KU 112444, 112445; Cerro Quia, 740 m., KU 112446, 112447; Cerro Sapo,

3000 ft., ANSP 22966; Laguna, 820 m. [camp between upper Río Tapaliza and Río Pucro, Serranía del Darién], KU 75742–75744, 112448; north end Serranía de Pirre, 500 m., KU 112442, 112443, 112451; Tacarcuna, Pucro Ridge, 1100 m., KU 75745. *Panamá*: south slope Cerro Campana, 740 m., KU 75740, 75741. *Veraguas*: Cocuyos de Veraguas, ANSP 3473.

ECUADOR: *Pichincha*: Río Blanco, 20 km. from Mindo, USNM 166933.

Rhadinaea dumerilii

No locality data ("Cuba," in error), MNHN 733.

COLOMBIA: *Antioquia*: Medellín, AMNH 35490. *Chocó*: Peña Lisa, Condoto, BMNH 1914.5.21.46; Quebrada Pangala, Río San Juan, AMNH 103823.

Rhadinaea flavilata

Localities previously listed in Myers, 1967, pp. 55, 56.

Rhadinaea forbesi

MEXICO: No specific locality ("Guadalajara? Probably near Orizaba, Veracruz"), USNM 29124. *Veracruz*: 15 km. N Jalapa, UMMZ 89378–89380; Las Vigas, 8500 ft., KU 26732; nr. Las Vigas, FMNH 100748; Tequeyutepec, 7 mi. W Jalapa, FMNH 100725, USNM 110364, 110365; 4 km. W Tlapacoyan, 1700 ft., KU 23963.

Rhadinaea fulviceps

PANAMA: No specific locality, USNM 61187. *Canal Zone*: Barro Colorado Island, MCZ 34881, UF 7533, UMMZ 63761; Camp Chagres, KU 112457; Curundu, KU 80266; nr. Fort Clayton, UIMNH 41725; Fort Gulick, KU 112456; Gigante Island, Gatun Lake, ANSP 24748; Juan Mina, MCZ 26647; Madden Dam, UMMZ 76023; Madden Forest, AMNH 103779. *Colón*: Agua Clara nr. Chagres River, ANSP 22274. *Darién*: Boca de Cupe, MCZ 38226; Cana, USNM 50121; upper Río Tuira at Río Mono, 130 m., KU 112453–112455.

Rhadinaea fulvivittis

MEXICO: *Oaxaca*: Cerro de la Corona, Santiago Lapaquia, UIMNH 37164; Cerro San Felipe, AMNH 100903–100905, FMNH 105654–105658, UIMNH 36198–36200, 52974, 52975, 53113–53115, 56132, 60783–60785, USNM 110347; Cerro San Felipe, 6000–10,000 ft., AMNH 97972; *ca.* 6 mi. E Cerro San Felipe, *ca.* 10,000 ft., AMNH 94717; south slope Cerro San Felipe, N San Felipe Agua, AMNH 91081–91084; vivero on Arroyo San Felipe, above town, 5700 ft., AMNH 89590; 6.5 mi. NE El Carrizal, 7700 ft., AMNH 100898; "El Pacifica" [=San José del Pacifico?], UIMNH 6318; 1.2 mi. E Ixtlán de Juárez, 7400 ft., AMNH 106954, 106955 (data not included in text); 2 mi. E Ixtlán de Juárez, *ca.* 7800 ft., AMNH 94716; La Cofradía, 8900–9000 ft., Sierra de Cuatro Venados, AMNH 97963, 97964; Llano de las Flores, 3150 m., KU 70883; Mt. Zempoaltepec, USNM 46434; 18 km. N, 33 km. W Oaxaca, 7200 ft., TCWC 17191; 24 km. NNE Oaxaca, 2350 m., UMMZ 124757 (2 spec.); 3 mi. E Ojo de Agua, 8600 ft., Sierra de Cuatro Venados, AMNH 103140; Quiegolani, AMNH 65138, 65139; San Andres Chicahuastla, UIMNH 50493; 7–8 mi. N San Juan del Estado, 8000–8400 ft., AMNH 106956, 106957 (data not included in text); 3 rd. mi. NW Santa Inez del Monte, Sierra de Cuatro Venados, AMNH 100899; 5 mi. NW Santa Inez del Monte, 9000 ft., AMNH 103041, 103042 (live color data only in text); Santo Tomás, Teipan, UIMNH 40903; "vicinity Tehuantepec," UIMNH 50494; Tejocotes, 7600 ft., Distrito Etla, AMNH 100900–100902; Tejocotes, 7900–8100 ft., AMNH 103684–103687 (data not in text); Tejocotes and vicinity, 8000–8600 ft., AMNH 102989–103040, 106943–106953 (live color data only in text); 6–8 km. S Tejocotes, AMNH 100887–100897; Tlalixtac Cañon, 3 mi. NE El Estudiante, 7700 ft., AMNH 104383 (data not included in text); 2 mi. SW Yuvila, 8600 ft., Distrito Ixtlán, AMNH 104384 (data not included in text). *Puebla*: 4 mi. W Zoquitlán, 8400 ft., CU 4966 (data not in text). *Veracruz*: Orizaba, USNM 6333, 7075; Potrero Viejo, FMNH 124498; Puerto Morelos, Cumbres de Acultingo, 7500 ft., UMMZ 114658.

Rhadinaea gaigeae

MEXICO: *Hidalgo*: Barranca de los Horcones, km. 239, 10 km. S Durango, USNM 110366; Durango, FMNH 100123; 6 mi. NE Jacala, Puerto de La Zorra, 6000 ft., KU 61099; La Placita, S Jacala, FMNH 100684; 1.5 mi. N Zacualtipan, LSU 11010. *San Luis Potosí*: Alvarez, 2000–8800 ft., FMNH 73384, MCZ 19047, 24982–24984; mts. of Alvarez, 16 leagues SE San Luis Potosí, UMMZ 90668; Cerro Conejo, LSU 4206; Ciudad del Maiz, FMNH 100685; 11 mi. E, 2 mi. N Ciudad del Maiz, 5400 ft., KU 28086; Xilitla, LSU 603; Xilitla, Cueva Salitre, LSU 602; Xilitla region, LSU 262, 264, KU 24016, 24017. *Tamaulipas*: cave at El Pachón, 8 rd. km. NNE Antiguo Morelos, UAZ 26582; Rancho del Cielo, 8 mi. NW Gómez Farías, AMNH 102490; WNW Rancho del Cielo, *ca.* 3550 ft., LSU 11009; numerous localities in Gómez Farías region, 3300–6000 ft. (for list and map see Martin, 1958, pp. 7, 72, under *Rhadinaea crassa*), UMMZ 98944, 98945, 100188–100191, 101206, 101208, 101368–101370, 102988, 102989 (4 spec.), 102990–102993, 108514, 108792–108796, 110821, 111054–111093, 111100, 112921–112924.

Rhadinaea godmani

MEXICO: *Chiapas*: Catharinas, SMF 43774; F.

Catharina, Distrito Libertad, UMMZ 95155, 95156; 18.9 km. NW Comitán, 5990 ft., TNHC 29667; Prusia, SMF 43773. *Oaxaca*: above Zanatepec, UIMNH 56142; 12 air mi. NNE Zanatepec, 4900 ft., LSU 7576.

GUATEMALA: No specific locality, MCZ 5830, UMMZ 96650. *Chimaltenango*: Chichivac, 5 mi. N Tecpan, CAS 6720–6725; Chichivac, 8700 ft., FMNH 20263. *El Progreso*: Finca Bucaral, UMMZ 106731. *Sacatepéquez*: Dueñas, BMNH 1946.1.9.14–1946.1.9. 17; Dueñas, Finca San Rafael, *ca.* 3 km. NW Casa Grande, UMMZ 100516. *San Marcos*: 3 km. E Tejutla,2350–2600 m., UMMZ 96647–96649.

EL SALVADOR: *Santa Ana*: Hacienda Monte Cristo, UMMZ 117290, 117291.

COSTA RICA: *Alajuela*: Volcán Poás, 1920 m., UMMZ 123351. *Cartago*: Tres Rios, USC 2983 (5 spec.). *Cartago–San José*: El Empalme, Pan-Amer. Hwy., 2208 m., USC 2629; edge National Forest Preserve, Pan-Amer. Hwy., Talamanca Range, 7000–8000 ft., KU 30962. *Heredia*: 2.2 km. N La Concordia, 1950 m., KU 63865.

PANAMA: No specific locality, FMNH 68103. *Chiriquí*: Boquete district, 6000–7000 ft., MCZ 34369; El Volcán (=town of Hato del Volcán), 1200 m., ANSP 22575, 22583, 22584, KU 75747; Finca Lérida, 1600 m., 9 km. N Boquete, KU 75748; Finca Lérida, 5300 ft., ANSP 22913–22915, 24773; Nueva Suiza, 6000 ft., FMNH 68102.

Rhadinaea guentheri

NICARAGUA: *Zelaya*: Eden Mine, AMNH 7412.

COSTA RICA: *Cartago*: IICA campus nr. Turrialba, USC 151; La Suiza, nr. Turrialba, ANSP 22431. [*Cartago* or *San José*]: Irazú, BMNH 1946.1.8.15. *Heredia:* Finca la Selva nr. junc. Río Sarapiquí and Río Puerto Viejo, USC 1546. *Limón*: La Lola, KU 31938, USC 209. *Puntarenas*: Palmar, KU 31939; 4 mi. NW Villa Neily, USC 7108. *San José*: Cerro de La Muerte, 12 mi. S Georgiana Motel, 6900 ft., LSU 8761; rd. to San Isidro General, southern slopes [of Cerro de La Muerte], USC 277.

PANAMA: *Bocas del Toro*: La Loma, 1500 ft., MCZ 19345. *Chiriquí*: Puerto Armuelles, ANSP 24252. *Coclé*: La Mesa area, trail to Las Minas, El Valle, 2400 ft., FMNH 83480.

Rhadinaea hannsteini

MEXICO: *Chiapas*: Unión Juárez, Volcán Tacaná, UIMNH 55016.

GUATEMALA: *San Marcos:* Finca La Paz, UMMZ 106698, 106699, 106701 (4 spec.), 106702 (2 spec.); Finca La Paz, 1450 m., MCZ 53778, UMMZ 98753, 98754, 98756, 98757; Finca La Paz, 1050–1300 m., UMMZ 106700 (3 spec.). *Suchitepéquez*: west slope Volcán Santa Clara, Finca El Naranjo, UIMNH 46126–46129.

Rhadinaea hempsteadae

MEXICO: *Chiapas:* Rancho Nuevo, 7800 ft., 8.6 mi. SE San Cristóbal de Las Casas on Hwy. 190, JFC 66-60; 9 mi. by Hwy. 190 SE San Cristóbal de Las Casas, UAZ 26581.

GUATEMALA: *Alta Verapaz*: Finca Chichén, *ca.* 5700 ft., about 10 km. S and slightly E of Cobán, UMMZ 89080; Finca Chichén, 1850 m., UMMZ 89081; Finca Volcán, 1200 m., UMMZ uncatalogued (field no. LCS 182). *Huehuetenango*: Paraiso, *ca.* 1970–2200 m., UMMZ 127271–127276; 3 km. E San Juan Ixcoy, 2200 m., UMMZ 120014; Todos Santos, 8000 ft., UMMZ 89078, 89079; 2 km. E Todos Santos, 2600 m., UMMZ 120015.

Rhadinaea hesperia

MEXICO: *Colima*: Queseria, UMMZ 80226, 80227. *Guanajuato*: Guanajuato, USNM 15429, 15430. *Guerrero*: mts. W Acahuizotla, 3500 ft., TCWC 7489; Agua del Obispo, 3300 ft., TCWC 7490, 11574; Chilpancingo, FMNH 38349, 38350, UIMNH 35002, UMMZ 84701–84709; vicinity Chilpancingo, AMNH 72496; 5 mi. N Chilpancingo, FMNH 105093; El Treinte, FMNH 100028; Omilteme, Sierra de Burro, MCZ 42660–42662. *Jalisco*: *ca.* 15 mi. SE Autlán, 5000 ft., Sierra Nevada Autlán, UMMZ 101921; 21 mi. S Guadalajara, KU 29503; Magdalena, USNM 67373; 20 km. WSW Purificación, KU 73619. *Morelos*: Barranca, nr. Cuernavaca, USNM 20166; 20 km. NE Cuautla, 6500 ft., TCWC 7378, UIMNH 25929; Huautla, USNM 122060; Tepoztlán, 6000–6100 ft., TCWC 7000, 7377. *Michoacán*: 1 mi. N Arteaga, 2900 ft., UMMZ 119281 (3 spec.); 0.5 mi. NE Coalcomán, slope Cerro de Avillos, 3500 ft., UMMZ 104502; Hacienda El Sabino, FMNH 105092, UIMNH 18933; Uruapan, Cupatitzio Natl. Park, UMMZ 92342; north slope Volcán Jorullo, *ca.* 3600 ft., UMMZ 104494; 2 mi. W Volcán Jorullo, UMMZ 104682. *Sinaloa*: 2 km. E Loberas, km. 1175, 6000 ft., AMNH 102518; Plomosas, USNM 46456; Santa Lucia, KU 75629; 12.3 km. (Hwy. 40) SW Santa Lucia, 1200 m., KU 80870; 19.2 km. NE Santa Lucia, 1891 m., KU 80871. *Zacatecas*: Mezquital del Oro, Zacatecas, BMNH 92.2.8.57.

Rhadinaea kinkelini

GUATEMALA: *Alta Verapaz*: Finca Chichén, 5100 ft., about 10 km. S and slightly E of Cobán, UMMZ 89077.

HONDURAS: *Ocotepeque*: 21 km. E Nueva Ocotepeque, 1900 m., LSU 23828. *Yoro:* Portillo Grande, FMNH 34739.

EL SALVADOR: *Santa Ana*: Hacienda Monte Cristo, 2200 m., KU 63866, 63867.

NICARAGUA: *Jinotega*: Jinotega, JV 69398 (data not included in text). *Matagalpa*: Santa María de Ostuma nr. Fuente Pura, JV 66399 (data not included in text).

Rhadinaea lachrymans

No specific locality, ANSP 5539.

MEXICO: *Chiapas*: No specific locality, UMMZ 94604. Chicomusela, UMMZ 94609; El Chiciquite, UIMNH 54847; Letrero, Ciltepec, UMMZ 94606, 94607; Mt. Ovando, FMNH 104622, UMMZ 116570, USNM 110367–110369; Mt. Ovando, Soconusco, UMMZ 87699; Saxchanal, UMMZ 94605, 94608.

GUATEMALA: *Chimaltenango*: 5 mi. N Tecpán, 8650 ft., CAS 67016–67019. *Quezaltenango*: Finca Lorena, UMMZ 107325; 10.5 km. SSW San Martín Sacatepequez, 2050 m., KU 63868. *San Marcos*: Finca La Paz, UMMZ 106697, 120441 (3 spec.); Finca La Paz, 1050–1300 m., UMMZ 106696 (4 spec.); Finca La Paz, 1150 m., UMMZ 106695; Finca La Paz, 1285 m., 2 km. NW Casa Grande, UMMZ 107326; Finca La Paz, 1140 m., 2 km. SE Casa Grande, UMMZ 107327; Finca La Paz, 2 km. NW La Reforma, UMMZ 98305–98307; Loma de La Paloma, 4000 ft., above El Porvenir, FMNH 35059.

Rhadinaea lateristriga

No locality data ("Cuba," in error), MCZ 297.

COLOMBIA: *Boyaca*: Muzo [100 km. N Bogotá, 800–825 m.], UMMZ 78263; *Cauca*: Pacific side, Río San Juaquim, 1500 m., FMNH 54886 (data not included in text); *Valle*: Río Raposo, USNM 151680.

ECUADOR: No specific locality, ANSP 3348. Between Huigra to Río Chiquancay, ANSP 18125. *Chimborazo*: Pallatango, AMNH 23028. *Esmeraldas*: Intac, BMNH 78.1.25.51; San Javier, UIMNH 55723, 55724. *Guayas*: Guayaquil, USNM 62793, 62794 (data not included in text). *Loja*: Alamor, AMNH 22233. *Napo-Pastaza*: Mera, Río Pastaza, AMNH 49106 (data not included in text). *Pichincha*: Quito, ANSP 5600.

PERU: No specific locality, ANSP 5581.

Rhadinaea laureata

MEXICO: No specific locality, ZMB 2109 (data not included in text). *Durango*: Coyotes, 8000 ft., Sierra Madre, FMNH 1498; 10 mi. E El Salto, AMNH 68360; 10 mi. SW El Salto, 10,100 ft., KU 40337; Laguna de Progreso, UMMZ 113625–113627. *México*: 123 km. W, 6 km. S Mexico City, 2640 m., KU 39966. *Michoacán*: 4.4 mi. N Capácuaro, 7450 ft., UMMZ 114656; 9 km. S Carapan, km. 9 on Uruapan Rd., UIMNH 18935; 5 mi. S Carapan, USNM 110370–110372; 12 mi. S Carapan, 7600 ft., KU 62509, 62510; 29.2 mi. S Carapan, UIMNH 23854, 23855; Cherán, AMNH 64719; 6.4 mi. N Cherán, 6800 ft., UMMZ 112544, 112545; 2.4 mi. S Paracho, 7800 ft., UMMZ 114655; 3.8 mi. S Paracho, 7800 ft., UMMZ 119280; Pátzcuaro, FMNH 103232; 5 mi. W Lake Pátzcuaro, FMNH 103229; Tancítaro, 5000–6000 ft., FMNH 37127–37129, 39026–39029, 39031, 39032, 40816; km. 9 on Uruapan Rd., FMNH 103230, 103231. *Morelos*: 1.5 km. SE Huitzalac, 8000 ft., TCWC 4119; km. 63, 10 km. [from] Tres Cumbres, UIMNH 18934.

Rhadinaea macdougalli

MEXICO: No specific locality ("Chiapas or Oaxaca"), UIMNH 37163. *Oaxaca*: nr. Buena Vista, crest of Sierra Madre, N Río Grande, UIMNH 3775; Distrito de Villa Alta, Yelagago, *ca.* 3750 ft., AMNH 89618.

Rhadinaea marcellae

MEXICO: *San Luis Potosí*: Xilitla region, LSU 270.

Rhadinaea montana

MEXICO: *Nuevo Leon*: La Huacteca, 21 km. W Monterry, KU 92621; Monterry, ANSP 15355; Ojo de Agua, nr. Galeana, FMNH 30826, 40814.

Rhadinaea montecristi

EL SALVADOR: *Santa Ana:* Hacienda Monte Cristo, 2200 m., KU 62113–62120, 63869–63885, UMMZ 11792 (7 spec.).

Rhadinaea multilineata

VENEZUELA: *Aragua*: Parque Nacional Rancho Grande, AMNH 98284–98291, 98445; Rancho Grande, trail to Pico Periquito, UMMZ 124222; Rancho Grande, 0.5 mi. below (S) Portachuela Pass, UMMZ 124340. *Miranda*: Curupao Power Plant, AMNH 59445–59449; El Tanque, Curupao, MCZ 51475; Naiguate, Los Canales, CM 22775.

Rhadinaea myersi

MEXICO: *Oaxaca*: La Soledad, UIMNH 6317; Pluma Hidalgo, AMNH 19783; 3 mi. N Pluma Hidalgo, 5000 ft., LSU 7566.

Rhadinaea occipitalis

BRAZIL: No specific locality, USNM 120833. Chapada, ANSP 11123, 11124. Northern Brazil, Santos, SMF 19058. Central Brazil, SMF 19059. São Paulo [state or city?], MCZ 20721, 20724, 20725, 27675, UMMZ 62805.

PERU: *Loreto*: Orellana Reforma, AMNH 54593.

BOLIVIA: Manas, MCZ 24901. [*La Paz*]: Sorata, SMF 19060. *Santa Cruz:* Buenavista, FMNH 35644, MCZ 20623, UMMZ 69350 (2 spec.), 69351, 69352; Buenavista, 450–500 m., UMMZ 60711, 60712, 60714, 63250, 63251.

ARGENTINA: No specific locality, AMNH 17517.

Rhadinaea omiltemana

MEXICO: *Guerrero*: 18 rd. mi. W Asoleadero, 1900 m., Kraig Adler field nos. MN 4560, 4561 (data not included in text); Chilpancingo, FMNH 38351; mts. of Chilpancingo, UMMZ 84695, 84696; vicinity Chilpancingo, AMNH 72499; Omilteme, BMNH

94.11.14.14, 1946.1.1.7, FMNH 106858, UIMNH 18936, USNM 110374; Omilteme, 7300 ft., KU 87754; Sierra de Burro, MCZ 43282 (data not included in text).

Rhadinaea pachyura

COSTA RICA: *Heredia*: Cinchona, KU 31956. *Limón*: Cahuita, USC 2933; Guapiles, ANSP 22369; Penshurst, UCR 2935 (data not included in text); Sipurio, USNM 30618.

PANAMA: *Bocas del Toro*: nr. Almirante, KU 80240; 4.8 km. W Almirante, 40 m., KU 112458; La Loma, MCZ 19775. *Chiriquí*: Finca Lérida, ANSP 23880, 24774.

Rhadinaea persimilis

BRAZIL: *Espírito Santo*: Santa Teresa, SMF 32457.

Rhadinaea pilonaorum

GUATEMALA: *Santa Rosa:* Finca La Gloria, *ca.* 11 km. ENE Chiquimulilla, *ca.* 950 m., UMMZ 102635, 118262.

EL SALVADOR: *San Salvador*: San Salvador, 670 m., FMNH 64951.

Rhadinaea poecilopogon

BRAZIL: No Specific locality ("wahrscheinlich in der Provinz San Paulo"), ZMB 2101–2103 (data not included in text). *Rio Grande do Sul*: No specific locality, BMNH 82.10.4.78, 85.2.3.24. *Santa Catarina*: No specific locality, BMNH 88.11.30.3.

URUGUAY: No specific locality, ANSP 27344. Paysandú, USNM 31278.

Rhadinaea posadasi

GUATEMALA: *Sololá*: Olas de Moca, southern slope Volcán Atitlán, FMNH 20420. *Suchitepéquez*: western slope Volcán Santa Clara, UIMNH 46130; southern slope Volcán Zunil, CAS 66962–66966.

Rhadinaea pulveriventris

COSTA RICA: *Alajuela*: Cinchona, 1600 m., KU 103894; eastern slope Volcán Poás, 4500 ft., 14.1 mi. N Vara Blanca, UMMZ 117651 (4 spec.), 117652 (5 spec.). *Cartago*: Navarro, MCZ 15261. *San José*: Alto La Palma, UCR 2602 (data not included in text).

PANAMA: *Bocas del Toro*: northern slope Cerro Pando, 1450 m., KU 112459.

Rhadinaea quinquelineata

MEXICO: *Oaxaca*: nr. Sylacayoapam, MNHN 04.506, 04.507 (data not included in text). *Puebla*: Teziutlán, USNM 31350.

Rhadinaea sargenti

PANAMA: *Panamá*: Río Pequení, GML specimen; Pequení-Esperanza Ridge [divide] nr. head [Río] Adee, 1300 ft., MCZ 42789; Pequení-Esperanza Ridge nr. head Río Pequení, 1000 ft. and 1800 ft., MCZ 42787, 42788; Piedras-Pacora Ridge [divide], 2460 ft., MCZ 42764.

Rhadinaea schistosa

MEXICO: *Veracruz:* Cuautlapan, FMNH 100065, 100296–100298, USNM 109914.

Rhadinaea serperaster

COSTA RICA: *Cartago*: Navarro, 4000 ft., UMMZ 74301. *Heredia*: *ca.* 2 rd. km. N Caída El Angel, JV 66220; 3.8 km. S Cariblanco, Caída El Angel, 5000 ft., USC 75; Cinchona, EHT 4076, KU 31953, 35598; Conde de Tattenbach, KU 30958; Isla Bonita, 1450 m., KU 103895–103897. *San José*: between Alto La Palma and La Hondura, UCR 2218 (data not included in text); Rancho Redondo, USC 1204; nr. San José, ANSP 3739, MCZ 28069.

Rhadinaea, species inquirenda

COSTA RICA: *Cartago*: vicinity Finca de Jardín, 6 mi. S Villa Mills, USC 1036.

Rhadinaea taeniata aemula

MEXICO: No specific locality, UMMZ 100018. *Guerrero*: 2.5 mi. S Almolonga, 5600 ft., TCWC 11599, 11600; Chilpancingo, FMNH 38348, UIMNH 35003; mts. of Chilpancingo, UMMZ 84697–84700; vicinity of Chilpancingo, AMNH 72497, 72498; Omilteme, Sierra de Burro, FMNH 104996, MCZ 42659; 2 mi. E Omilteme, 6600 ft., KU 87753. *Morelos*: km. 58 on rd. to Cuernavaca, nr. Tres Cumbres, FMNH 104997, USNM 110373; 1.5 mi. SE Huitzalac, 8000 ft., TCWC 4118, UIMNH 16853; 5 km. N Tepotztlan, AMNH 58212; km. 63, 10 mi. S Tres Cumbres, UIMNH 18938; Tres Marías, FMNH 104995 (data not included in text). *Oaxaca*: Cerro San Felipe, UIMNH 18937, 53116, 53117; Cerro San Felipe, 6000–10,000 ft., AMNH 97970, 97971; above vivero on south slope Cerro San Felipe, *ca.* 8000 ft., AMNH 89591; *ca.* 20 km. NE Oaxaca, 2260 m., KU 116948; Quiegolani, AMNH 65101, 65102; Tejocotes and vicinity, 7200–7900 ft., Distrito Etla, AMNH 89834, 91086, 91087, 93232, 97966–97969, 100908, 102982–102988 (data not included in text), 103688–103696 (data not included in text), 106930–106942 (data not included in text); 1 mi. S Tejocotes, 7600 ft., AMNH 97965; *ca.* 6 mi. S Tejocotes, 7200 ft., AMNH 91085; Zapotitlan, FMNH 105301.

Rhadinaea taeniata taeniata

MEXICO: [*Distrito Federal?*]: City of Mexico, BMNH 68.4.7.13, 68.4.7.14. *Jalisco*: 6.4 km. W Atenquique, 2060 m., KU 102971; 9.2 rd. mi. W Atenquique, LACM 37325; La Cumbre de los Arras-

trados, BMNH 92.10.31.44–92.10.31.46; 4 mi. S Mazamitla, 6800 ft., KU 29509. *Michoacán*: 6.3 rd. mi. WSW Dos Aguas, UMMZ 121522; 14 mi. W Mil Cumbres, 9300 ft., TCWC 11585; Tancítaro, 5000–6000 ft., FMNH 37130, 39030.

Rhadinaea taeniata taeniata × *Rhadinaea taeniata aemula*

MEXICO: No specific locality (see text), ZMB 2115, 2117 (2 spec.). *Guerrero*: 1.5 mi. N San Vicente de Jesus, 1000 m., UMMZ 125731.

Rhadinaea vermiculaticeps

No locality data, ANSP 3741.

PANAMA: *Coclé*: El Valle, FMNH 47464; El Valle, Los Minos trail, 2750 ft., FMNH 109721. *Veraguas*: Cocuyos de Veraguas, ANSP 3534, 3535.

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