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A REVISION OF THE GENUS *ANADIA* (SAURIA, TEIIDAE)

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ABSTRACT

The concept of the microteiid genus Anadia *Gray, 1845, has been expanded to include* Argalia marmorata *Gray, 1846 and one species —* brevifrontalis *— heretofore referred to* Euspondylus. *Both newly referred forms are close to species that have always been placed in* Anadia. *Eleven species — one new — are recognized in five species groups: (1) the* ocellata *group including* ocellata *Gray,* vittata *Boulenger,* rhombifera *(Günther) and* petersi, *new species; (2) the* bogotensis *group with only* bogotensis *(Peters); (3) the* steyeri *group with only* steyeri *Nieden; (4) the* bitaeniata *group including* bitaeniata *Boulenger,* brevifrontalis *(Boulenger) and* pulchella *Ruthven; and (5) the* marmorata *group with* marmorata *Gray and* blakei *Schmidt.*

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INTRODUCTION

That the systematics of the "microteiids" is confused and demands extensive study is beyond doubt. Volume II (1885) of Boulenger's "Catalogue of Lizards in the British Museum" was the last comprehensive analysis of the Teiidae, and, in view of numerous species described since, is woefully outdated. The few genera that have subsequently been revised comprise *Alopoglossus, Cercosaura, Leposoma,* and *Pantodactylus* (Ruibal, 1953), *Placosoma* (Uzzell, 1959), *Echinosaura* (Uzzell, 1965), *Neusticurus* (Uzzell, 1966), *Arthrosaura* (Cunha, 1967) and *Ecpleopus* (Uzzell, 1969).

The genus *Anadia* has been as plagued by uncertainty as any. Not only has the generotypic locality remained a mystery since Gray's 1845 description of the genus, but the eleven nominal species and three subspecies subsequently added to the genus and still in use have not been subjected to comparative examination, despite the suggestions of several authors (Burt & Burt, 1930; Dunn, 1937, 1944a) that some of them might be invalid. An endeavor to construct a functioning key for the described forms from the existing literature only convinced Peters and Donoso-Barros (1970) of the low reliability of their information. Their key is inevitably inaccurate and misleading. Other keys published have been limited to early material (Boulenger, 1885), to Costa Rican forms (Taylor, 1955), or to Ecuadorian species (Peters, 1967), and are of little use. Since specimens of most described species are few and widely scattered, the tabular lists of scale counts presented by Loveridge (1929) and Dunn (1944a) were of necessity compiled (but not without error) from previously published values that were at best approximate. The sole attempt (Dunn, 1944a) at providing a "definite" locality for the type species of *Anadia* was unsuccessful due to his reliance on published accounts and a lack of familiarity with the genus. The remark of Burt and Burt (1930), that "it seems inadvisable to attempt anything like a generic revision of these highly variable and little known lizards," is indicative of the dilemma faced by microteiid systematists.

The aim of this investigation has been to determine the validity of the described forms of *Anadia* by an examination of all available material. Within the genus certain species have been found sufficiently similar to permit the delimitation of species groups. The genus itself, however, may be arbitrary in that the defining characters of *Anadia* as now conceived may be lacking in evolutionary significance. Yet since only an extensive analysis of the entire microteiid complex would permit an accurate evaluation of the generic boundaries, it has been necessary in this study to accept the genus as currently defined. Despite such unfortunate uncertainty, the genus serves a utilitarian function in bringing similar species together for placement in species groups that quite certainly reflect genuine evolutionary proximities. In this light, the transferal to *Anadia* of two species from other genera has seemed appropriate, as in both cases the species bear such close resemblance to species always referred to *Anadia* as to clearly belong to the same species groups. If future study should reveal that the species groups fall into distinct

genera then the current placement of these two species in *Anadia* is still a constructive step towards that end.

As herein revised, *Anadia* comprises eleven species ranging from Costa Rica south to Pacific Ecuador and from western Colombia to eastern Venezuela. No *Anadia* occur in the Amazonian drainage system. Such contrasting species as the slender, narrow-headed and semi-arboreal *A. ocellata* of moist Central American forests and the stout, broad-headed *A. brevifrontalis* inhabiting treeless paramo of the Venezuelan Andes characterize the genus.

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Finally, I wish to acknowledge the artistic skill of Laszlo Meszoely, who produced the illustrations for this review.

I. GENERIC DEFINITION

Anadia Gray, 1845 (type by monotypy *Anadia ocellata* Gray, 1845: 58).
Argalia Gray, 1846 (type by monotypy *Argalia marmorata* Gray, 1846: 67). *New Synonymy.*
Xestosaurus Peters, 1862 (type by monotypy *Ecpleopus* (*Xestosaurus*) *bogotensis* Peters, 1862: 217-220).
Chalcidolepis Cope, 1875 (type by monotypy *Chalcidolepis metallicus* Cope, 1875: 116-117= *ocellata* Gray, 1845: 58)

Historical Note

In 1845 Gray proposed the family *Anadiadae,* containing the monotypic genus *Anadia.* Based on a single specimen, his familial description contained a few species-specific and sex specific traits, but must otherwise be viewed as the first generic description of *Anadia.* Although the next worker, Wilhelm Peters (1862) placed the type species of *Anadia, A. ocellata,* in the subgenus *Euspondylus* of *Ecpleopus,* Boulenger (1885) revived *Anadia* for *ocellata* and three additional species, and provided a more adequate description comparable to his descriptions of other teiid genera. The only subsequent description of the genus, by Taylor (1955), was apparently drawn from Boulenger's Catalogue with few changes.

Definition of the Genus Anadia (figures 1 and 2)

Head scales smooth, flat and for the most part large and regular: a rostral; single frontonasal separating nasals; paired prefrontals; on occasion a small presupraocular; 2-4 supraoculars; a presuperciliary anterior to row of superciliaries; several large palpebrals forming translucent or pigmented disk in lower eyelid; a loreal, usually in contact with supralabials; a frenocular anterior to row of suboculars; a frontal; paired frontoparietals; an interparietal; variable parietals, postparietals and temporals; recessed tympana; 6-8 supralabials; 5-8 infralabials; a mental; single anterior and 4 pairs of chin-shields of which anterior 2-3 in contact along midline; gulars essentially homogeneous, with no obviously enlarged longitudinal rows; 1-2 enlarged collar rows. Lateral teeth bi- and tricuspid.

Dorsal scales smooth, juxtaposed or imbricate, essentially homogeneous, with posterior edges slightly pointed, rounded or squared. A few to numerous continuous annuli about trunk, formed by merging of ventral, lateral and dorsal transverse scale rows. Lateral scales equal to or somewhat smaller than dorsal scales, but no distinct band of much smaller lateral scales along entire side, nor any granular or convex scales aside from those about limb insertions. Ventrals smooth, quadrangular, juxtaposed or somewhat imbricate, arranged in transverse and longitu-

dinal rows. 3-9 large preanal scales along anterior border of vent. Adult males always with conspicuous femoral pores; females with none, fewer or as many less conspicuous pores. Maximum snout-vent length ca. 106 mm.

All limbs fully developed, pentadactyle with all toes clawed. Tail cylindrical.

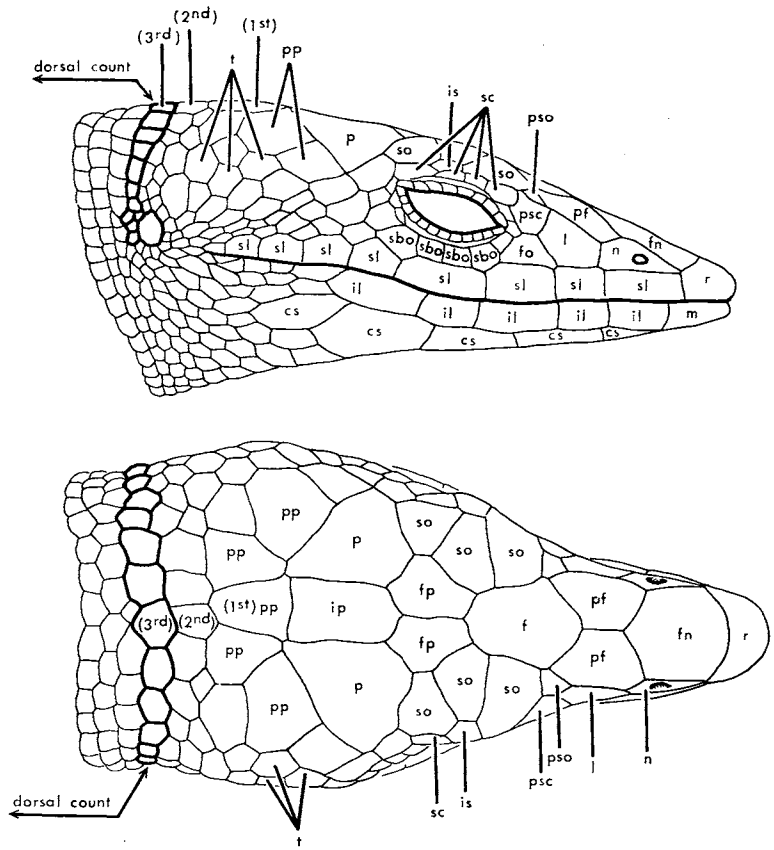

Fig. 1, lateral view of the head-scales of *Anadia;* 2, dorsal view. Drawn from *A. vittata* Nomenclature: cs, chin-shield; f, frontal; fn, frontonasal; fo, frenocular; fp, frontoparietal; il, infralabial; ip, interparietal; is, inserted scale between supraoculars and superciliaries; l, loreal; m, mental; n, nasal; p, parietal; pf, prefrontal; pp, postparietal; psc, presuperciliary; pso, presupraocular; r, rostral; sbo, subocular; sc, superciliary; sl, supralabial; so, supraocular; t, temporal.

Diagnostic Traits

1. Dorsal scales smooth, essentially homogeneous.
2. Lateral scales equal to or somewhat smaller than dorsal scales, but no distinct band of much smaller scales along entire side.
3. Ventral scales smooth, quadrangular.

4. Head scales smooth, without striation.
5. Single frontonasal separating nasals.
6. Paired prefrontals.
7. Clear or pigmented palpebral disk of several large scales on lower eyelid.
8. Gular scales smooth, essentially homogeneous, with no distinctly enlarged longitudinal rows.
9. 3-9 large preanal scales along anterior border of vent.
10. Femoral pores conspicuous in adult males, and either present or absent in females.
11. Limbs well developed, pentadactyle with all toes clawed.

In Boulenger's (1885) analysis of the Teiidae, *Anadia* falls in group II, and may be distinguished from:

1. Genera of group I by the frontonasal separating the nasals.

2. Genera of groups III and IV by the well developed limbs with five fully developed clawed digits. [1]

Within group II generic boundaries are in need of re-evaluation and redefinition. At present *Anadia* may be distinguished from group II genera by the diagnostic traits listed above. Certain of these criteria are especially useful, as some of the corresponding differences of other group II genera indicate: *Placosoma* has small feebly keeled dorsal scales; *Ptychoglossus* has elongate, narrow, quadrangular scales that are feebly keeled; *Alopoglossus, Arthrosaura, Cercosaura, Leposoma, Pantodactylus* and *Prionodactylus* all have distinctly keeled dorsal scales; *Echinosaura, Teuchocercus,* and *Neusticurus* (except *N. strangulatus*) have non-homogeneous dorsal scales; *Neusticurus strangulatus* has small lateral scales and only two large scales along the anterior border of the vent (Uzzell, 1961); *Proctoporus and Pholidobolus* lack prefrontals; *Amapasaurus* has several small frontonasal scales (Cunha, 1970); *Aspidolaemus* has two widened rows of gular scales and a complete lack of femoral pores (Uzzell, 1969b); *Ecpleopus* has small lateral scales, no femoral pores in the male, and smooth or slightly keeled dorsal scales; *Euspondylus* has lateral scales distinctly smaller than dorsals; *Opipeuter* has an undivided palpebral disk (Uzzell, 1969a). Several of Boulenger's genera are no longer recognized: *Oreosaurus* = *Proctoporus* (Andersson, 1914); *Loxopholis* = *Leposoma* (Ruibal, 1952); and *Argalia* = *Anadia* (this study).

The Problem of Generic Boundaries

For the most part, "microteiid" genera have been constructed on the basis of external morphological characteristics alone, and hence a first test for the validity of these genera is in the evolutionary significance

1. *Amapasaurus* has been placed in group II by Cunha (1970) even though it has but four digits on the anterior limbs.

of these traits. For example, much emphasis in setting the generic boundaries within the microteiid group has been put on the form of the body scales, even though in other families (e.g. Iguanidae, Agamidae) such characteristics have been found to be variable within genera. Is it evolutionarily sound to delimit a genus in this way? Given the low level of systematic certainty currently prevailing in our understanding of the microteiids, the author has found it necessary to accept body-scale form as a key characteristic in the definition of *Anadia*: only species with smooth, non-keeled, non-striated dorsal scales have been considered as possible candidates. Yet even among these *Anadia* there may be suggestions of a trend toward keeling in certain species (see p. 253), as well as variation in the shape of these smooth scales from species to species. The fact that groups of species within the genus are strikingly similar — in both body-scale and other traits — indicates that *Anadia* as a genus may represent a composite of distinct phyletic groups that have, by convergent evolution, come to share smoothness of the body scales. If this is the case, systematists in looking among the many keeled or striated microteiids may well find species bearing resemblance to the species-groups herein recognized within *Anadia,* and may wish to redefine the generic boudaries so as to better reflect phyletic relationships.

A study of Boulenger's *Catalogue* (1885) reveals, for example, that *Euspondylus* has been distinguished from *Anadia* by a greater subdivision of lateral scales, by dorsal scales sometimes feebly keeled, and by a strong collar fold. Yet experience with the species of *Anadia* suggests such traits to be but species-specific characters not reliable for generic distinction. Hence *despite* the slightly smaller lateral scales of Boulenger's *Euspondylus brevifrontalis,* this species is herein transferred to *Anadia* in view of its close relationship to *A. bitaeniata,* and *despite* the somewhat pronounced collar fold of Boulenger's *Argalia marmorata,* this latter species has been removed from *Argalia* to *Anadia* to reflect its close affinity to *Anadia blakei.*

Furthermore, an examination of the type of *Euspondylus guentheri* reveals that, excepting somewhat smaller lateral scales, it could well fit into *Anadia.* Recalling that Peters (1867) placed *E. acutirostris* (which he described), *E. maculatus, A. ocellata* and *A. rhombifera* all in the subgenus *Euspondylus* of the genus *Ecpleopus,* it might have been reasonable to include the three *Euspondylus* of Boulenger's work (*acutirostris, guentherii* and *maculatus* [*strangulatus* has already been transferred to *Neusticurus* by Uzzell, 1961]) in *Anadia* as one or two species groups, modifying the generic definition to include dorsal scales with striation and slight keeling, and greater lateral subdivision. However, since I have not examined in series these *Euspondylus,* which are under study by Thomas Uzzell, I refrain from taking any action here.

A similar case where smooth vs. slightly keeled dorsals seems a weak ground for generic distinction is that of *Ptychoglossus nicefori.* Originally described as *Anadia nicefori* by Loveridge (1929), it was transferred to *Ptychoglossus* by Dunn (1944a) in view of the elongate and feebly keeled nature of the dorsal scales and its apparent similarity

to *Ptychoglossus festae*. Both ***Anadia*** *marmorata* and *Anadia blakei* have elongate dorsals, however, and the dorsals of the former even hint occasionally at keeling. *P. nicefori* does differ in some respects from *Anadia* as currently defined: it has two enlarged longitudinal rows of gular scales, for example. However, a few specimens of *Anadia rhombifera* have some enlarged gulars that suggest longitudinal rows. Moreover, the differences among species within the genus *Ptychoglossus* are equally large. A generic revision of the latter might clarify not only relationships within *Ptychoglossus*, as Uzzell (1958) anticipated, but also relationships to genera such as *Anadia*. Clearly the problem of generic boundaries in the microteiids can only be solved by close examination of all the species with an eye open to characters in addition to those in current use.

A final comment might be made in regard to generic boundaries. Two genera of the Peruvian and Ecuadorian Andes, *Proctoporus* and *Pholidobolus* have as key defining criteria the absence of prefrontals (Boulenger, 1885). Yet a rough correlation is found in *Anadia* between increasing elevation and decreasing prefrontal size: *bogotensis* and *brevifrontalis*, both of high altitudes, show reduced prefrontals relative to the lowland species (*ocellata, vittata, steyeri*). Furthermore, *brevifrontalis* and *bogotensis* have greater pigmentation of the palpebral scales on the lower eyelid than low elevation *Anadia*, a condition approximating the non-transparent nature of the palpebral disk in the *Proctoporus* and *Pholidobolus* of Boulenger (some subsequently described *Proctoporus* have clear disks, according to Uzzell, 1970). Such observations suggest that these morphological criteria used in setting off the two genera may merely reflect adaptive strategies for living at high elevations. If this be the case, might not these species be phyletically close to microteiids of lower elevations which possess prefrontals and greater transparency of the palpebral disk?

II. SPECIES ACCOUNTS

The following section of this review has been organized in such a manner as to facilitate comparison of the species of *Anadia*. By placing the discussion of the methods of study and of scale nomenclature to the fore the author intends to emphasize that some of the techniques and designations utilized throughout this review differ from those previously used by microteiid systematists.

The species accounts themselves are intended to be directly comparable one to the other. Thus the descriptions of the species are all presented in similar style. The lists of diagnostic traits serve further to point out distinguishing characteristics of each species.

The key to the species is of course constructed on the basis of available specimens, and may prove slightly inaccurate as further collections are made. But with the back-up of the tabular and graphic presentations of important meristic traits (table 1; fig. 4), the map showing geographic distributions of the species (fig. 3), and the accounts of the species themselves, there should be no reason for further confusion or misidentification of specimens of *Anadia*.

Methods of Study and Scale Nomenclature

As there have been no standard procedures for making scale counts of microteiids, the published figures are not comparable. It is in the hope of facilitating study and comparison of these species that the procedures herein utilized are given in detail:

1. Supraocular count refers to the large, regular shields above the eye only; for the 1-2 smaller scales often formed in front of the supraoculars (fig. 1, 2) by division of the presuperciliary (discussed below) the name presupraocular is proposed. Previous systematists of *Anadia* have often included a presupraocular in the supraocular count, with the result that for those specimens in which the presuperciliary is divided the count is increased by one even though the large, regular shields above the eye have not changed in size or number. It is to clarify the nature of this variation that a new term is employed.

2. Superciliary count refers to the small scales lying between the supraoculars and the eye opening. The enlarged scale along the upper anterior border of the orbital region (figs. 1, 2) is termed the presuperciliary, which in some specimens may divide to form in addition the presupraocular. The presuperciliary has been considered the anterior

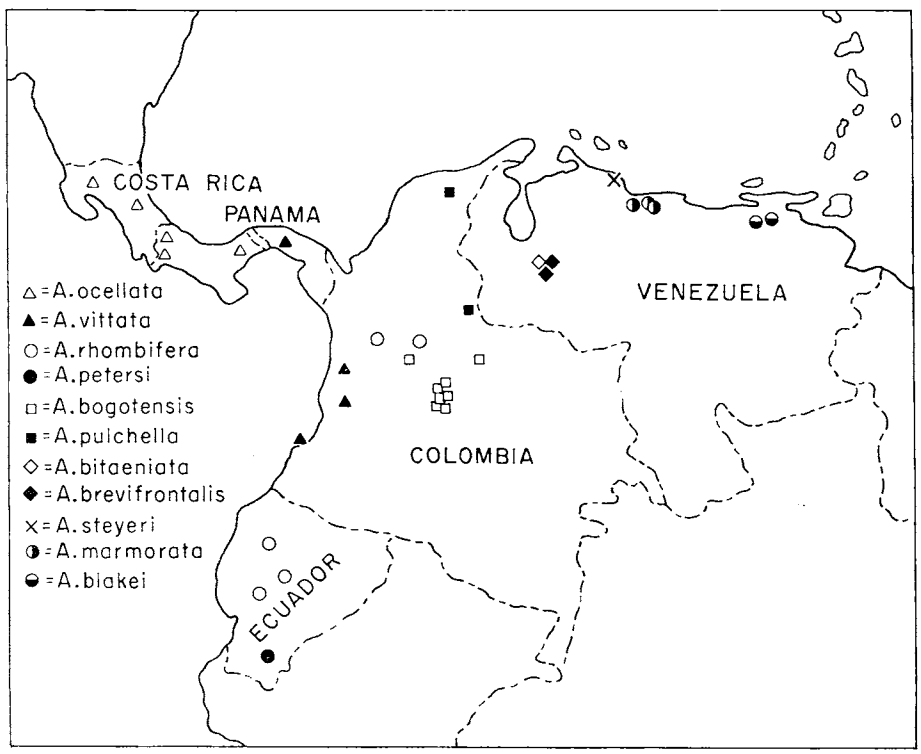

Fig. 3, Geographic distribution of the species of *Anadia*.

superciliary by, for example, Uzzell (1970), but neither this scale nor any scale lying behind the eye is here included in the superciliary count.

3. The term palpebrals is used for the enlarged scales on the lower eyelid which collectively form the more or less translucent disk.

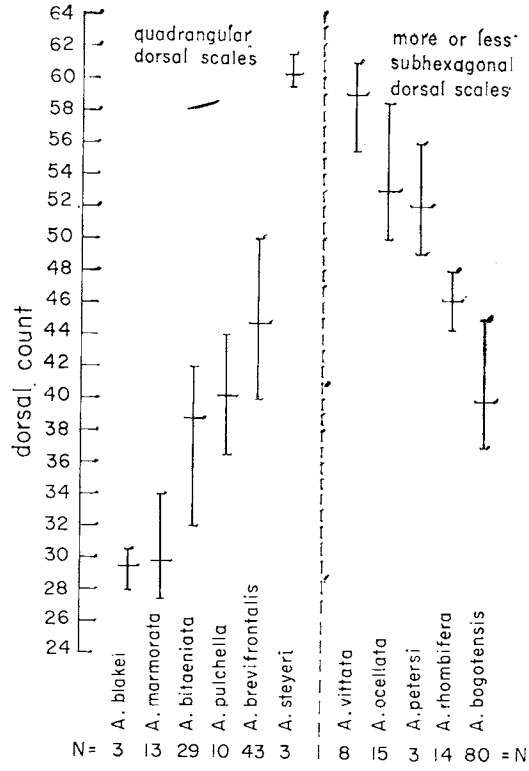

Fig. 4, Distribution of dorsal counts.

4. The subocular count refers only to scales in contact with both the eye opening and the supralabials but excludes the large frenocular scale which, though often in contact with the eye opening lies anterior to it (figs. 1, 2). Previous authors have frequently used the term infra-orbital in place of subocular.

5. Gular scale count refers to the number of transverse rows from (and including) the apex formed between the large chin-shields where they meet mid-ventrally to (and including) the enlarged collar row. Due to a degree of disorderly arrangement of scales in this area, the gular count is of necessity approximate. In general, an irregular insertion of one or a few scales has not been considered a row.

6. Dorsal count is a standardization of the traditional occiput to base of the tail count. The count refers to the number of transverse scale rows from (and including) the third row behind the interparietal (this

is most often the first row passing behind the ear, as in figures 1 and 2) to (and including) the row determined by the vertical plane connecting the rear edges of the hind limbs when the latter are held perpendicular to the body axis. As occasional irregularities along the middorsal line sometimes result in an unequal number of transverse rows on the right and left sides, it has been necessary to count both sides, and average the result. The dual figures (e. g., 45r, 44) occasionally given in the typed tables represent the counts for both right and left sides, prior to averaging.

7. Ventral count refers to the number of transverse rows lying between the enlarged, overlapping collar row and the vent, hence encompassing both the traditional ventral and preanal counts. These traditional counts have been combined so as to overcome the ambiguity that arises in trying to distinguish the two. In *Anadia* it is frequently unclear which scales could be considered preanal, whereas the collar to vent count is unmistakenly clear. Thus the ventral counts presented in this study represent combined figures that exceed in size the traditional counts reported by previous investigators by an amount of two or three rows. In certain specimens irregularities along the ventral midline have necessitated counting the transverse rows on both sides of the midline, and averaging these two figures to give the ventral count.

8. Midbody count refers to the number of scales encircling the trunk at midbody. The exact location of this midbody annulus is important since neighboring annuli may differ in the number of scales they include. The following procedure for determining the midbody annulus has been adopted:

a) Count the number of transverse ventral rows that lie between the fore and hind limbs, i. e. those rows which laterally pass up the side between the limbs. Occasional irregularities along the ventral midline may cause this figure to differ on the right from on the left side. In such an event count on the right side of the specimen.

b) Halve this figure. If the figure to be halved is odd, add one before halving such that the resultant halved figure is an integer.

c) Beginning at the anteriormost transverse ventral row included in the initial count, count towards the tail this halved figure. The transverse row thus located is the midbody annulus.

9. Measurements were all made with a dial caliper of 1/10 mm calibration, with the exception of tail length which was measured with a straight rule in mm.

Key to *Anadia*

1. Ventral scales squared off (i. e. posterior edges not rounded or pointed), or if at all rounded, venter light 2

   Ventral scales quite rounded and imbricate, at least on posterior portion of belly; venter slate, dark grey or grey-brown. (Colombian Andes.) ..... *bogotensis*

2. Dorsal count less than 55, or if greater than 55, midbody count less than 40 and suboculars uneven in size, one extending downward between 4th and 5th supralabials as an angular (wedge-shaped) protrusion (fig. 25A) 3

   Dorsal count more than 55; midbody count more than 40; sub-oculars uniformly large and regular, none extending downward between 4th and 5th supralabials as an angular (wedge-shaped) protrusion (fig. 25B). (Coastal north-central Venezuela) .... *steyeri*

3. Dorsal scales much larger than ventral scales (*marmorata* group) 4
   Dorsal scales smaller than or same size as ventral scales 5

4. Suboculars large and regular (fig. 20A); tip of snout light; dark markings on infralabials. (Northcentral Venezuela) .... *marmorata*

   Suboculars very small and irregular (fig. 20B); tip of snout same color as head; only occasional marking on infralabials. (Northeastern Venezuela). ..... *blakei*

5. Dorsal scales somewhat hexagonal in shape (fig. 23); (*ocellata* group) 6

   Dorsal scales quadrangular (fig. 23). Suboculars in an uneven row, one extending downward between the 4th and 5th supralabials as an angular (wedge-shaped) protrusion (fig. 16); dorsal ground color slate, grey-brown or bluish. (*bitaeniata* group) 9

6. Ventral scales quadrangular, juxtaposed or but very slightly imbricate; dorsum having light dorsolateral lines on darker ground, or uniformly light brown or rust 3

   Ventral scales with rounded posterior edges and clearly imbricate; no light dorsolateral lines; dorsum brown with or without dark markings (figs. 11, 12). (Southcentral Ecuador.) .... *petersi*

7. Dorsal count more than 49 8
   Dorsal count less than 49 (Central Ecuador) ..... *rhombifera*

8. Light dorsolateral line 3 or more scale rows wide, sometimes indistinct due to paleness of dorsum; mid-dorsal region pale or marked with dark specks more or less fused into 3 longitudinal lines (fig. 8). (Eastern Panama and Pacific Colombia.) .... *vittata*

   Light dorsolateral line not much wider than 2 scale rows across; mid-dorsal region uniformly dark or heavily marked with spots, blotches or zigzag pattern (fig. 5). (Central and western Panama, Costa Rica.) ..... *ocellata*

9. Palpebrals unpigmented or with but a few speckles of pigment; ventral surface of thighs cream-colored or with colorful hues, but not slate-grey, blue-grey or blue. (Elevations of 2500-3050 m in the Venezuelan Andes.) ..... *bitaeniata*

   Palpebrals well speckled with pigment; ventral surface of thighs slate-grey, blue-grey or blue. (Elevations of 2900-3500 m in the Venezuelan Andes.) ..... *brevifrontalis*

Anadia ocellata Gray

Anadia ocellata Gray, 1845: 58 (Type locality: "Tropical America?", corrected herein to "Costa Rica or Panama."); Gray, 1851, pl. vi, fig. 1; Boulenger, 1885: 398-399.
Ecpleopus (*Euspondylus*) *ocellatus;* Peters, 1862: 212.
Chalcidolepis metallicus Cope, 1875: 116-117, pl. 24, fig. 5; pl. 28, fig. 2. (Type locality: "Aguacate Mountains", Costa Rica). *New Synonymy.*
Ecpleopus (*Chalcidolepis*) *metallicus;* Duméril & Bocourt, 1879: 371-372.
Leposoma ocellatum; Cope, 1885: 97.
Leposoma metallicum; Cope, 1885: 97-98; 1887: 45.
Anadia metallica; Günther, 1885: 30; Boulenger, 1885: 400.
Anadia metallica metallica Taylor, 1955: 535-537.
Anadia metallica attenuata Taylor, 1955: 537-542. (Type locality: Pacuare, Rio Pacuare, Cartago Province, Costa Rica). *New Synonymy.*
Anadia metallica arborea Taylor, 1955: 542-545. (Type locality: Las Flores, Tenorio, Guanacaste Province, Costa Rica). *New Synonymy.*

Diagnostic Traits: 1. high dorsal count: 50-58.5; 2. midbody count: 27-32; 3. dorsal scales quadrangular-subhexagonal, with posterior edges somewhat rounded (fig. 23); 4. nasal with subnostril groove, or divided vertically through nostril (fig. 25A); 5. long suture between prefrontals; 6. usually 1-2 small scales between superciliary row and supraoculars (fig. 25A); 7. suboculars unequal in size, one protruding downward between 4th and 5th supralabials (fig. 25A); 8. narrow dorsolateral light line (fig. 5); 9. prevalence of dark marking in the middorsal area; 10. dark stripe passing through eye and onto side of body, containing light ocelli (fig. 5); 11. venter light; 12. femoral pores 8-11 in male, 2-6 in female; 13. head and body slender, tail long (fig. 5).

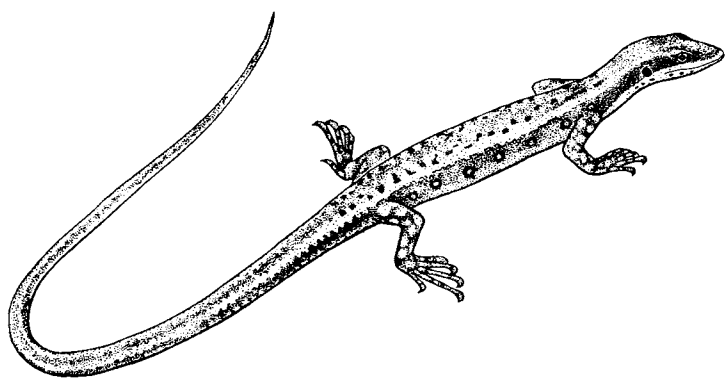

Fig. 5, Color pattern of *A. ocellata.* Drawn from KU 113567 (snout-vent length 54.5 mm, female).

A. ocellata may be distinguished from: 1. *A. rhombifera, A. bogotensis, A. pulchella, A. bitaeniata, A. marmorata* and *A. blakei* by the high dorsal count; 2. *A. steyeri* and *A. brevifrontalis* by the shape of dorsals, the subnostril groove, the dark lateral stripe and the lateral ocelli; 3. *A. petersi* by the light dorsolateral lines; 4. *A. vittata* by the narrowness of the dorsolateral line and the prevalence of dark markings in the mid-dorsal region.

Description (N=15)

Each nasal single with groove from nostril to supralabial below, or divided vertically through nostril. Nasal sometimes in contact with rostral. Midline suture between prefrontals long. 3 supraoculars and a presupraocular. 3-5 superciliaries. 0-2 small scales inserted between superciliary row and supraoculars. 3-5 unpigmented palpebrals. 4-6 suboculars, one forming angular protrusion downward between 4th and 5th supralabials. 14-20 transverse gular rows. No sexual dimorphism in head size.

Dorsal scales smooth, quadrangular-subhexagonal, with somewhat rounded posterior edges, arranged in 50-58.5 very slightly imbricate transverse rows from ear to tail. Lateral scales slightly smaller, more rounded, less regular than dorsals, such that many transverse rows pass about body as annuli without lateral irregularities. 27-32 scales in mid-body annulus. Ventrals quadrangular, arranged in 35-41.5 juxtaposed transverse rows from collar to vent. 3-8 quite large scales along anterior border of vent. Femoral pores 8-11 (including 1-2 on interfemoral scales) in male, 2-6 in female. 14-18 lamellae under fourth toe of hind limb. Maximum snout-vent length, 74.4 mm (female).

Variation

Of 15 specimens: nasal fully divided in 6, contacting rostral in 3; no inserted superciliary between outer superciliary row and suproculars in 2; third pair of chin-shields in contact along midline in 10.

Color Pattern (fig. 5)

Coloration, both of live and preserved material, has been discussed in detail for several specimens by Taylor (1955). In life, the dorsum may be a metallic olive, brownish-olive or bronze, this being usually a consequence of dark mottling or dense dark flecking on a lighter background, though one preserved specimen is uniformly dark in the mid-dorsal region. A narrow (about 2 scales wide) and somewhat irregular dirty-white or clay-colored dorsolateral line extends on each side from above the orbit onto the tail and is bordered below by a dark longitudinal stripe passing through the eye, above the arm-insertion along the lateral surface and onto the tail. The latter dark stripe contains 3-8 light, often black-bordered ocelli arranged in a more-or-less linear fachion. The chin and venter are unblemished or with fine speckles of dark pigment and usually of a creamy color, but one live male (51.4 mm in snout-vent length) from El Valle, Panama was yellow ventrally and had a dull-red tail. Photographs of 3 specimens are to be found in Taylor (1955).

Range and Habitat

This species has been found from northwestern Costa Rica to central Panama west of the Canal Zone, in low montane regions (fig. 6). Estimated elevations are available for three Panamanian localities: 2500 ft. (ca. 760 m), 910 m, and 4300 ft. (ca. 1310 m), and for one Costa Rican: 1200 m.

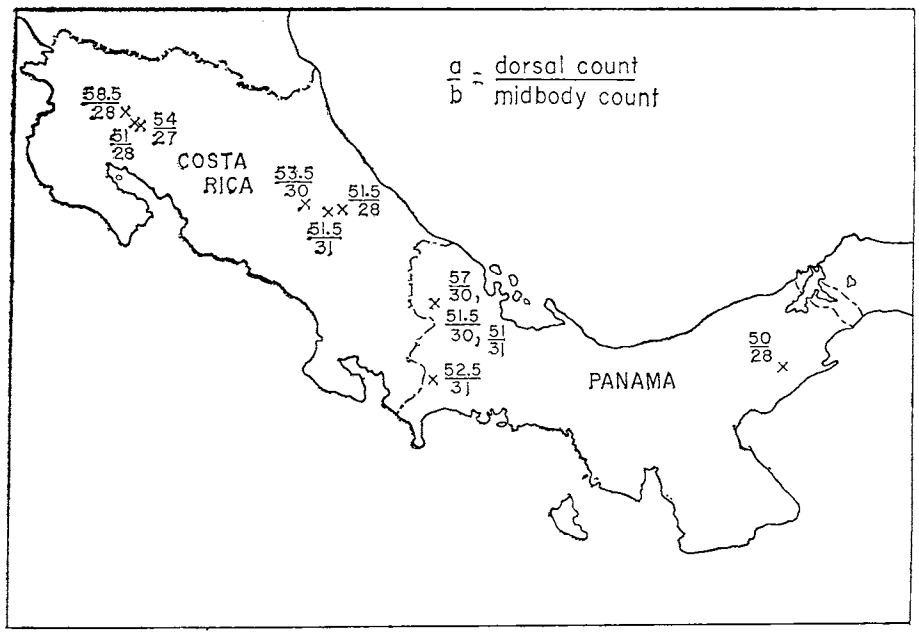

Fig. 6, Geographic distribution of dorsal and midbody counts of *A. ocellata*.

Apparently *A. ocellata* is largely arboreal, as noted by Taylor (1955). He reported Costa Rican specimens being collected on a tree bole some eight feet (2.4 m) from the ground, from a bromeliad in a forest tree at some distance from the ground, and in a field recently cleared of forest trees. On the basis of three additional specimens, including one taken in a bromeliad 30 feet (9.1 m) up in a tree in open forest, Heyer (1967) suggested a correlation of the distribution of this species with that of large tank bromeliads. The single central Panamanian specimen, from El Valle, Cocle Province, was located (by Dr. G. B. Fairchild and the author) during the day about 1 meter from the ground concealed beneath the still clasping base of a dead frond of a banana plant not far from uncleared forest; in captivity it showed preference for moist places.

Discussion

By 1845 an adult specimen from "Tropical America?" had found its way into the hands of John Edward Gray at the British Museum. Recognizing its uniqueness, Gray erected a new family (Anadiadae) for

the "Eyed Anadia." The family was short-lived (Wilhelm Peters, 1862), but the British Museum specimen remains a type of the genus, and hence deserves a more definite designation of locality.

An attempt at such a designation of locality was made by Dunn (1944a) on the basis of a specimen from Jericó, Antioquia, Colombia (originally described as *Euspondylus acutirostris* by Burt, 1932) which Dunn referred to *A. ocellata.* Yet the discrepancies between the two in meristic counts are too great; this second specimen has turned out to be *A. rhombifera* (for further discussion of this specimen, see p. 223). Somewhat later James Peters (1959) was confronted with two Ecuadorian specimens of *Anadia petersi* which he erroneously assigned to *A. ocellata.* This explains the two erroneous localities for *A. ocellata* given in Peters' check list (1967) and in his more recent catalogue (Peters and Donoso-Barros, 1970).

Examination of the type (BM 1946. 8.2.2) revealed it to be conspecific with what has been called *A. metallica* (Cope) as verified by supraocular, superciliary, nasal, dorsal, ventral and midbody scale counts, femoral pore counts, head and body proportions, and coloration. As the latter species was described by Cope (1875), 31 years after *A ocellata, A. metallica* must be regarded as a junior synonym (New Synonymy). The two could stand side by side in Boulenger's *Catalogue* (1885) only as a result of ambiguity in Cope's (1876) description which led Boulenger to misinterpret the dorsal count. [1] As specimens of this species have been collected from Panama west of the Canal Zone to northwestern Costa Rica, it is quite certain that the type locality also lies within this region, and that Colombia and Ecuador are not within the range of *A. ocellata.*

Taylor (1955) on the basis of 5 specimens, Cope's type description of *metallica,* and notes on Cope's holotype furnished by Doris Cochran, erected three subspecies of *A. metallica.* The criteria given do not however, withstand further investigation. Dorsal and midbody counts show variation but these are not correlated with geographic distribution, as Taylor supposed (fig. 6). The holotype of *A. metallica arborea,* though having an extreme dorsal count (58.5), was collected from an area that has since yielded three specimens of lower dorsal counts (51, 51.5 and 54) (refer to fig. 6 for locality designation of two of these). Femoral pores reflect sexual dimorphism and hence are not suitable as key characters unless sex is specified, which Taylor did not do. Furthermore, the variation in coloration of the additional material does not support Taylor's subspecies. Hence these subspecies are here synonymized.

A. ocellata is the northernmost species of the *ocellata* group (see p. 253) and one of the two Central American representatives of the genus. The other species, which makes an intrusion only into eastern Panama, is not only geographically closest, but most similar morphologically as

1. Cope's description of "twelve transverse rows between the large postoccipital row and the line of the axillae, and forty-three to the line of the posterior faces of the femora" was taken by Boulenger (1885) to mean "forty-three from occiput to sacrum, inclusively" rather than fifty-five (43+12) as Cope intended.

well. Indeed, *A. ocellata* and *A. vittata* seem as closely related as any pair of species in *Anadia,* and were confused in the initial examinations of this study. Yet the greater number of body scales (especially dorsal and midbody counts - see table 1), the greater number of femoral pores in the male, and the differing coloration of *A. vittata* clearly set the latter species apart from *A. ocellata* (see the discussion of *A. vittata,* p. 221). It is likely that *ocellata* and *vittata* represent a fairly recent invasion of Central America.

Specimens examined

Holotype. "Tropical America?" BM 1946.8.2.2.

Additional specimens. COSTA RICA: "Aguacate Mountains", USNM 30568 (holotype, *Chalcidolepis metallicus*). *Guanacaste Province*: Las Flores, Tenorio, KU 34225 (holotype, *A. metallica arborea*); Silencio, by trail to La Laguna, 9 mi. W. of La Casa, USC-CRE 6237; San Bosco Forest, USC-CRE 6277; Tilaran, 2.7 mi. NNE on Arenal road, USC-CRE 8082. *Cartago Province:* Pacuare, Rio Pacuare, KU 34223 (holotype, *A. metallica attenuata*); Moravia de Chirripo, KU 34224; Moravia de Turrialba (1200m), KU 67346; "Santa Teresa Jungle," MCZ 32180. PANAMA: *Chiriqui Province*: Pan-American highway, 10 mi. from Costa Rican border (4300'), AMNH 73343. *Bocas del Toro Province:* Rio Claro near junction Rio Changera (910m), KU 113566-68. *Cocle Province:* El Valle (ca. 2500'), NMC 10870.

Anadia vittata Boulenger

Anadia vittata Boulenger, 1913: 1033, pl. 107, fig. 2 (Type locality; Peña Lisa [300'], Condoto, Chocó Province, Colombia.); Dunn, 1944a: 67.
Anadia angusticeps Parker, 1926: 550-552. (Type locality: Gorgona Island, Cauca Province, Colombia). *New Synonymy;* Dunn, 1944a: 67.

Diagnostic Traits: 1. high dorsal count: 55.5-61; 2. midbody count: 30-37; 3. dorsal scales quadrangular-subhexagonal, with posterior edges slightly rounded (fig. 23); 4. nasal with subnostril groove, or divided vertically through nostril (fig. 16); 5. long suture between prefrontals; 6. usually 1-2 small scales between superciliary row and supraoculars (fig. 25A); 7. suboculars unequal in size, one protruding donwnward somewhat between 4th and 5th supralabials (fig. 25A); 8. moderately broad light dorsolateral lines, or entire mid-dorsal region pale (fig. 8); 9. dark stripe passing through eye and onto side of body often containing ocelli, but sometimes "faded" (fig. 8); 10. venter light; 11. femoral pores 11-14 in male, 2-4 in female; 12. head and body slender, tail long (fig. 8).

A. vittata may be distinguished from: 1. *A. rhombifera, A. bogotensis, A. pulchella, A. bitaeniata, A. brevifrontalis, A. marmorata,* and *A. blakei* by the high dorsal count; 2. *A. steyeri* by the lower midbody count, the shape of the dorsals, the subnostril groove, the condition of the

suboculars, and the dorsal and lateral coloration; 3. *A. petersi* by the light dorsolateral line or pale mid-dorsal coloration; 4. *A. ocellata* by the breadth of the dorsolateral line and/or the relative paucity of dark markings in the mid-dorsal region.

Description (N=8)

Each nasal single with shallow groove from nostril to supralabial below, or divided vertically through nostril. Nasal not in contact with rostral. Midline suture between prefrontals long. 3 supraoculars and 0-2 presupraoculars. 3-5 superciliaries. 0-2 small scales inserted between

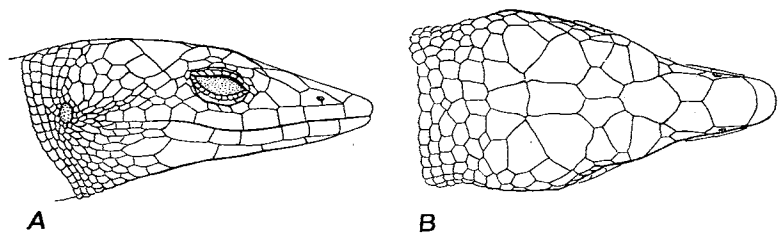

Fig. 7, Head scales of *A. vittata*. Drawn from FM 664.

superciliary row and supraoculars. 4-6 unpigmented palpebrals. 4-6 suboculars, one forming slight angular protrusion downward between 4th and 5th supralabials. 17-20 transverse gular rows. No sexual dimorphism in head size.

Dorsal scales smooth, quadrangular-subhexagonal, with slightly rounded posterior edges, arranged in 55.5-61 very slightly imbricate transverse rows from ear to tail. Lateral scales somewhat smaller, more rounded and less regular than dorsals, such that many transverse rows pass about body as annuli without lateral irregularities. 30-37 scales in mid-body annulus. Ventral scales quadrangular, arranged in 37-42.5 juxtaposed transverse rows from collar to vent. 4-6 quite large scales along anterior border of vent. Femoral pores 11-14 (2 on interfemoral scales) in male, 2-4 in female. 14-17 lamellae under fourth toe of hind limb. Maximum snout-vent length 67.0 (male).

Variation

Of 8 specimens, nasal divided on both sides in 2, on one side in 1; two presupraoculars on one side in 1, on both sides in 1; no presupraocular in 1; third pair of chin-shields in contact along midline in 3.

Color Pattern (fig. 8)

Characteristic of this species is the relatively wide, 3 or more scales across, light dorsolateral line extending along each side from above the eye, which in specimens from Gorgona Island, Colombia, and eastern

Panama is more or less merged in the overall light greyish-brown dorsal ground. In the case of darker mid-dorsal markings, these are arranged in three longitudinal rows, one middorsal and one on each side bordering the inner edge of the light dorsolateral line. Below the light line a brown lateral stripe passes through the eye and onto the lateral surface of the head and body. Within this stripe are found 2-11 usually black bordered ocelli, except in the pale Gorgona Island forms which lack both the distinct stripe and the ocelli. The chin and belly are whitish and unmarked

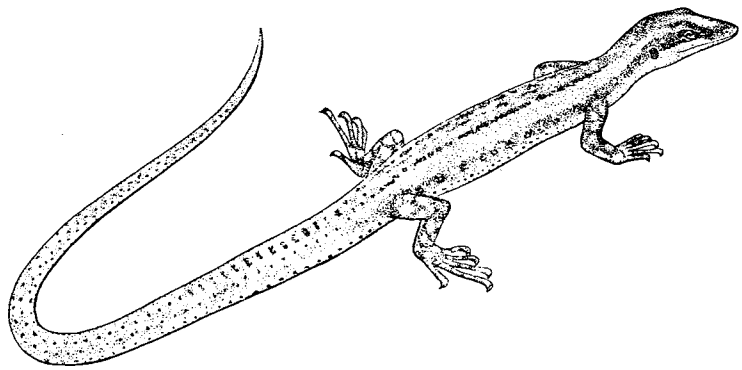

Fig. 8, Color pattern of *A. vittata*. Drawn from FMNH 165797 (snout-vent length 55.7 mm, male).

or with but a few venterolaterally situated darker specks. In life, one of the pale Gorgona Island individuals was "dorsally rusty colored, ventrally whitish" (F. Medem, field notes). If additional specimens from this island continue to exhibit this distinctly pale, seemingly faded coloration, it may be appropriate to regard this population as a separate subspecies (see discussion below). A few notes on the coloration of the holotype may be found in Boulenger's description of *A. vittata* (1913) and of a Gorgona Island specimen in Parker's description of *A. angusticeps* (1926).

Range and Habitat

The few scattered localities at which *A. vittata* has been obtained would suggest this species to range from east-central Panama to southern Colombia. Apparently a lowland species (recorded elevations: 10 m, and 300 ft = ca. 90 m), *A. vittata* has been collected on the ground (FM 649, 663, 664 — field notes) in tropical rain forest. F. Medem (field notes) records it as climbing on small branches and feeding on small crickets in captivity.

Discussion

A. vittata was described in 1913 by Boulenger, one of the few systematists with a familiarity with the genus. The new species was, he noted, "closely allied to *A. ocellata* Gray." Subsequently, Parker (1926)

described the species *A. angusticeps* which he believed differed from the former "in its more slender form, longer snout (and consequently differently proportioned head-shields), and coloration." Dunn, however, in his 1944 survey of *Anadia* and *Ptychoglossus* in Colombia, remarked on the similarities of the two species, and suggested that "as both are known only from a single specimen they may not be distinct."

Examination of the types (Table 3) and additional material confirms Dunn's suggestion. The more slender form and longer snout cited for the *angusticeps* type relative to that of *vittata* merely reflect slight individual variability much less than the distinct difference in snout length and shape discernible between these specimens and those of *A. ocellata*. While the indistinctly marked and pale appearance of the *angusticeps* type may be characteristic of the Gorgona Island population (a second specimen subsequently collected is similarly pale), this difference does not seem to justify regarding the Gorgona population as a separate species in light of the tendency of *A. vittata* as a species to reduce dark pigmentation relative to *A. ocellata* and the agreement of the meristic counts of the Gorgona material with those of mainland specimens. Nonetheless, since the gene flow between the island and mainland populations may be limited or negligible, selective forces may have molded this species on Gorgona Island into a distinguishable insular subspecies. If additional specimens from Gorgona Island also bear out the differences in coloration between Gorgona Island and mainland Colombian specimens, the name *angusticeps* is available for purposes of subspecific recognition. A paucity of specimens from Gorgona Island and the lack of differences in scale counts and scale traits between the insular and mainland forms make any systematic alterations beyond the placement of *A. angusticeps* into synonymy with *A. vittata* inapropriate.

The reduction of dark dorsal pigmentation and the greater width of the light dorsolateral stripes are in fact the most immediately apparent traits that differentiate this species from its closely related Central American neighbor, *A. ocellata*. In addition, the latter tends to have lower dorsal and midbody scale counts (Table 1) and fewer femoral pores in the male. As mentioned above, the snout of *A. vittata* is somewhat more narrow and longer than that of *A. ocellata*. As well as geographic non-overlap, the two species occupy different elevations (*A. vittata* has been recorded from 10 m and 90 m, *A. ocellata* from 760 m, 910 m, and 1310 m) and possibly different ecological niches, *A. ocellata* being perhaps more arboreal.

To the south, in Ecuador, occur the two other species of the *ocellata* group, *A. rhombifera* and *A. petersi*. The former is distinguished by its different coloration, stouter body and lower dorsal and midbody counts, while *A. petersi* differs in the more imbricate nature of its dorsal and ventral scales, the darker ground color, the lack of light dorsolateral lines, and the sexual dimorphism of head and body size.

Specimens Examined

Holotype. COLOMBIA: *Chocó Province:* Condoto, Peña Lisa (300') BM 1913.11.12.34.

Additional specimens. COLOMBIA: *Chocó Province:* Condoto, Peña Lisa, BM 1946.8.2.35; *Valle Province:* lumber camp "Carton de Colombia", 7 km W. of Rio Calima on road to Buenaventura, FMNH 165797, FM 663-64; *Cauca Province*: Gorgona Island, BM 1946.9.1.2 (holotype of *A. angusticeps*); Gorgona Island, northern part (10 m), FM 649. PANAMA: *Panama Province:* trail between Atlas de Pacora and San Blas, GML specimen.

Anadia rhombifera (Günther)

Cercosaurus rhombifer Günther, 1859: 406-407, pl. 20, fig. A (Type locality: "W. Ecuador".)
Ecpleopus (Euspondylus) rhombifer; Peters, 1862: 208-209.
Leposoma rhombiferum Cope, 1885: 98.
Anadia rhombifera Boulenger, 1885: 399; Burt & Burt, 1931: 312.

Diagnostic Traits: 1. dorsal count: 44-48.5; 2. midbody count: 28-34; 3. dorsal scales subhexagonal; 4. nasal with shallow or indistinct subnostril groove (fig. 25A); 5. long suture between prefrontals; 6. often 1-2 small scales between superciliary row and supraoculars (fig. 25A); 7. palpebrals unpigmented; 8. dorsum light or dark brown, either without marking or with scattered to dense dark flecks (fig. 9); 9. dark lateral stripe passing from ear onto side of body, sometimes containing prominent black-bordered ocelli (fig. 9); 10. venter light, often dusted with pigment along its sides; 11. femoral pores: 8-15 in male, 0-2 in female.

A. rhombifera may be distinguished from: 1. *A. ocellata, A. vittata, A. petersi,* and *A. steyeri* by the lower dorsal count; 2. *A. bitaeniata, A. marmorata* and *A. blakei* by the higher dorsal count; 3. *A. pulchella* and *A. brevifrontalis* by the subhexagonal shape of the dorsals, the subnostril groove, and the higher male and lower female pore counts; 4. *A. bogotensis* by the less imbricate and rounded dorsals, the brown dorsum, the dark lateral stripes, and the light venter.

Description (N=14)

Each nasal single with shallow or indistinct groove from nostril to supralabial below, or divided vertically through nostril. Nasal sometimes in contact with rostral. Midline suture between prefrontals long. 3-4 supraoculars and 0-1 presupraoculars. 3-6 superciliaries. 0-2 small scales inserted between supercialiary row and supraoculars. 3-6 unpigmented palpebrals. 4-6 suboculars, one forming slight angular protrusion downward between 4th and 5th supralabials. 13-17 transverse gular rows. Little sexual dimorphism in head size.

Dorsal scales smooth, subhexagonal, with rounded posterior edges, arranged in 44-48.5 somewhat imbricate transverse rows from ear to tail. Lateral scales slightly smaller and more rounded than dorsals, such that many transverse rows pass about body as annuli without lateral irregularities. 28-34 scales in midbody annulus. Ventral scales qua-

drangular, arranged in 31-35 juxtaposed or slightly imbricate transverse rows from collar to vent. 4-7 quite large scales along anterior border of vent. Femoral pores 8-15 (0-1 on interfemoral scale) in male, 0-2 in female. 15-19 lamellae under fourth toe of hind limb. Maximum snout-vent length 68.0 mm (male).

Variation

Of 14 specimens: nasal divided in 3, contacting rostral in 4; no presupraocular in 2; no scales inserted between supercialiary row and supraoculars in 1; loreal not connected to supralabials in 1; third pair of chin-shields in contact along midline in 5.

Color Pattern (fig. 9)

Coloration was described for the type by Günther (1859). This species demonstrates distinct sexual dimorphism in color pattern.

In the adult female the brown dorsum is heavily marked with brown or dark brown flecks in the middorsal region, giving the appearance in some specimens of a dark vertical band flanked by lighter, grayish tan dorsolateral stripes. From the orbit a dark brown, readily apparent

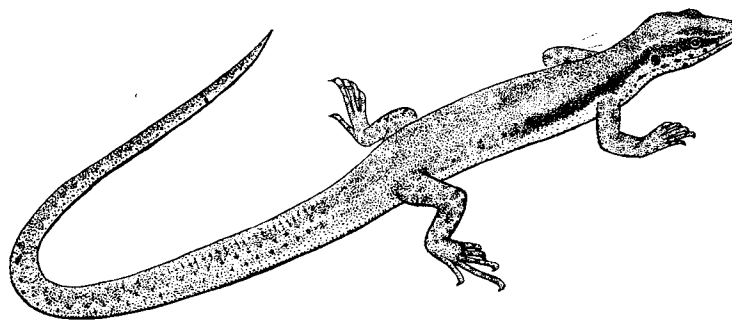

Fig. 9, Color pattern of *A. rhombifera* male. Drawn from KU 109711 (snout-vent length 59.3 mm, male).

stripe extends laterally along the body to the base of the tail, although it may become indistinct as it approaches the latter. This stripe may contain a few or many longitudinally aligned light, cream-colored spots, but there are no pronunced ocelli. Venter white or cream, often heavily dusted with brown pigment along its sides. Juvenile specimens resemble the females, except that the ventral surface of the tail is salmon (field notes of William E. Duellman for KU 142758-60).

The adult male is considerably less marked dorsally (fig. 9). The dorsum is brown and unmarked or with scattered small dark specks which in some specimens suggest a faint vertical band. The dark lateral stripe often contains one to six or more prominent ocelli, these consisting of very dark rings about a cream-colored center. The venter in life is more vividly colored than that of the female: "throat pale yellow; belly yellow

becoming pale orange posteriorly and on ventral surface of tail" (field notes of William E. Duellman for KU 142755-57).

The specific name apparently refers to the markings on the tail of the type: "the dorsal line appears spotted with darker, the spots assuming the regular form of rhombs at the origin of the tail, and forming a continuous band to its tip" (Günther, 1859). Such a distinct pattern is characteristic of the female alone. Some specimens of *A. ocellata* and *A. vittata* have a similar pattern on the tail.

In poorly preserved material fading of pigmentation of the scales can cause dark pigmentation of underlying tissue to show through. Thus the Jericó specimen (ILS 333) referred to by Burt (1932) as having a slate colored ventrum does in fact seem very slate-blue. Even the spots on the sides which were apparently cream colored in life seem bluish in preservation. In freshly preserved material the underlying tissue is apparently bluish-green.

Range and Habitat

This species has been collected from the slopes of the Cordillera Real in Ecuador at altitudes of 500m, 700m and 1570m as well as from the Cordillera Oriental in central Colombia at an altitude of 1760m. Presumably this species ranges at intermediate altitudes between the lowland *A. vittata* of Pacific Columbia and the montane *A. bogotensis.* The Rio Verde specimens were taken from arboreal bromeliads during daytime (field notes of W. E. Duellman).

Discussion

The dorsal scale shape, the head scales, the coloration pattern, the body size and proportions, and the arboreal habitat of this species clearly indicate its proximity to other *ocellata* group species such as *A. ocellata* and *A. vittata.* Yet unlike these latter two species, *A. rhombifera* is sexually dimorphic in head and body size, the adult male having a proportionately larger head as well as being of greater size than the female. In *A. petersi* this dimorphism is even more greatly pronounced, however.

In 1944 Dunn referred to *A. ocellata* a specimen, described by Burt (1932) as *Euspondylus acutirostris.* Examination of this specimen (ILS 333) reveals that it does in fact belong to the *ocellata*-group, but to the species *A. rhombifera* rather than *A. ocellata.* This fact is most clearly demonstrated by the dorsal and ventral counts which are 45r, 46 (45 to the right of the midline, 46 to the left) and 32 respectively. (The counts given by Burt were 47 and 30; see discussion of methods of study, p. 211).

Specimens Examined

Holotype. "W. Ecuador", BM 1946.9.1.4.

Additional specimens. ECUADOR: *Pichincha Province:* Santo Domingo de Los Colorados (500m), KU 109711, 142753, *Bolivar Province:*

Balzapamba (700m), AMNH 24201, 32779, *Tungurahua Province*: 1.3 km W. Rio Verde (1570m), KU 142754-60. COLOMBIA: *Antioquia Province:* Jericó (1760m) ILS 333; *Boyacá Province:* Otanche, in the Muzo district ILS 334.

Anadia petersi, sp. n.

A. ocellata (in error) Peters, 1959: 121-133.

Holotype: USNM 193221, adult male from San Ramon, near Loja, Loja Province, Ecuador.

Paratypes: USNM 193222, female from same locality; ZSM 47/1928 "Ost-Ecuador".

Diagnostics Taits: 1. high dorsal count: 49-56; 2. midbody count: 31-33; 3. dorsal scales elongate subhexagonal, with posterior edges rounded, imbricate; 4. ventral scales with posterior edges rounded and quite imbricate, at least on rear portion of belly; 5. moderately long suture between prefrontals; 6. 0-2 small scales between superciliary row and supraoculars (fig. 25A). 7. palpebrals unpigmented; 8. suboculars unequal in size, one protruding between 4th and 5th supralabials (fig. 25A); 9. dorsum brown, unmarked or with short transverse dark bars, but without distinct light dorsolateral lines (figs. 11, 12); 10. prominent, black-bordered lateral ocelli (figs. 11, 12); 11. venter light, unmarked; 12. femoral pores: 9-10 in male, 1-2 in female.

Anadia petersi may be distinguished from: 1. *A. bogotensis, A. pulchella, A. bitaeniata, A. marmorata* and *A. blakei* by the high dorsal count; 2. *A. steyeri* by the lower midbody count; 3. *A. brevifrontalis* by the presence of prominent, black-bordered lateral ocelli; 4. *A. vittata, A. ocellata* and *A. rhombifera* by the elongate, more overlapping dorsal and ventral scales.

Description (N=3)

Each nasal single with or without shallow vertical groove from nostril to supralabial below, not contacting rostral. Midline suture between prefrontals moderately long. 3 supraoculars, but no presupraocular. 3-5 superciliaries. 0-2 small scales inserted between superciliary row and supraoculars. 4-5 unpigmented palpebrals. 4-5 suboculars, one forming angular protrusion downward between 4th and 5th supralabials. 15-17 transverse gular rows. Head of male expanded posterolaterally, and proportionately larger than that of female.

Dorsal scales elongate subhexagonal with posterior edges rounded, arranged in 49-56 imbricate transverse rows from ear to tail. Lateral scales slightly smaller, more rounded and less regular than dorsals, such that many transverse rows pass about body as annuli without lateral irregularities. 31-33 scales in midbody annulus. Ventral scales quadrangular, posteriorly somewhat rounded and quite imbricate (at least on

rear portion of belly), arranged in 35.5-36 transverse rows from collar to vent. 6 quite large scales along anterior border of vent. 9-12 femoral pores in male, 1-2 in female. 19-20 lamellae under fourth toe of hind limb. Maximum snout-vent length 74.3 (male).

Variation

The important counts and measurements have been tabulated to illustrate the variation of the specimens. It will be noted that the data for two of these specimens given by Peters (1959) are not equivalent with those given here; his method of counting was different.

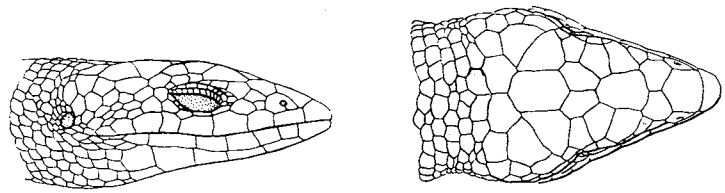

Fig. 10, Head scales of *A. petersi*. Draw from paratype USNM 193222.

Color Pattern (figs. 11, 12)

Peters (1959) gave a Spanish description of the coloration of two specimens. The adult males and the adult female are quite differently marked, suggesting sexual dimorphism in coloration similar to that in *A. rhombifera*.

The dorsum is brown, in the male unmarked, but in the female marked with two longitudinal rows of short dark transverse bars and a few scattered whitish flecks. In both cases a defined light dorsolateral

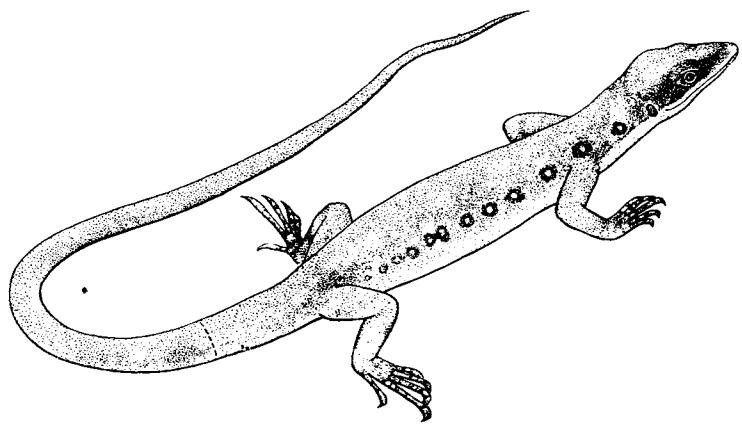

Fig. 11, Color pattern of *A. petersi*, holotype. Drawn from USNM 193221 (snout-vent length 67.5 mm, male).

line is absent. The lateral surface of the head of the male is unmarked, while the female has a somewhat darker stripe extending from the eye to above the forelimbs at which point the stripe merges with the brown ground color. On the side is a longitudinally aligned row of 6 (in the female) to 9-12 (in the male) prominent, black bordered white ocelli. All ventral surfaces are light and unblemished, except for some darker flecks to the sides in one male.

Range and Habitat

The type and one paratype are from south central Ecuador, near Loja in Loja Province. The city of Loja is situated at 2200 m. The Münich specimen has only the indefinite locality "Ost-Ecuador."

Discussion

The referral by J. A. Peters (1959) of two Ecuadorian *Anadia* to the species *ocellata* was made before examination of the type of that species demonstrated that *ocellata* is a Central American form. Since it

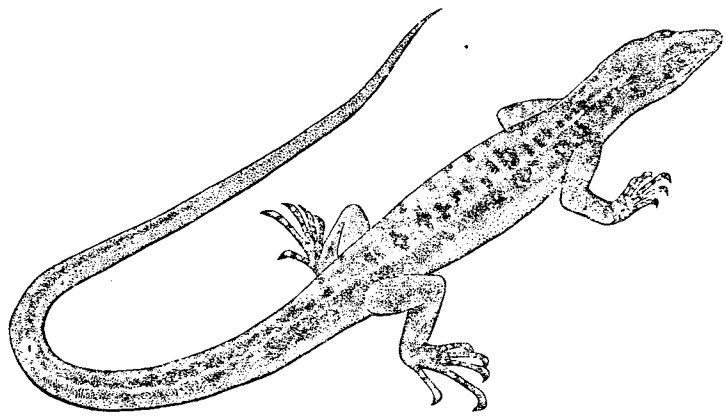

Fig. 12, Color pattern of *A. petersi*, paratype. Drawn from USNM 193222 (snout-vent length 60.5 mm, female).

appears that no published name is available for these specimens, they are designated as type and paratype of a new species, *Anadia petersi*. A specimen in the Staatsmuseum, Munich, bearing a manuscript name by Lorenz Müller proves to be a second paratype of *A. petersi*.

The affinities of this species to members of the *ocellata* species-group (see p. 253) are borne out by: 1) the subhexagonal shape of the dorsal scales, 2) the subnostril groove on one nasal of the holotype, 3) the moderately long suture between the prefrontals, 4) the 0-2 small scales inserted between the superciliary row and the supraoculars, 5) the high dorsal count, 6) the reduced number of femoral pores of the female, 7) the downward angular "wedge" intrusion of a subocular

between the supralabials, 8) the unpigmented palpebrals, and 9) the conspicuous lateral ocelli.

Yet the overlapping condition of both dorsal and ventral scales approaches that of *A. bogotensis* (fig. 13), suggesting that *A. petersi* is to a certain extent intermediate between the other *ocellata* group species and *A. bogotensis*. The points 1, 3, 4, 6, and 8 above are common elements to both the *ocellata* group and *bogotensis*. Like *bogotensis*, *petersi* occurs at high elevations.

Anadia bogotensis (Peters)

Ecpleopus (*Xestosaurus*) *bogotensis* Peters, 1862: 217-220, pl. 3, fig. 3 (Type locality: Sta. Fé de Bogotá, Department of Cundinamarca, Colombia).

Anadia bogotensis; Boulenger, 1885: 400; Werner, 1916: 305; Loveridge, 1929: 100; Burt & Burt, 1931: 311; Dunn, 1944b: 17-18; 1944b: 65; Valdivieso & Tamsitt, 1963: 33.

Diagnostic Traits: 1. dorsal count: 35-45.5; 2. midbody count: 24-32; 3. dorsal scales with distinct rounded posterior edges, imbricate (fig. 13); 4. ventral scales quite rounded and imbricate, at least on rear portion of belly; 5. nasal with subnostril groove, or divided vertically through nostril (fig. 25A); 6. 2 (occasionally 3) supraoculars; 7. palpebrals pigmented, forming a non-transparent disk; 8. suboculars unequal in size, one protruding downward between 4th and 5th supralabials (fig. 25A); 9. venter bluish-slate or blue-black (brownish, after long preservation) sometimes with pattern of light marking on the scale edges; 10. femoral pores: 10-16 in male, 0-2 (occasionally 5-8, indistinct) in female.

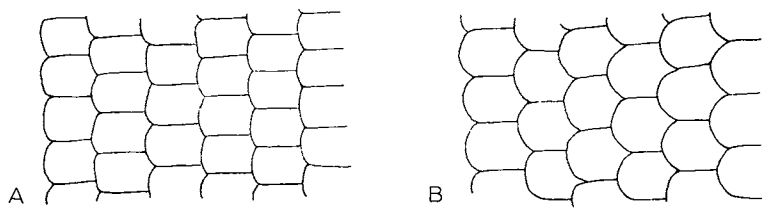

Fig. 13, Comparison of the dorsal scales of *A. petersi* (A) and *A. bogotensis* (B). Illustrated are the scales of the midback, on the rigt side of the middorsal line.

A. bogotensis may be distinguished from: 1. *A. ocellata, A. vittata, A. petersi* and *A. steyeri* by the lower dorsal count; 2. *A. marmorata* and *A. blakei* by the higher dorsal count; 3. *A. rhombifera* and *A. pulchella* by the imbricate arrangement of the dorsals and ventrals, the subnostril groove, the pigmented palpebrals and the slate or dark grey venter; 4. *A. bitaeniata* and *A. brevifrontalis* by the imbricate and rounded dorsals, the subnostril groove, and the higher male and lower female femoral pore counts.

Description (N=80 for body scale and pore counts, otherwise N=46)

Each nasal single, with groove from nostril to supralabial below, or occasionally divided vertically through nostril. Nasal may or may not contact rostral. Prefrontals usually meet to form midline suture. 2 (occasionally 3) supraoculars, no presupraocular. 2-5 pigmented palpebrals forming a non-transparent disk. 3-5 suboculars, not equal in size (1-3 distinctly smaller), one forming angular (wedge-shaped) protrusion downward between 4th and 5th supralabials. 14-20 transverse gular rows. Head of male expanded posterolaterally and proportionately somewhat larger than that of female.

Dorsal scales subhexagonal, with distinctly rounded (sometimes even wedge-like) posterior edges (fig. 13), arranged in 35-45.5 overlapping transverse rows from ear to tail. Lateral scales smaller than or nearly equal to dorsal scales, such that many transverse rows pass about body as annuli without lateral irregularities. 24-32 scales in midbody annulus. Ventral scales quadrangular, posteriorly quite rounded and imbricate (at least on rear portion of belly), arranged in 28.5 to 35.5 transverse rows from collar to vent. 4-8 quite large scales along anterior border of vent. Femoral pores: 10-16 in males, 0-2 (occasionally 5-8, indistinct) in female. 13-19 lamellae under fourth toe of hind limb.

Variation

This species is abundantly represented in collections; not all specimens have been examined. Dorsal, ventral, midbody and femoral pore counts were taken from 80 specimens, but of these only 46 were completely examined.

Of 46 specimens: nasal divided on one or both sides in 4; nasal not contacting rostral in 18; prefrontals not meeting to form midline suture in 6; prefrontals separated by a small, anomalous scale in 1; two superciliaries on one or both sides in 4; small scale inserted between superciliary row and supraoculars one or both sides in 7; only 4 scales along anterior border of vent in 1; stub feet (and hence no lamellae) in 1.

Color Pattern

The type description is still useful:

"The dorsal color is either uniform olive-brown, or flecked with blackish, or there are formed by these flecks three to five more or less regular longitudinal stripes, between which appear on certain specimens a pale longitudinal line on each side. The venter is slate-blue or blue-black, the scales often grey on the edges, the tail is as the body..." (Wilhelm Peters, 1862, pp. 220-221; translated from German).

The degree to which pale markings are present is highly variable. Certain specimens are uniformly dark brown above and slate below. The specimen from Lagunas del Chisacal (3600m), on the other hand, has numerous irregular light flecks arranged in 4 longitudinal rows on the

back, the flecks apparently having been "clear green" on a dark brown background in life. This same lizard had a blackish throat and belly with "clear yellowish spots" (corresponding to the grey edges described by Peters, quoted above), dark eyes, and dark yellow coloration under the feet (field notes of P. A. Olivares). Several of the syntypes have so much light greenish pigmentation on the back as to appear to be dorsally light with brown irregular flecks arranged in 3-4 longitudinal, occasionally fused rows, rather than vice versa; and unlike the Lagunas del Chisacal specimen, their heads are also light above. Even these, however, are laterally and ventrally dark, though having thin light markings on the edges of the scales.

Range and Habitat

A. bogotensis occupies the Cordillera Oriental (East Andes) of Central Colombia (Departments of Caldas, Cundinamarca and Boyacá), reaching elevations of at least 3600 meters. Due to a paucity of altitudinal data, the lower limit of its range is uncertain, the two lowest recorded localities, Choachi and Aquadita, being at about 2000 meters, according to Dunn (1944a). The majority of specimens have been taken near Bogotá (elevation of the city: 2317-2599m; Valdivieso and Tamsitt, 1963).

Ecological data for *A. bogotensis* are sparse: "this lizard inhabits rocky areas overgrown with grass and was taken at both localities under rocks with frogs..." (Valdivieso and Tamsitt, 1963), "specimens seen in the field were under flat stones on the ground" (Dunn, 1944a), and "on a clump of grass in a pasture" (field notes of P. A. Olivares, translated from Spanish).

Discussion

Of all *Anadia*, the species one might at first sight select as most distinctively different is *A. bogotensis*, since both the degree of roundedness of the posterior edges of the dorsal scales, and the extent to which both dorsal and ventral scales overlap is not matched by any of the other species. In fact, Wilhelm Peters (1862) went so far as to place *bogotensis* in a separate subgenus (*Xestosaurus*) from *ocellata* and *rhombifera*. Nonetheless the presence in *bogotensis* of a number of traits (dorsal scales more or less hexagonal; subnostril groove; occasional inserted scale between superciliaries and supraoculars; few femoral pores in female) characteristic of the *ocellata* species-group (see p. 253), and the somewhat intermediate status of *A. petersi* suggest at least a distant relationship of *A. bogotensis* to the species of this group (i.e. to *ocellata, vittata, rhombifera* and *petersi*). Hence despite its distinctiveness, this species is not so phyletically mysterious as, say, *A. steyeri*, which has traits apparently unique to itself among the described forms of *Anadia*. In fact, at least some of the differences between *A. bogotensis* and the *ocellata*-group species may be adaptations to more montane climatic conditions: *A. bogotensis* has in common with the species (*A. brevi-*

frontalis) found above the tree-line in Venezuela such characteristics as slate coloration below, reduction of supraocular number, reduction in size of the prefrontals, pigmentation of the disk on the lower eyelid and sexual dimorphism in head size.

Specimens Examined

Syntypes. COLOMBIA: *Department of Cundinamarca*: Sta. Fé de Bogotá, Berlin 4654 (2 specimens), 4655, 4656 (3 specimens), 4657 (2 specimens), 4658 (2 specimens), 4659 (2 specimens), 4660 (4 specimens).

Additional specimens. COLOMBIA: *Department of Cundinamarca*: Bogotá, Berlin 30043, Basel 3763, 8872-73, MCZ 13790, 14170, 17120-22, 17160-68, 17170-74; Aquadita, south of Bogotá, ANSP 24164; La Mesa, near Bogotá, MCZ 46421 (4 specimens); Lagunas del Chisacal, Cordillera Oriental (3600m), untagged FM specimen. *Department of Caldas*: La Dorada, AMNH 27612. *Department of Boyacá*: shore of L. Tota, AMNH 91763.

Specimens examined only for 4 counts (see *Variation*, above). COLOMBIA: *Department of Cundinamarca*: Bogotá, BM65.6.12.15-16, MCZ 42182 (9000'), USNM 92498; Paramo Cruz Verde, Bogotá, ANSP 26258; Bogotá, hill behind Univ. de Los Andes, LACM 39784-86; Gutierrez (S.E. of Bogotá), AMNH 32715-22; Pantanos Martos, Finca Vista Hermosa, site 13, AMNH 9747-49; Choachi, MCZ 19219-28 (+3 specimens without number).

Anadia steyeri Nieden

Anadia steyeri Nieden, 1914: 365 (Type locality: "Puerto Cabello," Carabobo Province, Venezuela.); Roux, 1927: 259; Shreve, 1947: 526.

Diagnostic Traits: 1. high dorsal count: 59.5-61.5; 2. high midbody count: 41-45; 3. dorsal scales quadrangular, quite small; 4. long suture between prefrontals; 5. suboculars large and quite uniform in size, none protruding downward between 4th and 5 th supralabials (fig. 25B); 6. dorsum with reddish brown spots *or* transverse brown bands *or* brown vertebral band bordered by white dorsolateral (figs. 15, 16); 7. 2 thin dark lines from eye to the ear (figs. 15, 16); 8. venter white; 9. in female, femoral pores in 2 sets: one inner and one outer.

A. steyeri may be distinguished from: 1. All *Anadia* except *A. ocellata* and *A. vittata* by the high dorsal count; 2. *A. ocellata* and *A. vittata* by the quadrangular dorsal scales, the size and shape of the suboculars, the absence of subnostril groove, and the two thin dark lines (rather than a dark stripe) passing from eye to ear.

Definition (N=3)

Each nasal single, contacting rostral. Midline suture between prefrontals long. 3 supraoculars and a presupraocular. 4-7 superciliaries, sometimes with several small scales inserted between superciliary row

and supraoculars. 5-6 unpigmented palpebral scales. 4-6 large suboculars, none forming more than a trace of angular protrusion downward between 4th and 5th supralabials. 17-22 transverse gular rows. No sexual dimorphism in head size.

Dorsal scales quadrangular with posterior edges straight, arranged in 59.5-61.5 juxtaposed transverse rows from ear to tail. Lateral scales only slightly smaller and less regular than dorsals, such that many transverse rows pass about body as annuli without lateral irregularities. 41-45 scales in midbody annulus. Ventral scales quadrangular, larger than dorsals, arranged in 39.5-41.5 juxtaposed or slightly imbricate transverse rows from collar to vent. 6-9 scales along anterior border of vent. All specimens apparently female, with 4-7 femoral pores in two separate sets on each hind limb: inner of 1-2 pores and outer of 3-5 pores. 17-19 lamellae under fourth toe of hind limb. Maximum snout-vent length 81.0 (female).

Variation

Row of 3 scales inserted between superciliaries and supraoculars in one; anterior chin-shield (usually single) divided irregularly in one. Counts for all 3 specimens are tabulated in Table 7.

Color Pattern (figs. 14, 15)

Nieden (1914) commented on the coloration of the type: "Coloration above greybrown, on the sides lighter, with numerous irregular reddish--brown spots on the dorsum which are arranged in 2-3 quite distinct longitudinal rows. Venter white" (translated from German). The specimen has faded considerably, but one might add to the above that laterally adjacent to the dorsal spots are pale whitish blotches which extend down the side.

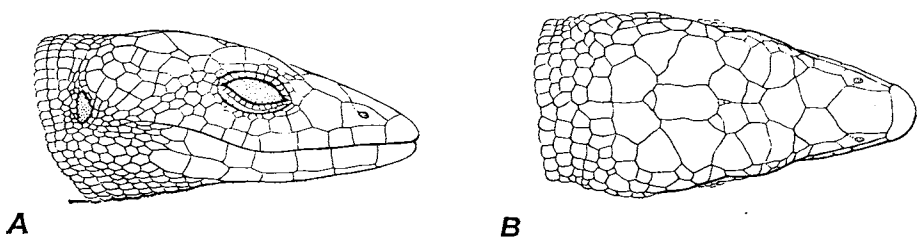

Fig. 14, Head scales of *A. steyeri*. Anomalous division of frontoparietals and parietal of this specimen atypical. Drawn from MCZ 48901.

The Basel specimen mentioned by Roux (1927) differs considerably. The dorsal marking is both denser and more distinct, such that in correspondence to spots in the above are found irregular blotches arranged in *transverse* brown bands (fig. 15). Transverse banding would seem, at first, a significantly different pattern from longitudinal rows of spots, yet examination of the type reveals the rather large spots to be transversely aligned. Hence transverse fusing would account for the banding

pattern. In between the irregular bands of the Basel specimen are blotches of light color (light brownish-grey, according to Roux, 1927). The sides are irregularly spotted with brown on a light background. Venter unmarked white (Roux, 1927). Scattered dark markings dorsally on the head, forming 2 thin dark lines extending from the orbit to the ear.

MCZ 48901 is startlingly different in coloration from the two above, as noted by Shreve (1947). He suggests that the "series of dorsal spots mentioned by Nieden and Roux appear to have fused to form a brown vertebral band about 12 scales in width at midbody." This longitudinal band is solid, quite unlike the spotting or blotching patterns, and is bordered on each side by a thin (2-3 scales in width) white dorsolateral line, which passes from the occiput to the base of the tail (fig. 15). Sides light brownish grey with scattered dark flecks. Venter light with some thin dark markings along the longitudinal sutures, between the ventral scales. The scattered dark markings on the head are very

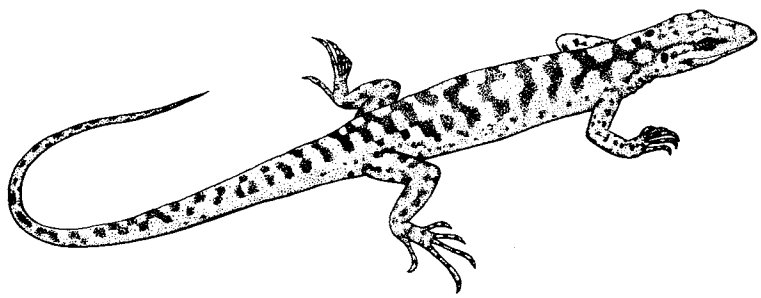

Fig. 15, Banded color pattern of *A. steyeri*. Drawn from Basel 9229 (snout-vent length 70.5 mm, female).

similar in size and placement to those of the Basel specimen (the type has faded too much to discern head markings), also forming the two thin lateral lines from orbit to ear. The coloration of this specimen may represent a juvenile pattern (table 7 for measurements of size).

Range and Habitat

All 3 specimens have been taken at low altitudes in Falcon and Carabobo States along the coast of Venezuela.

Discussion

This species, described from a single type by Nieden (1914), is represented in collections by only 3 specimens, each of which has been discussed in the literature (Nieden, 1914; Roux, 1927; Shreve, 1947); Distinguished by the small size of the dorsal scales, which are clearly smaller than the ventrals, the three specimens have high dorsal counts (table 7). Among *Anadia*, only certain specimens of *A. vittata* and *A. ocellata* have comparable dorsal counts, yet the latter may be distin-

guished by a subocular which protrudes downward in a broad but shallow wedge between the supralabials (no subocular in *steyeri* protrudes downward), by the lower midbody counts, by the slimmer bodies and by the dark longitudinal line passing through the eye and ear and onto the sides.

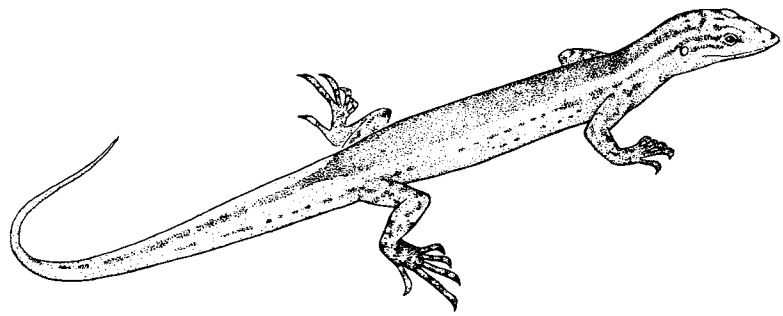

Fig. 16, Solid middorsal color pattern of *A. steyeri*. Drawn from MCZ 48901 (snout-vent length 55.5 mm, female).

As mentioned above, the three specimens differ considerably in pattern. Yet that they are a single species is apparent from the similarity of meristic counts (dorsal, ventral, midbody, femoral pore), head scales (supraoculars, superciliaries, suboculars, prefrontals, palpebrals) and body proportions, and also from the close similarity of the markings on the head of the Basel and MCZ specimens. The three localities are also very close.

Specimens Examined

Holotype. VENEZUELA: *Carabobo State*: "Puerto Cabello", Berlin 24293.

Additional material. VENEZUELA: *Falcon State*: El Mene, Basel 9229; Acosta District, Pauji, MCZ 48901.

Anadia pulchella Ruthven

Anadia pulchella Ruthven, 1926: 1-3 (Type locality: La Cumbre, Santa Marta Mountains (7000'), Magdalena Province, Colombia.); Dunn, 1937: 11; 1944a: 64-65.

Anadia pamplonensis Dunn, 1944a: 64 (Type locality: Pamplona (2340m), Norte de Santander Province, Colombia). *New Synonymy.*

Diagnostic Traits: 1. dorsal count 36.5-44; 2. midbody count: 34-41; 3. dorsal scales quadrangular; 4. ventral scales larger than dorsals, juxtaposed; 5. 3 supraoculars; 6. 4-5 unpigmented palpebrals; 7. suboculars all fairly large, none protruding downward between 4th and 5th supralabials; 8. dorsum tan, olive or brownish (very dark in some preserved material), marked sparsely or heavily with darker pigment; 9. venter somewhat lighter than dorsum, tan or greenish-yellow; 10. 5-9 femoral pores in both sexes.

A. pulchella may be distinguished from: 1. *A. ocellata, A. vittata, A. petersi,* and *A. steyeri* by the lower dorsal count; 2. *A. marmorata* and *A. blakei* by the dorsal scales that are smaller than the ventral scales; 3. *A. bogotensis* by the quadrangular dorsal scales, the juxtaposed ventral scales, and the absence of a subnostril groove; 4. *A. rhombifera* by the quadrangular dorsal scales, the suboculars, none of which protrude downward between the 4th and 5th supralabials, and the greater number of femoral pores in the female; 5. *A. brevifrontalis* by the absence of bluish or greyish color ventrally, the unpigmented palpebrals, and the suboculars, none of which protrude downward; 6. *A. bitaeniata* by the suboculars, of which all are similarly large, and none protrude downward.

Description (N=10)

Each nasal single, without groove below nostril, and contacting rostral. Prefrontals may or may not meet to form midline suture. 3 supraoculars and one or no presupraocular. 4-6 superciliaries. 4-5 unpigmented palpebral scales. 3-4 fairly large suboculars, none forming more than trace of angular protrusion downward between 4th and 5th supralabials (fig. 25). 15-17 transverse gular rows. Head in male greatly enlarged posterolaterally, and relatively larger than in female.

Dorsal scales smooth, quadrangular, with posterior edge slightly rounded, arranged in 36.5-44 very slightly imbricate transverse rows from ear to tail. Lateral scales of equal size with or but slightly smaller than dorsals, such that many transverse rows pass about body as annuli without lateral irregularities. 34-41 scales in midbody annulus. Ventral scales quadrangular, approximately equal in size to dorsals, arranged in 30.5-35 juxtaposed transverse rows from collar to vent. 5-6 quite large scales along anterior border of vent. 5-9 femoral pores, in both sexes. 17-20 lamellae under fourth toe of hind limb. Maximum snout-vent length 105.9mm (male).

Variation

Of 10 specimens: prefrontals meet to form common suture in 4 specimens; a small scale between superciliaries and supraoculars on one side in one specimen.

Color Pattern

A detailed description of the coloration and marking of the type was given by Ruthven (1926). As all the preserved material of *A. pulchella* on hand appears discolored, this description is largely repeated here: "Color above light olive, with deep brown markings; on the back the brown is in the form of narrow transverse bands, interrupted on the median line, while on the tail it forms two rows of spots.... On the sides are numerous pale spots which are better defined in a single row on each side of the tail. There is a brown band on each side of the head and neck from the end of the snout to the fore limb, below which the labial region and the neck are pale yellow... Ventral surface pale greenish yellow

with numerous dark spots mostly arranged in two rows." The brief comments of Dunn (1944a) on 14 specimens from Pamplona were: "The color is a rather uniform light tan, some of the specimens showing scattered dark streaks, two or three scales long." As mentioned above, markings of the preserved material seem obscured by discoloration effects, yet it does appear that some specimens were uniformly tan above and somewhat lighter below, with but a few scattered flecks on the side of the neck and above fore-arm insertions, yet lacking a brown lateral band, while others were quite heavily flecked dorsally with dark pigment or were even marked with narrow transverse bands, as was the case of the type, and were of lighter ventral coloration. Of the specimens, only two other than the type show a dark lateral band on each side. A topotypic *A. pulchella* has narrow, light dorsolateral lines, and the vertebral midline also appears slightly lighter, though not distinctly so, than the remainder of the back.

Range and Habitat

A. pulchella has been collected at elevations of about 2130-2740 meters in the Santa Marta Mountains, Magdalena Province, Colombia and in the vicinity of Pamplona, Norte de Santander Province, Colombia.

The type was found in a bromeliad (Ruthven 1926).

Discussion

Two specimens have been discussed in the literature under the name of *A. pulchella*: the type, described by Ruthven (1926) and a second specimen from the type locality, mentioned by Loveridge (1929). Though Dunn (1937), in noting affinities of an *Anadia* from Pamplona, Prov. Norte de Santander, Colombia to *A. pulchella* and *A. bitaeniata,* came originally to regard *A. pulchella* (misspelled as *A. pulchra*) as but a race of *A. bitaeniata,* he later (1944a) reversed this decision, upholding the validity of *A. pulchella* while describing a new species, *A. pamplonensis,* on the basis of 13 additional Pamplona specimens. Ruthven (1926) had noted a similarity of the type to *A. rhombifera.*

This review has permitted examination of a long series of *A. bitaeniata,* 3 specimens of *A. pulchella* from the Santa Marta Mountains, Colombia, including the two *pulchella* mentioned above, 7 specimens from Norte de Santander, Colombia as well as 14 *A. rhombifera.* While *A. rhombifera* is clearly distinct (table 1), the similarity of *A. bitaeniata* to the Santa Marta Mountains and Norte de Santander specimens is apparent. Nonetheless, *A. bitaeniata* may be distinguished by the subocular that protrudes downward between the supralabials, by the lower ventral scale row count and by different coloration (*A. bitaeniata,* except in badly faded specimens, is grey-brown or slate above, often with bluish tinges while *A. pulchella* is tan, olive or brownish above). The other scale counts also differ somewhat (table 1). *A. bitaeniata* is Venezuelan, while *A. pulchella* is Colombian. The specimens from Norte de Santander, though differing slightly in meristic counts (table 9), are not distinguish-

able from the specimens from the Santa Marta Mountains. The differences mentioned by Dunn (1937) for a single Norte de Santander specimen, and which were, he felt, borne out by 13 additional specimens subsequently collected (Dunn, 1944a) do not stand up in the current investigation. The table below reveals considerable overlap in the distribution of supraocular, dorsal, midbody and preanal border scale counts (the differentiating criteria according to Dunn), and it is suggested that the differences in distribution that do occur are a consequence either of 1) sampling error, due to small size of population samples, or 2) geographical variation. Hence, the name *Anadia pamplonensis* established by Dunn (1944a), is here reduced to a synonym. If future investigation reveals the distributional difference of scale counts of specimens from the two areas to be significant and a consequence of geographical variation, it may at that time be considered desirable to re-erect *pamplonensis* as a subspecies of *A. pulchella.*

Specimens Examined

Holotype. COLOMBIA: *Magdalena Province*: La Cumbre, Hacienda Vista Nieve, Santa Marta Mountains, 7000', UMMZ 63333.

Additional specimens COLOMBIA: *Magdalena Province*: La Cumbre, Santa Marta Mountains, 7500', MCZ 22409; near San Sebastian, Mt. Figueroa, Santa Marta Mountains, 9000', UMMZ 85598; *Norte de Santander Province*: (no more exact locality) ILS 20835; Pamplona, USNM 127094-127096, MCZ 112371-112373.

Anadia bitaeniata Boulenger

Anadia bitaeniata Boulenger, 1903: 430-431 (Type locality: Culata (3000 m), Merida Province, Venezuela.).

Diagnostic Traits: 1. dorsal count 32-42; 2. midbody count: 31-41; 3. dorsal scales quadrangular; 4. ventral scales larger than dorsals, juxtaposed; 5. 3 supraoculars; 6. 4-5 palpebrals, unmarked or with only a few speckles of pigment; 7. suboculars unequal in size, one protruding downward between 4th and 5th supralabials; 8. dorsum slate-grey, grey-brown, often with barely distinct light dorsolateral lines; 9. venter light, often with yellow, orange or other hue; 10. ventral surface of thigh light or with non-blue hue; 11. 7-11 femoral pores in both sexes.

A. bitaeniata may be distinguished from: 1. *A. ocellata, A. vittata, A. rhombifera, A. petersi* and *A. steyeri* by the lower dorsal count; 2. *A. marmorata* and *A. blakei* by the dorsal scales that are smaller than the ventral scales; 3. *A. bogotensis* by the quadrangular dorsal scales, the juxtaposed ventral scales, and the absence of a subnostril groove; 4. *A. pulchella* by the unequal suboculars, one of which protrudes downward, and the frequently greyish dorsum; 5. *A. brevifrontalis* by the light (non-blue) ventral surface of the thigh, the scant pigmentation of the palpebrals, and the somewhat lower dorsal count.

Description (N=29)

Each nasal single without groove below nostril, contacting rostral. Prefrontals may or may not meet to form midline suture. 3 supraoculars and 0-1 presupraocular. 3-5 superciliaries. 4-5 palpebrals, unpigmented or with few speckles of pigment. 3-5 large suboculars, one forming angular protrusion downward between 4th and 5th supralabials. 12-16 transverse gular rows. Head in male somewhat enlarged posterolaterally and relatively larger than in female.

Dorsal scales quadrangular, with posterior edges straight or somewhat rounded, arranged in 32-42 juxtaposed or very slightly imbricate transverse rows from ear to tail. Lateral scales slightly smaller,

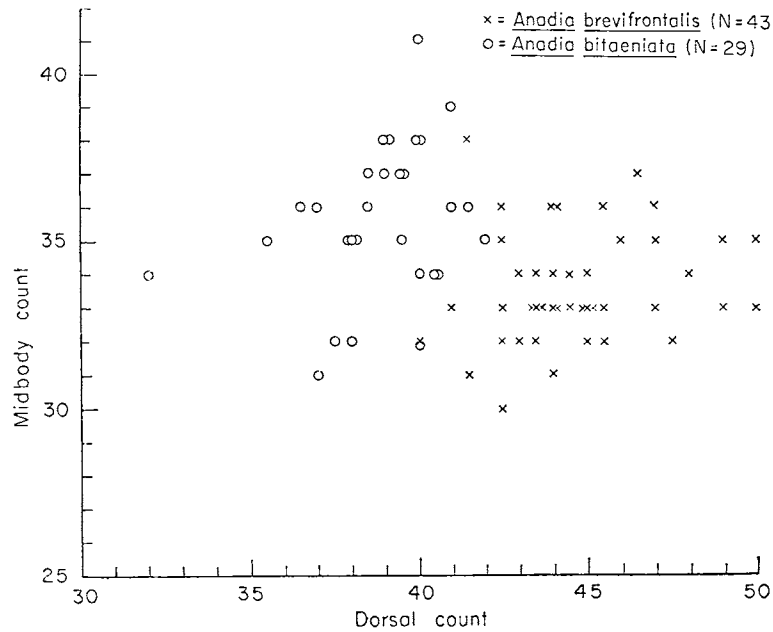

Fig. 17, Plot of midbody versus dorsal counts for *A. brevifrontalis* and *A. bitaeniata*.

more rounded than dorsals, such that many transverse rows pass about body as annuli without lateral irregularities. 31-41 scales in midbody annulus. Ventral scales quadrangular, larger than dorsals, arranged in 27-31 juxtaposed transverse rows from collar to vent. 5-8 quite large scales along anterior border of vent. Both sexes with 7-11 femoral pores. 16-20 lamellae under fourth toe of hind limb. Maximum snout-vent length 87.8 mm (male).

Variation

Of 29 specimens: prefrontals fail to form midline suture in 5; loreal does not contact supralabials in 3: presupraocular on one or both sides in 18.

Color Pattern

A description of coloration in life has been drawn up from an examination of 3 living adults and the field notes of Juan Rivero on 4 others:

Dorsally slate-grey, grey-brown or brown. On each side a pale dorsolateral line, in some specimens barely distinguishable from the ground color. Otherwise uniform above and unmarked, or having scattered dark flecks, some arranged in longitudinal rows. Sides as back or slightly lighter, unmarked or with scattered flecks, but no ocelli. Head similar to body, unmarked. Iris yellow-brown.

Ventral surfaces light, with many possible hues of color: cream, grey, bluish, violaceous, brownish-cream, light orange, or orange-brownish cream. Most intense coloration occurs posteriorly on belly and on thighs: vivid yellowish-tan, orange-brown or intense cream. Ventral surfaces unmarked or with scattered spots.

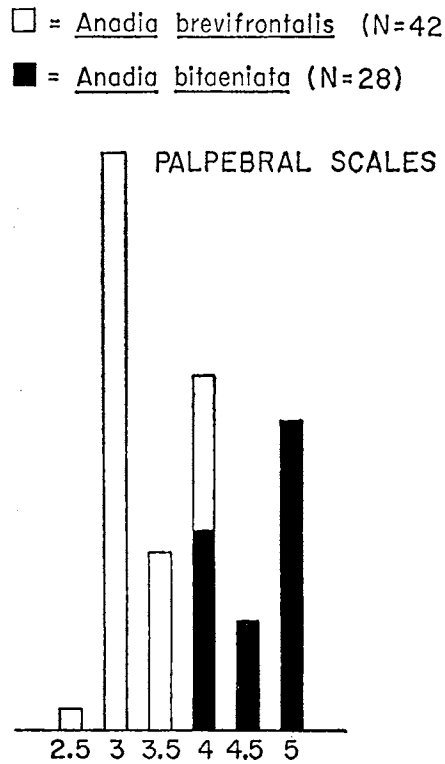

Fig. 18. Histogram showing the distribution of palpebral counts of *A. brevifrontalis* and *A. bitaeniata*

In preservation the ventral hues fade to brownish-cream, greyish or slightly bluish. The dorsum becomes progressively more brown: the syntypes, though described as brownish or olive (Boulenger, 1903), are now chocolate-brown above. Several preserved juveniles have distinct, yellow dorsolateral lines bordered with dark brown.

The hind limbs are in no case bluish or grey beneath, as in *A. brevifrontalis*, but are always cream (brownish cream in preservation) with or without yellowish-tan, orange, brownish, or some similar non-blue hue.

Range and Habitat

This species has been collected at elevation of 2500 to 3050 meters in the Merida region of the Venezuelan Andes.

A. bitaeniata apparently occupies the temperate zone. Seven specimens from La Culata were taken in a temperate zone, grassy area with no forest nearby, at 2900-3000m. Of these, one was found under rocks in a muddy area within a fast-moving stream, and the others under rocks near the stream (field notes and personal communication of Juan Rivero).

Rivero recently collected two specimens out of a large bromeliad, 6 m up in a tree in rather open forest, the sparse trees being in a thicket of 4.5 m high spiny bushes, though heavy forest was but 15 m away. This site, at an elevation of 2700 m in Valle de la Culata, was not more than 100 m from a place where *A. bitaeniata* had been taken on the ground.

Discussion

The similarity of *A. bitaeniata* to *A. brevifrontalis* has led to confusion of the two species (p. 242). Both are dorsally grey, slate or brownish and usually marked with darker flecks or light dorsolateral lines. The midbody, ventral and dorsal counts overlap, the latter in the range of 40 to 42 (fig. 17). The dorsal scales of both are similarly shaped and similarly arranged. Both may have reduced prefontals, as well as some pigmentation of the palpebrals. There is no sexual dimorphism in femoral pore number in either species.

The most simple distinction lies in the coloration of the ventral surface of the hind limbs: *A. bitaeniata* has cream, yellowish or orangish thighs, that become brownish cream with preservation, whereas *A. brevifrontalis* has vivid blue, bluish or grey thighs. The difference in distribution of the dorsal and midbody counts is most clearly illustrated in a plot of midbody vs. dorsal counts (fig. 17), the ratio dorsal count/midbody count being lower for *A. bitaeniata* than for *A. brevifrontalis*. *A. bitaeniata* has three supraoculars while *A. brevifrontalis* usually has but two, this being the case on one or both sides of the head in 27 of 43 specimens. The number of palpebral scales also differs (fig. 18).

Although a paucity of detailed ecological data prevents confirmation, it is my belief that these two inhabitants of the Venezuelan Andes occupy different altitudinal zones. Rivero (1963) differentiated the Temperate Zone from the Paramo Zone on the basis of climatic, vegetational and zoological data, the former extending from about 2000 to 3000 meters and the latter from about 3000 to 4600 meters. Rivero's field data suggest that the *A. bitaeniata* occupies moist microhabitats (bromeliads, beneath rocks near or in streams), within the Temperate Zone at elevations of 2500-

3050 m. The fact that the altitudinal ranges overlap does not necessarily indicate that the two species overlap in distribution, for the altitudinal location of the boundary between Temperate and Paramo Zone fluctuates according to local conditions (Rivero, 1963). On the other hand, according to Boulenger's data, both species have been collected at Escorial at 3000 meters, although I suspect not at the same time. There is, of course, no reason why at the transition between the zones contact between the species should not occur, and Escorial might be such a locality.

A. bitaeniata is also close to *A. pulchella.* However, *A. pulchella* is not a race of *A. bitaeniata* as Dunn (1937) once suggested, and *A. pamplonensis* is a synonym of *A. pulchella* (p. 235; table 9), not of *A. bitaeniata* as Peters and Donoso-Barros (1970) have stated.

Specimens Examined

Syntypes. VENEZUELA: *Merida Province:* Culata (3000 m), BM 1946.8.2.11-13; Escorial (3000 m), BM 1946.8.31.25-28.

Additional specimens. VENEZUELA: *Merida Province:* La Culata (=Culata), BM 1905.5.31.32 (10,000ft.), BM 1905.5.31.34 (10,000ft.), BM 1905.5.31.38-41 (10,000ft.), MCZ 101701-07 (2900-3000 m), MCZ 104398, MCZ 112413-14, MCZ 121245-47; Facqueros (2500 m), BM 1905. 5.31.42-43.

Anadia brevifrontalis (Boulenger)

Euspondylus brevifrontalis Boulenger, 1903: 431-432 (Type locality: Escorial (10,000ft.), Merida Province, Venezuela.) ; Lancini, 1968: 5.
Anadia bitaeniata (in error) Burt & Burt, 1930: 30.

Diagnostic Traits: 1. dorsal count: 40-50; 2. midbody count: 30-38; 3. dorsal scales quadrangular or elongate quadrangular; 4. ventral scales larger than dorsals, juxtaposed; 5. 2-3 supraoculars; 6. 3-4 palpebrals dusted with pigment; 7. suboculars unequal in size, one protruding downward between 4th and 5th supralabials; 8. dorsum slate-grey or dark olive, with dark flecks or dark bordered light dorsolateral lines; 9. venter blue or grey, unmarked; 10. ventral surface of thigh greyish or bluish (after long preservation brownish) ; 11. 5-10 femoral pores in both sexes.

A. brevifrontalis may be distinguished from: 1. *A vittata* and *A. steyeri* by the lower dorsal count; 2. *A. marmorata* and *A. blakei* by the dorsal scales that are smaller than the ventral scales. 3. *A. ocellata, A. rhombifera,* and *A. petersi* by the quadrangular dorsal scales, and the blue or grey venter; 4. *A. bogotensis* by the quadrangular dorsal scales, the quadrangular and juxtaposed ventral scales, and the absence of subnostril groove; 5. *A. pulchella* and *A. bitaeniata* by the greyish or bluish ventral surface of the thigh, the well-pigmented palpebrals, and the somewhat higher dorsal count.

Description (N=43)

Each nasal single, often in contact with rostral. Prefrontals may or may not meet to form short midline suture. 2-3 supraoculars, 0-1 presupraocular. 3-5 superciliaries. 3-4 palpebrals dusted with pigment. 3-5 suboculars, one forming angular protrusion downward between 4th and 5th supralabials. 13-18 transverse gular rows. Head in male enlarged posterolaterally and relatively larger than in female.

Dorsal scales quadrangular or elongate-quadrangular, with posterior edges slightly rounded, arranged in 40-50 very slightly imbricate transverse rows from ear to tail. Lateral scales somewhat smaller and less regular than dorsals, but some tranverse rows pass about body as annuli without lateral irregularities. 30-38 scales in midbody annulus. Ventral scales quadrangular, larger than dorsals, arranged in 29-37 juxtaposed transverse rows from collar to vent. 4-8 quite large scales along anterior border of vent. 5-10 femoral pores in both sexes. 16-20 lamellae under fourth toe of hind limb. Maximum snout-vent length, 76.8 mm (male).

Variation

Of 43 specimens: nasal fails to contact rostral in one; prefrontals meet to from midline suture in 25; presupraocular on one or both sides in 37; 5 palpebrals on one side in one; second and third chin-shield fused on one or both sides in 6; reduced number of femoral pores in 7.

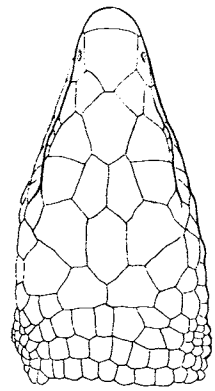

Fig. 19, Head scales of *A. brevifrontalis*. Drawn from MCZ 112441.

Range and Habitat

Found solely in the Andes of Merida Province, Venezuela, *A. brevifrontalis* is apparently restricted to the paramo at elevations of 2900 to 3600 m (Lancini, 1968). The paramo zone, according to Juan Rivero (1963), extends from 3000 m (roughly the upper limit of tree growth) or occasionally as low as 2400 m, to 4600-4700 m (the snow line).

A. brevifrontalis has been taken "thrashing about in the grass" (Fouquette, 1968), "under rocks in damp places" (Burt and Burt, 1930), "under rocks near Laguna Mucubaji but not close to water" (field notes of Juan Rivero for MCZ 101709-12), and "under a dried out Espeletia" (E. E. Williams, personal communication).

Color Pattern

Dorsally slate grey or dark olive in life, becoming brownish with extended preservation. Two extremes in dorsal markings may be observed: a) on the back a few to numerous dark flecks usually arranged in parallel longitudinal rows, or b) two of the longitudinal rows on each side are fused to form dark borders of a light dorsolateral line, extending from above the eye well along the length of tail; the middorsal and lateral regions lack dark markings. Most specimens lie between these extremes, having traces of light dorsolateral lines bordered by partially fused rows of dark flecks, as well as having rows of flecks present on the middorsal and lateral surfaces. It was the latter condition Boulenger (1903) described for the types. Head of same color as back, relatively unmarked.

Belly in life bright blue or grey, fading to greyish-blue, slate or brownish in preservation, but not cream or light. Along the sides under the tail few to many flecks roughly arranged in longitudinal rows.

Discussion

Inasmuch as Boulenger (1903) described *Anadia bitaeniata* and *Euspondylus brevifrontalis* in the same paper, he was well aware of the similarities and dissimilarities of the two. *E. brevifrontalis* was probably included in *Euspondylus* as a consequence of slightly greater subdivision of the lateral scales than is the case in *A. bitaeniata*. Yet this is but one of the traits alleged by him (1885) to distinguish *Euspondylus* from *Anadia*, the other two being a) dorsal scales sometimes feebly keeled, and b) a strong collar fold, neither of which are apparent in *brevifrontalis*. In fact Boulenger did mention (1903) that "this species connects *Euspondylus* with *Anadia*."

The extent of that "connection" was demonstrated by the confusion resulting in the British Museum, shortly thereafter. Of 23 specimens catalogued in 1905 as either *A. bitaeniata* or *E. brevifrontalis*, more than half were misidentified: 13 specimens identified as *A. bitaeniata* are *brevifrontalis*, while one specimen thought to be *E. brevifrontalis* is *Anadia bitaeniata*. Similarly Burt and Burt (1930) discussed several specimens (USNM 66842-43) as *Anadia bitaeniata*, but these are in fact *brevifrontalis*.

It was this discovery of two species under the name *A. bitaeniata*, that triggered my study of *Anadia*. Fortunately Thomas Uzzell called attention to *Euspondylus brevifrontalis*, and the investigation did not stray too far afield; nonetheless it struck me as illogical that two such closely related species should be set in separate genera.

I have mentioned above the three traits that I understand Boulenger (1885) to have used to separate *Euspondylus* from *Anadia,* of which but one applies to *brevifrontalis.* Comparative examination of the *Anadia* further reveals that the size and shape of the lateral scales varies considerably from species to species as does the degree to which unbroken annuli or rings of scales pass about the body. What one may point out, though, is that in none of the species of *Anadia* is there a distinct band of much smaller or granular lateral scales: there is not in *brevifrontalis.* Since I have been unable to set *brevifrontalis* clearly apart from the *Anadia* by any description of the size or subdivision of the lateral scales, and since such an act, even if it were possible, seems to me nonsensical in light of the close similarity of *brevifrontalis* to *A. bitaeniata,* I have removed the species *brevifrontalis* from *Euspondylus* and place it in the genus *Anadia.*

Anadia bitaeniata is similar, but not identical, to *Anadia brevifrontalis* both in appearance and scale counts (for comparison of the two, see discussion of *A. bitaeniata*). The differences that do occur appear to reflect, to some extent at least, the adaptation of *A. brevifrontalis* to environmental conditions at higher elevations. For example, reduction of the prefrontals and of the number of supraoculars, increase in pigmentation of the palpebrals, decrease in number of palpebrals, and the smaller adult size of *A. brevifrontalis* relative to *A. bitaeniata* mirror parallel developments in *A. bogotensis* and certain *Proctoporus,* all of which are high altitudinal forms.

Within *Anadia,* it seems that sexual dimorphism in head size may also be correlated to a montane habitat. Fouquette's field observation of aggressive behavior between two males of *A. brevifrontalis* in which "one of the lizards had its jaws clamped near the base of the tail of the other, and the two were rolling on the ground" (Fouquette, 1968: 881) suggests that expansion of the head in the male serves a territorial function. *A. brevifrontalis* is one of the few species for which a number of specimens are available; this may reflect a greater population density, which would support the likelihood of territorial behavior.

Specimens Examined

Syntypes. VENEZUELA: *Merida Province:* Escorial (10,000 ft.) BM 1946.8.2.32-33; Rio Albireggas (11,500 ft.) BM 1946.8.31.62.

Additional specimens. VENEZUELA: *Merida Province:* Chama River (10,300 ft.) USNM 66842-43; Culata BM 1905.5.31.33 (10,000 ft.), BM 1905.5.35-36, BM 1905.5.31.36a; Escorial (=El Escorial), BM 1905.5.31.44-52, (3000 m), MCZ 28668, MCZ 107685, MCZ 112412, (2900-3000 m), MCZ 121248-56; "Merida," Berlin 25917; Edo Merida, MCZ 112441; *Trujillo Province:* Mucubaji (3350 m), MCZ 101708-12; Lago Mucubaji, MCZ 112122; MCZ 112409; between Mucubaji and Laguna Negra, near Apartaderos (ca. 3300 m), ASU 08074-76; Sto. Domingo, MCZ 121256.

Anadia marmorata (Gray)

Argalia marmorata Gray, 1846: 67 (Type locality, as herein corrected: north-central Venezuela).
Argalia olivacea Gray, 1847: 96-97. (Type locality: near Colonia de Tova (8000'), Aragua Province, Venezuela); Gray, 1858, pl. xv, fig. 1; Boulenger, 1885: 408-409.
Gerrhonotus poecilochlus Lichtenstein, 1856: 16.
Ecpleopus (Argalia) olivaceus; Peters, 1862: 213.
Ecpleopus (Argalia) marmoratus; Peters, 1862: 213.
Ecpleopus (Argalia) poecilochilus; Peters, 1862: 213-216.
Leposoma olivaceum; Cope, 1885: 98.
Leposoma marmoratum; Cope, 1885: 98.
Leposoma poecilochilus; Cope, 1885: 98.
Anadia duquei Lancini, 1963: 1-2, fig. 1, 2 (Type locality: Quebrada El Cedro, tributary of Catuche River, Cerro El Avila, (1450 m) N. of Caracas, Distrito Federal, Venezuela). *New Synonymy.*

Diagnostic Traits: 1. low dorsal count: 27.5-34; 2. midbody count: 30-37; 3. dorsal scales larger than ventral scales; 4. dorsal scales quadrangular; 5. suboculars large and distinct (fig. 20A); 6. sutures between infralabials outlined with dark markings (figs. 21, 22); 7. tip of snout cream or yellow (figs. 21, 22); 8. some specimens with marbled dorsal coloration (fig. 21); 9. ventrum light, sometimes heavily marked; 10. femoral pores 8-12 in both sexes; 11. body stout; 12. adult male with enlarged head having prominent swelling of the posterolateral parts (fig. 21).

A. marmorata may be distinguished from: 1. *A. ocellata, A. vittata, A. rhombifera, A. petersi, A. steyeri, A. pulchella* and *A. brevifrontalis* by the low dorsal count; 2. *A. bogotensis* and *A. bitaeniata* by the large size of the dorsals, the light tip of the snout, the dark markings on the labials, and the lack of bluish or slate coloration dorsally and ventrally; 3. *A. blakei* by the large suboculars, the dark markings on the labials, the light tip of the snout, the higher midbody count, and the higher femoral pore count in the female.

Description (N=13)

Each nasal single, often contacting rostral. Prefrontals usually meet to form midline suture. 3-4 supraoculars and 0-1 presupraocular. 4-6 superciliaries. 4-6 palpebrals, with speckles of pigment. 3-5 large suboculars, one forming angular (wedge-shaped) protrusion downward between 4th and 5th supralabials. 12-16 transverse gular rows. Head of male greatly expanded posterolaterally, and proportionately much larger than head of female.

Dorsal scales quadrangular, much longer than broad and occasionally thickened posteriorly, with posterior edges straight, arranged in 26.5-34 juxtaposed transverse rows from ear to tail. Lateral scales somewhat

smaller and less regular than dorsals, such that many transverse rows pass about body as annuli without lateral irregularities. 30-37 scales in midbody annulus. Ventral scales quadrangular, somewhat smaller than

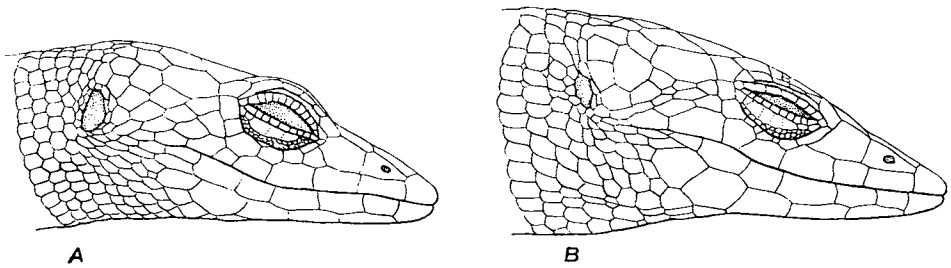

Fig. 20, Head scales of *A. marmorata* and *A. blakei*. Drawn from UMMZ 120329 and KMNH 17795 (type of *A. blakei*).

dorsals, in 27-30 juxtaposed transverse rows from throat to vent. 4-8 quite large scales along anterior border of vent. Femoral pores 8-12 in both sexes. 18-22 lamellae under fourth toe of hind limb. Maximum snout-vent length 94.9 mm (male).

Variation

Of 13 specimens: nasal not contacting rostral in 2; prefrontals not meeting to form short midline suture in 7; third pair of chin-shields in contact along midline in 7.

Color Pattern (figs. 21, 22)

Variation in the prevalence of dark markings on this microteiid encouraged Gray (1846, 1847) to describe two species: *Argalia marmorata* and *Argalia olivacea*. As these names suggest, the former was dorsally marbled with black-brown, while the latter was olive-green above. Boulenger reduced *olivacea* and an additional species (*poecilochilus*) to synonymy with *marmorata*, noting coloration to be: "Olive-brown above,

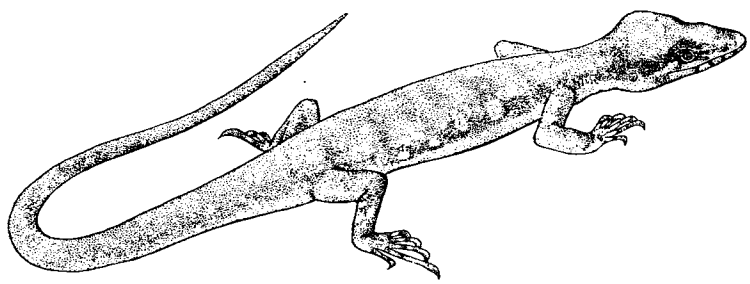

Fig. 21, Plain color pattern of *A. marmorata*. Drawn from AMNH 96248, male.

with or without reddish brown marblings; flanks with equidistant groups of cream-colored spots; the sutures of the head-shields generally dark brown; lower surfaces yellowish." (Boulenger, 1885: 409). Examination of the types of these three species confirms Boulenger's description, although of course the specimens have faded during more than a century of preservation. It might be added, however, that the lateral cream colored spots are not visible in all, and that remnants of dark blotches, rather than marbling, are evident in several.

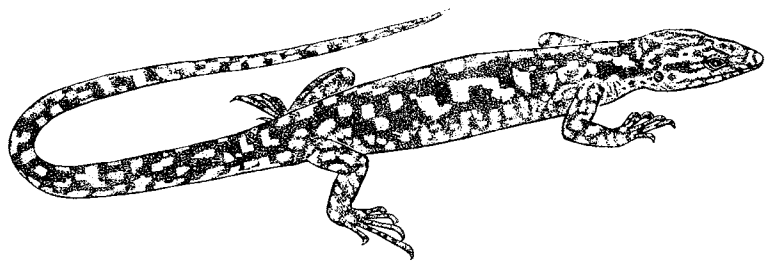

Fig. 22, Marbled color pattern of *A. marmorata*. Drawn from AMNH 96249, female.

On the basis of observations of freshly preserved material, Test, Sexton and Heatwole (1966) elaborate somewhat on Boulenger's description. Of four specimens, only one was olive dorsally with reddish brown marbling, the others being grayer and darker and having blackish marbling. Furthermore, "in all, the facial bars and the subterminal ring on the snout are black. The tip of the snout is whitish, slightly clouded in one. Field notes give the fresh color of this tip as yellow (in UMMZ 120324)" (Test, Sexton, and Heatwole, 1966: 20). The ventral surfaces are described as immaculate and yellowish, or dusty. These specimens are without cream-colored spots on the flank. On the basis of these descriptions and additional preserved material one may characterize *Anadia marmorata* in the following way: Olive, brownish or greyish dorsally with sparsely or densely scattered darker markings, or with reddish-brown or blackish marbling. Head with numerous dark markings on the lateral surfaces, almost all the sutures between the infralabials being more or less heavily outlined with dark pigment. Dark streak, or remnants of such a streak extending posteriorly from the orbit above the ear. From the lower border of the orbit a light stripe passes through ear to the forelimb and extends, in some specimens, along the side of the body in the form of light, irregular blotches. Tip of the snout light colored. Venter light, with or without dusting, spotting or irregular marbling.

Range and Habitat

Inhabiting the coastal range of Venezuela, *A. marmorata* has recently been taken at altitudes of 3600' (ca. 1100 m), 3690' (ca. 1125 m), 1500 m, 2000 m, and 3000' (ca. 2440 m) in the provinces of Aragua, Distrito Federal. The type locality of "Colombia" is erroneous, at least in its present

usage, and should be corrected to "northcentral Venezuela." Similarly I presume that the locality "Puerto Cabello" refers to the port from which the specimen was shipped in the mid-nineteenth century, and that the site of collection was in nearby Aragua province.

On the basis of field data for four specimens, Test, Sexton and Heatwole (1966) have suggested this species to be arboreal: "One individual was obtained about 2 m above the ground in the space between the still clasping base of a dead palm (*Iriartea*) leaf and the trunk, whereas another fell out of a tree from a height of 10-15 m.... Its morphology and what little we know of its habits suggest that *Argalia* [=*Anadia*] *marmorata* may be ecologically an arboreal counterpart of *Proctoporus achlyens,* living in the epiphytic leaf litter which accumulates on the larger branches of trees. Such habits could easily account for the small numbers of this species in collections" (Test, Sexton, and Heatwole, 1966, pp. 19-20). The pair of specimens mentioned by Gray (1847) were also found in a tree.

Discussion

In his *Catalogue of Lizards,* Boulenger (1885) recognized the genus *Argalia* erected by Gray (1846), though he reduced *Argalia olivacea* Gray to synonymy with *Argalia marmorata* Gray, leaving *Argalia* a monotypic genus. In his generic synopsis of the Teiidae, *Argalia* was distinguished from other similar microteiid genera by the large size of the dorsal scales, these being larger than the ventrals. Comparative examination of Boulenger's generic definitions further reveals *Argalia* to have been considered distinct from *Anadia:* 1) in having the body scales form transverse series on the back and belly but not complete annuli, 2) in having a "non-transparent disk" on the lower eyelid rather than a "more or less transparent disk composed of several scales" and 3) in having femoral pores not just in the male, but in both sexes.

Careful evaluation in the light of subsequently discovered species of *Anadia* reduces the significance and validity of these criteria. *Anadia pulchella* has dorsals equal in size to the ventrals, while the dorsals of *A. blakei* are larger than the ventrals. Indeed, within the *Anadia* one finds a gradation in size of the dorsals, from being clearly smaller than the ventrals (e.g. *A. steyeri*) to being clearly larger than the ventrals (e.g. *A. blakei*), such that generic distinction of *Argalia* on the grounds of size of dorsal scales alone cannot be maintained. Furthermore, several species of *Anadia* have annuli interrupted laterally to the same extent as *marmorata.* The so-called "non-transparent disk" on the lower eyelid of *marmorata* is but a disk divided into several large scales and speckled with pigment, as in the case in *Anadia bogotensis, Anadia brevifrontalis,* some *Anadia bitaeniata,* and some *Anadia blakei.* Finally, Boulenger's statement that femoral pores are absent in female *Anadia* is incorrect, femoral pores being found in both sexes of all species with the exception of certain female specimens of *A. bogotensis* and *A. rhombifera.*

The undermining of the criteria thought by Boulenger to distinguish *Argalia* from *Anadia,* suggests that *Argalia* should be synonymized with

Anadia. Such an alteration of taxonomic allocation is strongly supported by the close relationship of *A. marmorata* to *Anadia blakei* Schmidt. I have without hesitation placed them in the same species-group, as they are so similar in gross morphology, differing only in certain respects such as subocular size, sexual dimorphism, and midbody count (see discussion of *A. blakei*). Furthermore, there is a supposed new species of *Anadia* which this study reveals to be only a synonym of *marmorata*. Confusion of *Argalia* with *Anadia* has already taken place.

In 1963, A. R. Lancini described a new species, *Anadia duquei*, whose similarity to *Anadia blakei* was noted. Unfortunately but one specimen was available to Lancini at that time, and it was of different sex from the type and paratype of *A. blakei*. I have examined a subsequently collected specimen (MCNC 5397) also designated as *A. duquei* by Lancini and it is clear from the large size the suboculars, the dorsal, ventral and midbody counts (table 1), the high number of femoral pores in an apparently female specimen, and the markings on the head that this specimen belongs to *A. marmorata*. Although the type of *A. duquei* has not been examined, this specimen and the information contained in Lancini's type description and the accompanying photograph of the head scales and head markings have convinced me that *Anadia duquei* should be considered a synonym of *Anadia marmorata*.

Specimens Examined

Syntypes. "Colombia" (Venezuela) BM 1946.9.1.15-16.

Additional specimens. VENEZUELA: "Puerto Cabello," Berlin 1160 (syntype of *Gerrhonotus poecilochilus*); *Aragua Province*: near Colonia de Tova (8000'), BM 1946.8.8.97-98 (syntypes of *Argalia olivacea*); Rancho Grande AMNH 69039, UMMZ 120330 (3600'); Rancho Grande, near Portachuelo Pass UMMZ 120328, 120331; Rancho Grande, trail to Pico Periquito (3690'), UMMZ 120329; *Distrito Federal:* El Junquito (2000 m), AMNH 96248-49; between Carayaca and El Junquito (1500 m), MCNC 5397.

Anadia blakei Schmidt

Anadia blakei Schmidt, 1932: 161-162 (Type locality: Mt. Turumiquire, Venezuela).

Diagnostic Traits: 1. low dorsal count: 28-30.5; 2. low midbody count: 28-30; 3. dorsal scales larger than ventral scales; 4. dorsal scales quadrangular; 5. suboculars small and indistinct (fig. 20B); 6. dorsal coloration brown, with some scattered markings; 7. thin pencil line from the eye part way to the ear; 8. venter light; 9. femoral pores: 7-8 in male, 3-4 in female; 10. body stout; 11. adult male with enlarged head having prominent swelling of the posterolateral parts.

Anadia blakei may be distinguished from: 1. All *Anadia* except *A. bitaeniata* and *A. marmorata* by the low dorsal count; 2. *A. bitaeniata*

by the lack of bluish, slate or greyish coloration, the large size of the dorsal scales, and the small, indistinct nature of the suboculars; 3. *A. marmorata* by the small size of the suboculars, the lower midbody count, the absence of labial markings, the tip of the snout not being lighter than the head, and the reduced number of femoral pores in the female.

Description (N=3)

Each nasal single, contacting rostral. Midline suture between prefrontals short. 3 supraoculars and 0-1 presupraocular. 5 superciliaries. 3-4 lower palpebrals, with or without speckles of pigment. 4-6 suboculars, all very small, or indistinct, in a continuous or discontinuous row. 13-16 transverse gular rows. Head of male greatly expanded posterolaterally, and proportionately much larger than head of female.

Dorsal scales quadrangular, much longer than broad, with posterior edge straight, arranged in 28-30.5 juxtaposed transverse rows from ear to tail. Lateral scales slightly smaller, such that many transverse rows pass about body as annuli without lateral irregularities. 28-30 scales in midbody annulus. Ventral scales quadrangular, somewhat smaller than dorsals, arranged in 26-27 juxtaposed transverse rows from throat to vent. 5-6 quite large scales along anterior border of vent. Femoral pores 7-8 in male, 3-4 in female. 20-23 lamellae under fourth toe of hind limb. Maximum snout-vent length 90.9 mm (male).

Color Pattern

In the type description, Schmidt (1932) mentioned only that the type is "uniform brown above, paler beneath." This specimen has in addition a few specks of dark pigment scattered about the dorsal surface, and a thin line penciled from the corner of the eye slightly more than halfway to the ear. The paratype is more heavily marked, having virtually each longitudinal suture between adjacent dorsal scales outlined by a thin, dark longitudinal dash, as well as the thin line pencilled from the eye partway to the ear. The venter is light, with a tan hue and a few scattered markings. In both lizards the labials are essentially unmarked, and the tip of the snout is not conspicuously lighter than the head.

The single additional specimen is badly discolored such that markings are obscured.

Range and Habitat

Apparently inhabiting the mountainous area in Sucre and Monagas Provinces of northeastern Venezuela, *A. blakei* has been collected from elevations of 5000 and 6000 ft. (1520 and 1830 m).

Discussion

The easternmost representative of *Anadia* came into taxonomic view with its 1932 description by Schmidt. In addition to the two specimens

discussed by him, apparently but one additional example has been preserved.

A. blakei is in external morphology quite similar to *A. marmorata*, and it is on this ground that the inclusion in *Anadia* of the latter species is most strongly supported. An important similarity lies in the large size of the quadrangular shaped dorsals (reflected in the low dorsal count), a condition unique to these two species among *Anadia*. The head scales of the two are much alike (fig. 20), except for the suboculars, which are small, indistinct, and sometimes even in a discontinuous row in *A. blakei*, but are large, evident and continuous in *A. marmorata*. Body proportions of both are stout, and both exhibit pronounced sexual dimorphism. In *A. marmorata*, however, the females do not have a reduced number of femoral pores relative to the males, as is the case for *A. blakei*. The dark markings on *A. blakei* are reduced relative to *A. marmorata*, consisting solely of the thin pencil line from the eye partway to the ear, and scattered thin flecks and streaks, the labials being essentially unmarked. Unlike *A. marmorata*, the tip of the snout is not lighter in coloration than the remainder of the head.

Otherwise, *A. blakei* is morphologically closely allied to the *bitaeniata*-group, both in respect to the head scales (excepting the suboculars) and the quadrangular shape of the dorsal scales. Nonetheless *A. bitaeniata* is clearly distinct in such respects as scale counts and coloration.

Specimens Examined

Holotype. VENEZUELA: Mt. Turumiquire [which divides the provinces of Sucre and Monagas], 6000', FMNH 17795.

Additional specimens. VENEZUELA: Mt. Turumiquire (5000'), FMNH 17794 (paratype of *A. blakei*) ; *Monagas Province:* Cerro Negro, Caripe UIMNH 63561.

III. GENERAL DISCUSSION

The species accounts have put forward my observations of significant traits for systematic study. As the study of any species is only meaningful in the context of the relationship of this species to other similar ones, I have endeavored to present the results in such a fashion as to encourage direct comparison of the species of *Anadia*. Hence the essentially identical form of each species description, and the provision of a list of diagnostic traits.

Completion of this revision entails a more synthetic approach to the subgroupings within *Anadia*, for certain species seem naturally to fit together. On the one hand, on the basis of the dorsal scales, species fall into eastern and western groupings, while on the other closely related *Anadia* can be seen to form fairly clear species groups. It is the combined results of both that serve to indicate phyletic relationships.

The East-West Groupings

An interesting correlation exists between geographical distribution of the species and the shape of the dorsal scales. It appears that two groups may be roughly distinguished: the western species (of Ecuador, central and western Colombia, Panama and Costa Rica) have relatively short and somewhat imbricate, dorsal scales with more or less rounded posterior edges (fig. 23), while those species to the east (northeastern Colombia and Venezuela) have juxtaposed, or but very slightly imbricate, quadrangular dorsal scales with more or less straight posterior edges. Inasmuch as the one western species (*A. vittata*)

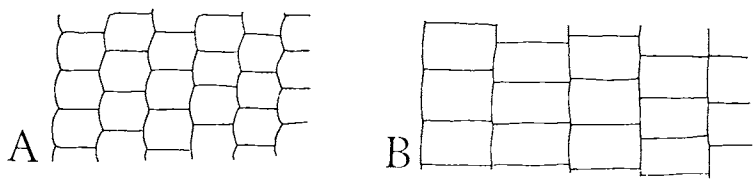

Fig. 23, The subhexagonal (A, *A. ocellata*) and quadrangular (B, *A. brevifrontalis*) dorsal scale types. Illustrated are the scales of the midback, on the right side of the middorsal line.

with dorsals most closely resembling the eastern quadrangular condition is the species geographically closest to the eastern group, one cannot rule out the possibility of an interrupted but continuous trend from east to west. Nonetheless, I have used the distinction to suggest a possible east-west division in the reconstruction of phyletic relationships (fig. 24). At the current state of "microteiid" research the importance of these trends in scale shape is at best hypothetical, but it is intriguing to suppose that 1) slight mid-scale thickening in some *A. marmorata* of the elongate, quadrangular dorsals, which in shape resemble the feebly keeled dorsals of some *Ptychoglosus*, and 2) the somewhat pointed nature of the posterior

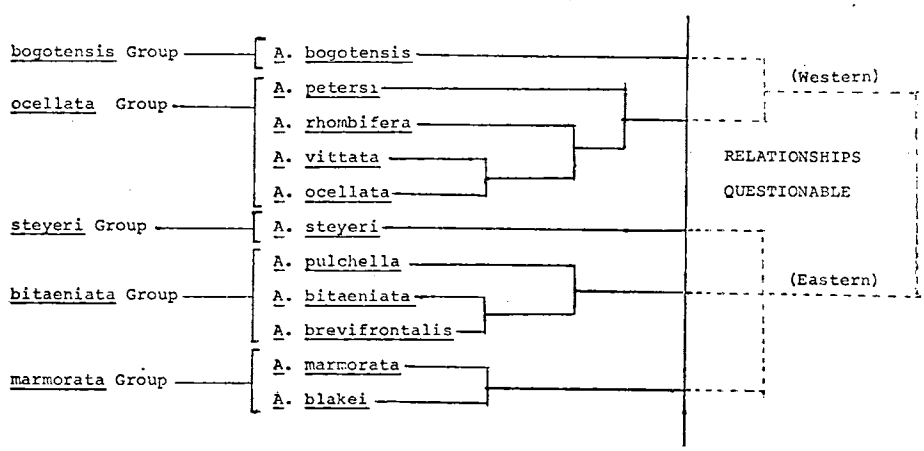

Fig. 24, Species groups in *Anadia* and suggested phyletic relationships.

rounding of the "subhexagonal" dorsals [1] of some *A. rhombifera* might represent traces of two keeled-scale types, the rectangular and the hexagonal, respectively. Thus the east-west division may have deeper phyletic significance than one of mere groupings of species; it may be that this division reflects convergence of at least two genera to a smooth-scaled condition.

The Species-Groups

The close similarities of certain species have led to the repeated misidentifications so prevalent in the systematic history of *Anadia*. The persistence of nomenclatural confusion testifies to the difficulties in distinguishing closely related species. Species-groups within *Anadia* are an unavoidable conclusion, yet the delimitation of the groups requires a recognition of useful criteria. The five species-groups discussed below are primarily distinguished by the condition of the prefrontals, the superciliaries, the suboculars, the femoral pores, by the scale counts on the trunk, and, of course, by the shape of the dorsal scales.

1. The *ocellata*-group — A western species-group comprised of four species *(ocellata, vittata, rhombifera,* and *petersi)* with "sub-hexagonal" dorsal scales (fig. 23). The prefrontals are always in contact, usually forming a long suture (of medium length in *petersi*). Most specimens have one or two small scales inserted between the superciliaries and the supraoculars, a condition otherwise found only in a few *bogotensis*. These, along with *bogotensis,* are the only *Anadia* in which a subnostril groove or divided nasal is found. The suboculars are fairly large and varied, with one protruding downward in a wedge between the 4th and 5th supralabials. In coloration, this group is characterized by dark dorsolateral lines, lateral occeli and a light venter, although all three characteristics need not be simultaneously present. The males have a series of up to 15 femoral pores per side, but these are reduced in number (no more than 5) in the females.

Within the group, *ocellata* and *vittata* are most similar, both being slender and narrow-headed. Among *Anadia,* these are the only species showing no sexual dimorphism in head size (the data for *A. steyeri* are inconclusive). *A. rhombifera* has an intermediate dorsal scale count, as opposed to the high counts of the other three species. Although. *A. rhombifera* is slightly dimorphic in head size, it is the higher altitude species, *A. petersi,* that distinctly shows expansion of the temporal region in the male, as would be expected if a correlation exists between head size dimorphism and altitudinal distribution (p. 243). The more imbricate condition of both the ventral and dorsal scales of the latter species relative to non-Bogotá *Anadia* suggests a partial step towards the condition of *A. bogotensis.*

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1. It is interesting to note that Boulenger's characterization (1885) of *Anadia* as having "subhexagonal" dorsals was appropriate for that time — the only western species then known *(A. marmorata)* was considered to be *Argalia.*

2. The *bogotensis*-group — The single high-altitude species *A. bogotensis* is distinct from the other species in that both the dorsal and ventral scales are considerably imbricate. The dorsals are rounded subhexagonal, placing *bogotensis* in the western division with the *ocellata*-group (fig. 23). Other than members of the *ocellata*-group, only *bogotensis* occasionally has a small scale inserted between the superciliaries and the supraoculars; *bogotensis* females, like *ocellata*-group females, have no or only a few femoral pores, while the males have up to 16. In view of these observations and the quite imbricate dorsal condition of *A. petersi* (fig. 13), it is attractive to consider *bogotensis* related to, and possibly derived from the *ocellata*-group. *A. bogotensis* is even more dimorphic in head size than *petersi*. In addition, the former is one of the two species (*A. brevifrontalis* being the other) that may have 2 rather than 3 or 4 supraoculars, and one of the four (the three *bitaeniata*-group species being the others) having the prefrontals regularly not connected — conditions probably correlated with the high altitudinal distributions of these species, and presumably representing the results of convergent evolution.

3. The *steyeri*-group — Like *A. bogotensis*, *A. steyeri* is distinctive and may be grouped by itself. A lowland lizard of coastal Venezuela, *A. steyeri* calls to mind *A. ocellata* and *A. vittata* in being long and in having a high dorsal count, a long prefrontal suture and a light venter, yet the head is relatively larger, the body more stout, and the dorsals rectangular and juxtaposed rather than subhexagonal. The higher midbody count and the large, regular suboculars which do *not* intrude downward between the underlying supralabials (fig. 25) are two characters which set *steyeri* apart. *A. pulchella* is the only other species with suboculars somewhat like *steyeri*. The only three specimens of *steyeri* preserved all have the row of femoral pores interrupted in the middle by a large gap leaving an inner and an outer set (all are probably female), a condition not otherwise observed in *Anadia*.

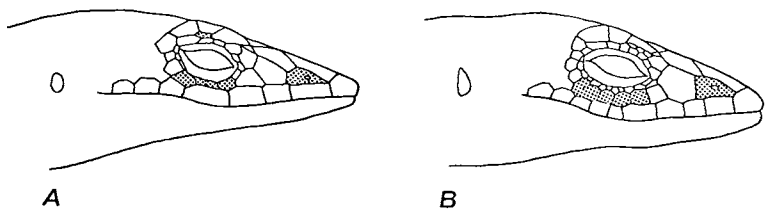

Fig. 25, Comparison of the distinguishing traits of the head scalation of *A. steyeri* (B) and species of the *ocellata*-group (A)

4. The *bitaeniata*-group — Three species (*A. pulchella, A. bitaeniata,* and *A. brevifrontalis*) constitute this group of *Anadia*. The dorsals are quadrangular and slightly rounded posteriorly (fig. 23); the suboculars may be equal or unequal in size, *pulchella* being *steyeri*-like in having no intruding wedge condition; the prefrontals may or may not connect. The dorsal count is much lower than for *steyeri* yet usually

higher than for the *marmorata*-group. Females of the *bitaeniata*-group have as many femoral pores as males (up to 11), a situation otherwise found only in *A. marmorata*. The sexes are dimorphic in head size, supporting the proposed correlation to high elevations.

A. bitaeniata and *A. brevifrontalis* are the two most closely related, having been repeatedly confused by systematists — even, it appears from identifications in the British Museum, by Boulenger, who described both species! *A. pulchella* is much like *bitaeniata* except in ground coloration and in the *steyeri*-like subocular condition. Dunn (1937) considered *pulchella* a race of *bitaeniata* although he subsequently (1944a) changed his mind.

5. The *marmorata*-group — *A. marmorata* and *A. blakei* of the Coastal Range of Venezuela are at first sight very similar, and might be considered one species if it were not for two observed differences that in this genus appear significant and characteristic of species rather than races. Both are large and stout *Anadia* with large elongate quadrangular dorsals and low dorsal count, but unlike *marmorata, blakei* has very small suboculars (fig. 20) and a reduced number of femoral pores in the female. On the other hand, in these characters, *marmorata* resembles the *bitaeniata*-group, having moderately large suboculars (with the intruding wedge condition), and an equal number of pores in both sexes. Both species are sexually dimorphic in head size.

The groups as described are conservative in that only clearly related species have been put together. Any further combining of species has been deemed inadvisable and unnecessary in view of the limited samples for many species (for *petersi, blakei* and *steyeri* n=3), the limitation of this study to external morphological characters, and the lack of any comparable study of closely related "microteiids" by which the significance of the distinguishing criteria might be evaluated. Traits such as the small inserted scale above the superciliary row, the nature of the suboculars and the sexual dimorphism are useful in distinguishing the species of *Anadia*, but their adaptive significance and evolutionary stability are unknown.

Figure 24 serves to summarize the phyletic relationships as discerned from the suggested east-west division and similarities within species-groups. Though it is by no means certain whether the *Anadia* are derived from a common generic ancestor, or are the result of several lines converging to a smooth scaled condition, it is conceivable that at some point the western group gave rise to the *bogotensis* and *ocellata* species-groups, while the *steyeri, bitaeniata* and *marmorata* species-groups arose out of the eastern group. As previously mentioned, it is my suspicion that examination of other microteiid genera will shed further light on the phyletic relationships between species-groups of *Anadia*, as will utilization of internal anatomic and structural features for systematic study.

Concluding Comments

The problems faced by systematists in attempting to clarify the specific, interspecific and generic categories of the lizards referred to as

"microteiids" are vast. Clearly, if the generic boundaries are as uncertain as they appear to be in my observation, then generic revisions of this sort can be of but limited value unless they establish relationships within these boundaries, for it is these relationships which then can provide the foundation for a phyletically accurate systematic arrangement.

It is with this approach in mind that the revision of *Anadia* has been presented. Thus the species descriptions are close to identical so as to allow easy location of the differing traits by inter-specific comparison. Thus a tabular list of diagnostic traits precedes each species description to permit clear understanding of the points of similarity and distinction. Thus the east-west groupings and species-groups are discussed.

It is the sincere hope of this author that these efforts at providing a stimulus for systematic overhaul of the microteiids will not be in vain. I have given but a preliminary indication of such difficulties as convergent evolution and altitudinal adaptation. The degree to which such phenomena prevail without acknowledgement is a measure of the ambiguity still present in microteiid systematics.

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Table 1. Scale counts for Anadia species

Species	Number of Specimens	Dorsal Scale Count	Ventral Scale Count	Midbody Count	Femoral ♂	Pores ♀
A. ocellata	15	50-58.5 (53.1)	35-41.5	27-32	8-11	2-6
A. vittata	8	55.5-61 (59.1)	37-42.5	30-37	11-14	2-4
A. rhombifera	14	44-48.5 (46.5)	31-35	30-34	8-15	0-2
A. petersi	33	49-56 (52.0)	35.5-36	31-33	9-12	1-2
A. bogotensis	80	35-45.5 (39.8)	28.5-35.5	24-32	10-16[1]	0-2(6?)[2]
A. steyeri	3	59.5-61.5 (60.3)	39.5-41.5	41-45	--	1-2+3-5[3]
A. pulchella	10	36.5-44 (40.2)	30.5-35	34-41	6-9	5-8?
A. bitaeniata	29	32-42 (38.8)	27-31	31-41	8-10	7-11
A. brevifrontalis	43	40-50 (44.7)	29-37	30-38	5-9	6(2?)-9
A. marmorata	13	27.5-34 (29.8)	27-30	30-37	8-12	8-11
A. blakei	3	28-30.5 (29.5)	26-27	28-30	7-8	3-4

Footnotes:

1. for 15 males
2. for 18 females
3. in two sets, one inner and one outer

Table 2. Counts and measurements for the holotypes of A. ocellata and its synonyms

	Pre-supra-oculars	Supra-oculars	Super-ciliaries[2]	Sub-oculars	Nasal[3]	Palpe-brals	Gulars	Dorsals[4]	Ventrals[4]
BM 1946.8.2.2 (holotype of A. ocellata)	1	3	5+1	4	2-c	5	17-18	56	37
USNM 30568[1] (holotype of A. metallica)	1	3	4?+1	?	2-x	?	16-17	55r,54	40
KU 34223 (holotype of A. metallica attenuata)	1	3	4+1	4	1-c	5	16-17	52r,51	39
KU 34225 (holotype of A. metallica arborea)	1	3	(4+0)r, 3-1	5r,4	1-c	4r,5	18-20	58r,59	42r,41

	Scales About Midbody	Sub-digital Lamellae[5]	Femoral Pores[5]	Sex	Snout-Vent Length (mm)	Snout-Ear Length (mm)	Tail Length (mm)
BM 1946.8.2.2	32	--	10	♂	48.2	10.0	broken
USNM 30568	?	?	3?	?	ca.52	ca.11	ca.107
KU 34223	31	16r,15	2r,10	♂	58.4	10.8	119
KU 34225	28	17r,18	5r,6	?	63.5	10.5	118

Notes:

1. specimen dried and distorted
2. the designation +1 indicates a small scale inserted between superciliary row and supraoculars (fig. 16).
3. the designations -c, -x, specify whether the nasal does (-c) or does not (-x) contact the rostral scale; the numbers 1, 2, refer to the condition of the nasal, whether single (1) or divided (2).
4. where two counts are given, one refers to the right side of the middorsal line (e.g. 55r), and the other to the left.
5. counts given are per hind limb, two counts indicating that right (r) and left differ.

Table 3. Counts and measurements for the types of A. vittata and a synonym

	Pre-Supra-oculars	Supra-oculars	Super-ciliaries	Sub-oculars	Nasal	Palpe-brals	Gulars	Dorsals	Ventrals
BM 1913.11.12.34 type of A. vittata	1	3	4+1	4	1-x	6	18	59	40r,39
BM 1946.9.1.2 type of A. angusticeps	2	3	(5r,4)+1	5	1-x	4	17	60r,62	42r,43

	Midbody	Lamellae	Femoral Pores	Sex	Snout-Vent Length	Snout-Ear Length	Tail Length
BM 1913.11.12.34	32	15r,16	4		39.5	9.0	broken
BM 1946.9.1.2	34	15	2?		48.0	9.8	injured

For clarification of notation see Table 2.

Table 4. Counts and measurements for the type of A. rhombifera

	Pre-supra-oculars	Supra-oculars	Super-ciliaries	Sub-oculars	Nasal	Palpe-brals	Gulars	Dorsals	Ventrals
BM 1946.9.1.4 (holotype)	1r,0	4	4+2r,5+1	4	1-c	5 or 6?	15	17r,49	35

	Midbody	Lamellae	Femoral Pores	Sex	Snout-Vent Length	Snout-Ear Length	Tail Length
BM 1946.9.1.4	34	15?	0-1?		51.3	10.8	117

For clarification of notation, see Table 2.

Table 5. Counts and measurements for A. petersi

	Supra-oculars	Super-ciliaries	Sub-oculars	Nasal	Palpe-brals	Gulars	Dorsals	Ventrals
USNM 193221, holotype	3	5+1r,4+2	4	(1r,2)-x	5	15-16	52r,50	36r,35
USNM 193222, paratype	3	4+1	3	1-x	4r,5	17	56	35r,36
MÜNCHEN 47/1928, paratype	3	3r,4	5r,4	1-x	5r,4	17	50r,48	36

	Midbody	Lamellae	Femoral Pores	Sex	Snout-vent Length (mm)	Snout-ear Length (mm)	Tail Length
USNM 193221	31	19	9r,10	♂	67.5	14.9	broken
USNM 193222	33	19r,20	2r,1	♀	60.5	11.8	116mm
MÜNCHEN 47/1928	32	20	12	♂	74.3	15.4	131mm

For clarification of notation, see Table 2.

Table 6. Summary of counts for 16 syntypes of Anadia bogotensis

	Supra-oculars	Super-ciliaries	Sub-oculars	Nasal	Palpebrals	Gulars
Berlin 4654 (16 specimens, syntypes)	2-3	3-5+(0-1)	3-5	1-c or 1-x	3-5	14-17

	Dorsals	Ventrals	Midbody	Lamellae	Femoral Pores ♂	Femoral Pores ♀
Berlin 4654	35-45.5	29-35	25-29	13-18	10-15	0-1

For clarification of notation, see Table 2.

Table 7. Counts and measurements of A. steyeri

	Pre supra-oculars	Supra-oculars	Super-ciliaries	Sub-oculars	Nasal	Palpebrals	Gulars
Berlin 24293, holotype	1	3	6	5	1-c	5	17 or 18
Basel 9229	1	3	5	5r,4	1-c	5	22
MCZ	2	3	7+3	5r,6	1-c	6	21 or 22

	Dorsals	Ventrals	Midbody	Lamellae	Femoral Pores	Sex	Snout-vent Length	Snout-ear Length	Tail Length
Berlin 24293	62r,61	42r,41	41	17r,18	2+5r, 1+4ℓ	♀	81.0	17.1	120
Basel 9229	60r,59	40r,41	44	18r,19	1+3	♀?	70.5	14.3.	113
MCZ 48901	60	40r,39	45	17	2+5	♀?	55.5	12.3	---

For clarification of notation, see Table 2.

Table 8. Counts and measurements of the type of A. pulchella

	Pre-supra-oculars	Supra-oculars	Super-ciliaries	Sub-oculars	Nasal	Palpebrals	Gulars
UMMZ 63333	0	3	6	3	1-c	4	15 or 16

	Dorsals	Ventrals	Midbody	Lamellae	Femoral Pores	Sex	Snout-vent Length	Snout-ear Length	Tail Length
UMMZ 63333 (holotype)	43r,44	31	41	18	5	♀	--	--	91

For clarification of notation, see Table 2.

Table 9. A Comparison of A. pulchella from the Santa Marta Mountains and from Pamplona

	Pre-supra-oculars	Supra-oculars	Super-ciliaries	Sub-oculars	Palpebrals	Gulars
Santa Marta Mountains A. pulchella (N=3)	0-1	3	6	3-3.5	4-4.5	15-16
Prov. Norte de Santander "A. pamplonensis" (N=7)	0-1	3-4	5-6.5	3-3.5	4-5	15-17

	Dorsals	Ventrals	Midbody	Femoral Pores (both sexes)	Scales bordering Vent (=preanals)
Santa Marta	39-44	31-32	37-41	5-8	6
Prov. Norte de Santander	36.5-41	30.5-35	35-39	6-8	5-7

Table 10. Summary of counts for the syntypes of A. bitaeniata

	Pre-supra-oculars	Supra-oculars	Super-ciliaries	Sub-oculars	Palpebrals	Gulars
BM 1946.8.2.11-13 and BM 1946.8.31.25-28 (syntypes of A. bitaeniata)	0-1	3	4-5	4	4-5	12-14

	Dorsals	Ventrals	Midbody	Lamellae	Femoral Pores
	32-39.5	27-30	32-37	16-19	8-10

Table 11. Counts and measurements of the types of A. brevifrontalis

	Pre-supra-oculars	Supra-oculars	Super-ciliaries	Sub-oculars	Palpe-brals	Gulars	Dorsals	Ventrals	Midbody
BM 1946.8.2.32 (syntype)	0	2	3	4	4r,3	16	45r,43	31	36
BM 1946.8.2.33 (syntype)	1	2	3	4	?	16-17	45	33r,32	33
BM 1946.8.31.62 (syntype)	0	2	4r,3	4	3	15	46r,48	30	35

	Lamellae	Femoral Pores	Sex	Length	Length	Tail Length
BM 1946.8.31.62	--*	7	♂	--*	--*	--*
BM 1946.8.2.33	--*	8	♂	--*	--*	--*
BM 1946.8.31.62	19	9	♀	74.4	14.1	94

* not recorded through oversight

Table 12. Counts and measurements for the types of Anadia marmorata and an additional specimen

	Pre-supra-oculars	Supra-oculars	Super-ciliaries	Sub-oculars	Palpebrals	Gulars
BM 1946.9.1.15 (syntype of Argalia marmorata)	1	3	4	4	5	15-16
BM 1946.9.1.16 (syntype of Argalia marmorata)	1	3	5	5r,4	5r,6	16
MCNC 5397 (specimen of "Anadia duquoi Lancini")	1	3	4	6	4	15

	Dorsals	Ventrals	Midbody	Lamellae	Femoral Pores	Sex	Snout-vent Length	Snout-ear Length	Tail Length
BM 1946.9.1.15	29	29r,27	35	19r,21	11r,9		72.1	17.7	132
BM 1946.9.1.16	28r,30	29	37	19	9r,11		79.4	17.6	128
MCNC 5397	29	27	33	17r,16	11r,8		--	--	--

For clarification of notation, see Table 2.

Table 13. Counts and measurements for the types of A. blakei

	Pre-supra-oculars	Supra-oculars	Super-ciliaries	Sub-oculars	Palpebrals	Gulars
FMNH 17795 (type of A. blakei)	1ℓ	3	6	6	4	14-15
FMNH 17794 (paratype)	1ℓ	3	6	7	3	15-16

	Dorsals	Ventrals	Midbody	Lamellae	Femoral Pores	Sex	Snout-vent Length	Snout-ear Length	Tail Length
FMNH 17795	30r,31	27	30	20r,21	4	♂	87.7	18.1	--
FMNH 17794	30	26	28	21r,20	3	♂	77.9	17.1	--

For clarification of notation, see Table 2.