

ANGUID LIZARDS OF THE GENUS
ABRONIA: REVISIONARY NOTES,
DESCRIPTIONS OF FOUR NEW
SPECIES, A PHYLOGENETIC
ANALYSIS, AND KEY

JONATHAN A. CAMPBELL AND DARREL R. FROST

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ABRONIA: REVISIONARY NOTES,
DESCRIPTIONS OF FOUR NEW
SPECIES, A PHYLOGENETIC
ANALYSIS, AND KEY

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ABSTRACT

We establish that *Abronia vasconcelosii* is a junior synonym of *A. aurita*. *Abronia fimbriata* is resurrected from the synonymy of *A. aurita* and shown to be one of the most distinctive species in the genus. *Abronia gaiophantasma* and *A. anzuetoi* are described, respectively, from the cloud forest of the western Sierra de las Minas, Department of Baja Verapaz, Guatemala, and the southern (Pacific) slope of the Volcán de Agua, Department of Escuintla, Guatemala. These species had previously been confused with *A. aurita* and "*A. vasconcelosii*," respectively. *Abronia smithi*, a new species from the Pacific versant of Chiapas, Mexico, and *A. leurolepis*, a new species from the Atlantic versant of Chiapas, Mexico, are described and distinguished from *A. ochoterenai*, from the Atlantic versant of Chiapas, Mexico, with which they had previously been confused. A more detailed diagnosis of *A. matudai*, of the Pacific versant of Guatemala and Chiapas, Mexico, is provided. *Abronia kalaina* is placed in the synonymy of *A. fuscolabialis*, and specimens previously reported as *A. montecristoi* from Honduras are shown to be representatives of *A. salvadorensis*.

We address the taxonomic history and provide synonymies and diagnoses for each of the problematical species. The natural history, conservation biology, and phylogeny of *Abronia* are discussed. The use of intraspecifically variable characters in phylogenetic inference is addressed

and alternative approaches to analysis are compared: (1) a reference approach in which only "fixed" characters are employed (i.e., all transformation series that contain polymorphic cells in the data matrix are excluded); (2) a "baseline" approach in which polymorphisms are optimized onto the resulting cladograms, but polymorphism is not allowed on interior stems; (3) an "any instance" approach in which only a priori apomorphies are coded, regardless of frequency; (4) an "unscaled," minimum turnover approach in which all character matches count equally a priori and origination of apomorphies is minimized; and (5) a "scaled" approach in which the transformation diameter from "fixed" plesiomorphy direct to "fixed" apomorphy is the same as from "fixed" plesiomorphy to "variable" within a terminal taxon to "fixed" apomorphy. A priori weighting of characters that exhibit no intrapopulational polymorphism over those showing polymorphism is done in order to evaluate the signal inherent in intraspecifically variable characters as well as characterization problems. Successive approximations is evaluated as a means of increasing the signal to noise ratio in data analysis. The technique recommended for incorporating intraspecifically variable morphological characters into a phylogenetic analysis is an unscaled, minimum turnover approach, combined with successive approximations.

RESUMEN

Se establece que *Abronia vasconcelosii* es un sinónimo de *A. aurita*. *Abronia fimbriata* es rescatada de la sinonimia de *A. aurita*, demostrando ser uno de los miembros más distintivos del género. Se describen las especies guatemaltecas, *Abronia gaiophantasma* del bosque nuboso del oeste de la Sierra de las Minas, Departamento de Baja Verapaz, y *A. anzuetoi* de la vertiente Sur (Pacífica) del Volcán de Agua, Departamento de Escuintla, especies que habían sido previamente confundidas con *A. aurita* y "*A. vasconcelosii*," respectivamente. A su vez, se describen *Abronia smithi* y *A. leurolepis*, nuevas especies mexicanas de las vertientes Pacífica y Atlántica de Chiapas, respectivamente, y se las separa de *A. ochoterenai*, de la vertiente Atlántica de Chiapas, con la que eran anteriormente confundidas. Una diagnosis más detallada de *Abronia matudai*, de la vertiente Pacífica de Guatemala y Chiapas, México, es presentada. *Abronia kalaina* es colocada en sinonimia con *A. fuscolabialis*, y el status taxonómico de los especímenes de "*A. montecristoi*" de Honduras es resuelto. La historia taxonómica, sinonimia y di-

agnosis de cada de las especies problemáticas es tratada, discutiendo también la historia natural y filogenia de *Abronia*. El uso de caracteres con variación intraespecífica en la inferencia filogenética es discutido, comparandose soluciones alternativas del análisis: (1) una aproximación de "referencia" en la cual solo los caracteres "fijados" son utilizados en análisis (i.e., excluyendo todas las transformaciones que involucran polimorfismos de la matriz de datos); (2) una aproximación de "baseline" en que los polimorfismos son optimizados dentro de los cladogramas resultantes, de tal manera de minimizar el cambio de caracteres, pero sin permitir polimorfismos en las ramas internas; (3) una aproximación de "cualquier instante" en la cual solamente los caracteres apomórficos a priori son codificados, pero sin importar la frecuencia; (4) una aproximación "sin escala" en la que todas las correspondencias de caracteres cuentan igualmente a priori y donde el origen de apomorfías es minimizado; (5) una aproximación a "escala" en la cual el diámetro de transformación desde un carácter plesiomórfico "fijado" a uno

apomórfico "fijado" es equivalente al diámetro de transformación existente entre estos dos estados pasando a través de un polimorfismo. El ponderamiento a priori de caracteres que no exhiben polimorfismo poblacional sobre aquellos que sí lo presentan es evaluado con el propósito de evaluar la señal inherente tanto en caracteres variables intraespecíficamente como en problemas de carac-

terización. El método de aproximaciones sucesivas es evaluado como medio de incrementar la señal de ruido en el análisis. La técnica recomendada para la incorporación de caracteres morfológicos variables intraspecíficamente dentro de un análisis filogenético es la aproximación sin escalas, y de mínimo cambio, combinada con el método de aproximaciones sucesivas.

INTRODUCTION

Studies on the anguid lizard genus *Abronia* have not been burdened with an overabundance of comparative material. Although species of *Abronia* are known to occur from southern Tamaulipas and Guerrero, Mexico, to southern Honduras (fig. 1), with few exceptions, most species of *Abronia* are known from few specimens, often from only the type or a few specimens from the immediate vicinity of the type locality. The literature of their natural history is dispersed and the most recent comprehensive systematic treatment (Good, 1988) committed or continued a number of taxonomic errors. We show that (1) *A. vasconcelosii* is a junior synonym of *A. aurita*; (2) that in Good's study *A. vasconcelosii* was based on one specimen of *A. aurita* (the holotype of *A. vasconcelosii*) and one specimen of an undescribed species, here named; (3) as with other authors, Good's phylogenetic analysis and diagnosis of "*A. aurita*" are based on another undescribed species, here named; (4) *A. fimbriata*, as treated by almost all recent authors, is not a synonym of *A. aurita*, but is one of the most distinctive members of the genus; (5) *A. ochoterrenai* as treated by recent authors is a composite of three species, two of which are here named; (6) *A. kalaina* is a junior synonym of *A. fuscolabialis*, the characteristics separating these nominal taxa being typical of individual variation, and the habitat of these nominal species being continuous; and (7) the report of *A. montecristoi* from Honduras by Wilson et al. (1986) was based on specimens of *A. salvadorensis*.

We document these conclusions and summarize the literature and our observations on the distribution, natural history, behavior, and reproduction of these largely arboreal lizards. Following, we discuss the use of intra-specifically variable characters in phylogenetic

analysis, as well as the details of characters used previously by us and other authors. Our phylogenetic analysis is refined over previous attempts by: (1) the addition of six additional species²; (2) having before us new and re-identified material; (3) correcting some previous observations; and (4) employing explicit phylogenetic algorithms.

In this manuscript we use a number of supraspecific collectives, some novel in their content with respect to groups defined by previous authors (e.g., Tihen, 1954; Good, 1988): (1) *Abronia reidi* group (= *A. reidi* and *A. ornelasi*); (2) *A. bogerti* group (= *A. bogerti* and *A. chiszari*); (3) *A. deppii* group (= *A. deppii*, *A. fuscolabialis*, *A. graminea*, *A. species* "Guerrero," *A. mixteca*, *A. oaxacae*, and *A. taeniata*); (4) *A. deppii* subgroup of the *A. deppii* group (= *A. deppii*, *A. species* "Guerrero," *A. mixteca*, and *A. oaxacae*); (5) *A. aurita* group (= *A. anzuetoi*, *A. aurita*, *A. fimbriata*, *A. gaiophasma*, *A. leurolepis*, *A. lythrochila*, *A. matudai*, *A. ochoterrenai*, and *A. smithi*). For purposes of our discussion three species are not referred to any species group: *A. mitchelli*, *A. montecristoi*, and *A. salvadorensis*.

Except where noted, scale definitions (fig. 2) and protocols for making scale counts follow Bogert and Porter (1967) and Campbell (1982, 1984).

² These include four species described herein (*Abronia gaiophasma*, *A. anzuetoi*, *A. smithi*, and *A. leurolepis*), one species resurrected from synonymy (*A. fimbriata*), and one species being described elsewhere (*A. species* "Guerrero"—Flores-Villela and Sanchez, MS). We know of at least three additional species currently being described, one each from the Sierra Madre Oriental, Chiapas, and Guatemala, that were discovered too late to be addressed in our manuscript.

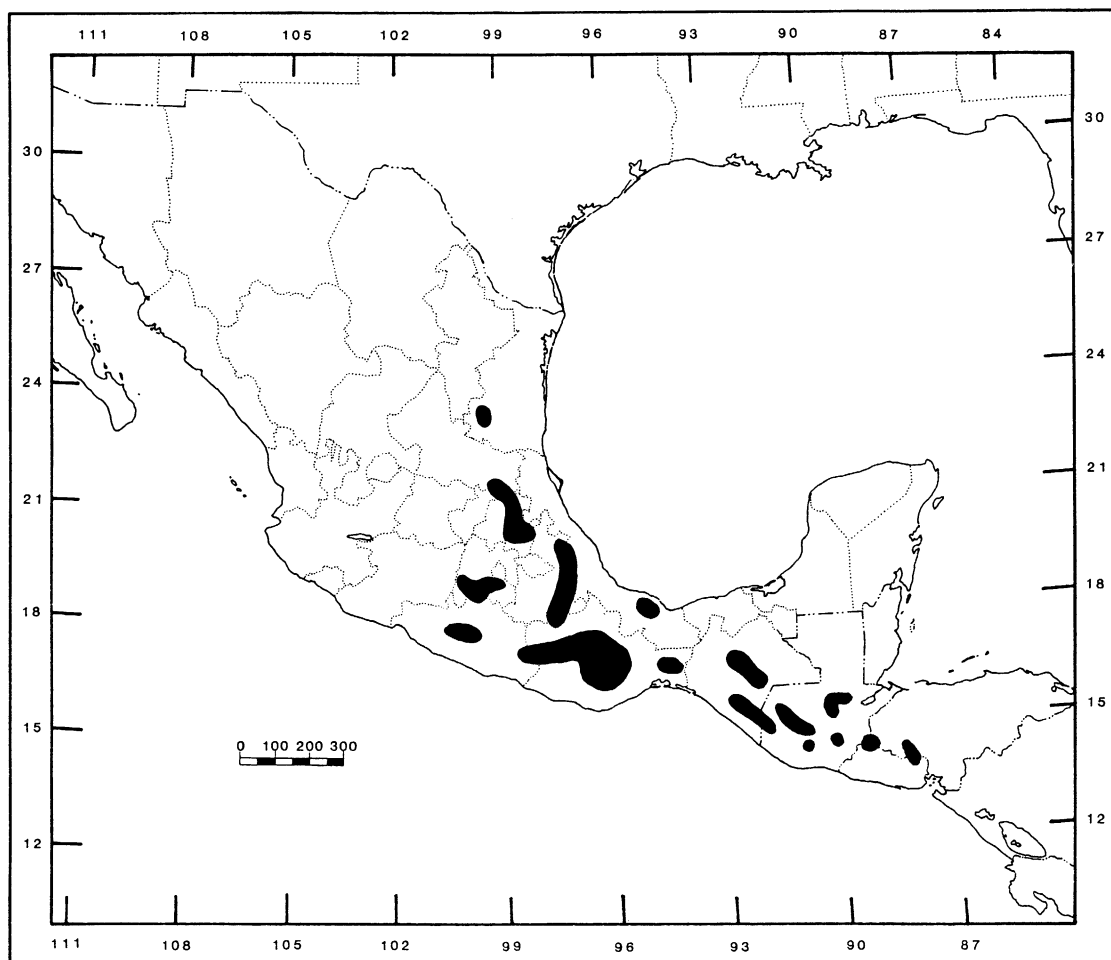


Fig. 1. Geographical distribution of *Abronia*.

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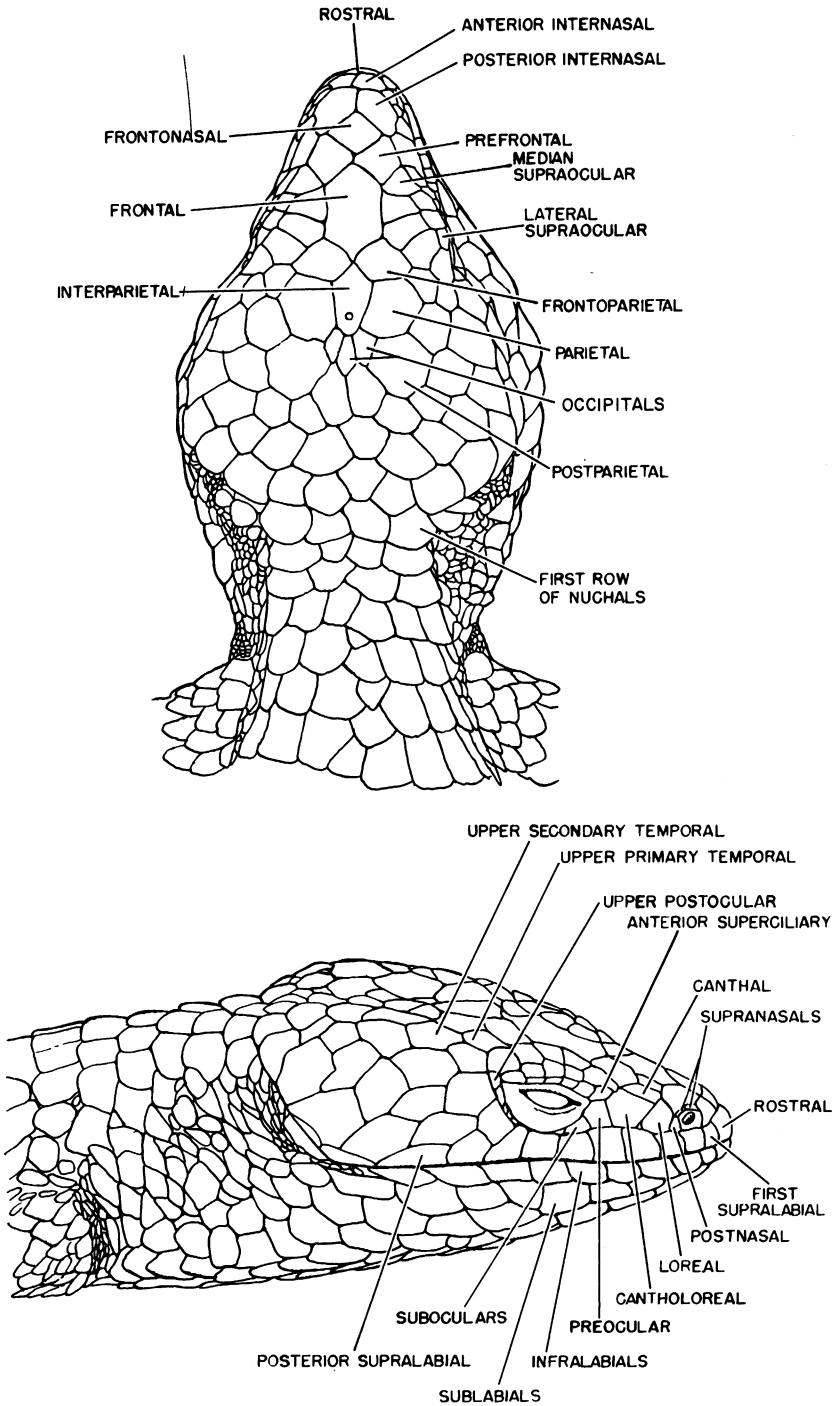


Fig. 2. Scale nomenclature of head and neck. Modified and reprinted from Bogert and Porter (1967).

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TAXONOMIC REVISION OF SOME SPECIES OF NUCLEAR CENTRAL AMERICA

CONSPECIFICITY OF *ABRONIA AURITA* AND *A. VASCONCELOSII*

Figures 3–5, 10A–C

Cope ("1868" [1869]) described *Abronia aurita* (as *Gerrhonotus auritus*) from the "vast forests of Vera Paz," Guatemala (figs. 3, 4). Salient features mentioned in his description include a "strong massive head"; a pea-green ground color "more or less shaded with yellow; the rugosities of the scales everywhere black"; and "eyelids and auriular [sic] processes yellow." Cope obviously was much impressed by this specimen, stating it "is equalled in beauty by *Gerrhonotus gramineus* [= *A. graminea*] of Mexico, which it resembles."

Abronia vasconcelosii was described (as *Gerrhonotus vasconcelosii*) by Bocourt (1871) on the basis of a specimen from "Argueta (Guatemala), à plus de 2,000 mètres d'alti-

tude" (fig. 5). Stuart (1951) reported that this small village (correctly spelled Argueta) was in the "pine-cypress zone between Sololá and Totonicapán" at an elevation of about 2900 m, although he also stated that he never visited the site. One of us (JAC) has been to the village, which is located a short distance from the Pan American Highway (Guatemala CA-1) in the Department of Sololá. The village lies at a somewhat lower elevation than previously reported by Stuart (1951) (about 2200 m) and although scattered patches of the original pine-oak forest still remain in the region, most of the immediate area around Argueta has been severely deforested. Secondary growth includes mostly stands of pines.

Bocourt (1871) described the coloration of *Gerrhonotus vasconcelosii* as "Teintes générales des parties supérieures du corps vert-pomme; plaques suscéphaliques maculées de noir; tubercules placés au dessus des oreilles

jaunes de Naples. Cou et tronc ornés de neuf larges bandes noirâtres en forme de chevrons; queue également traversée par une quinzaine de demi-anneaux de même couleur. Régions inférieures teintées de jaune verdâtre avec des points noirs sous la gorge." Bocourt (1871) also compared his *Gerrhonotus vasconcelosii* with the original description of *G. auritus* Cope and several specimens in the MNHN that he thought were *G. auritus* (but these were *Barissia fimbriatus* [= *Abronia fimbriata*])—see discussion for this species below). He noted that the "plaques inter-naso-frontales" were different (which indeed they are between *Gerrhonotus vasconcelosii*, sensu Bocourt [= *Gerrhonotus auritus* Cope] and *Gerrhonotus auritus*, sensu Bocourt [= *Barissia fimbriatus* Cope]) and that *Gerrhonotus auritus* possesses two postmentals, whereas *G. vasconcelosii* has but one (although this is shown below to be variable). Most subsequent authors (e.g., Bocourt, 1871; Tihen, 1954; Stuart, 1963) have distinguished *Abronia aurita* and *A. vasconcelosii* from each other primarily on the basis of a divided versus an undivided postmental scale, respectively.

We have secured a relatively large series of *Abronia* (40 specimens; see Specimens Examined, Appendix 1) from a forested valley of the upper Río Motagua watershed a few kilometers south of Chichicastenango, Department of Quiché, Guatemala. The Chichicastenango series of *Abronia* is nearly topotypic with *A. vasconcelosii*, lying only 17 km (airline) from the type locality (Argueta) of *A. vasconcelosii*. The highlands between Argueta and our Chichicastenango *Abronia* site are continuous and appear to have been covered originally with an unbroken, seasonally dry, pine-oak forest. Most individuals in this series agree well with the original description of the holotype of *A. vasconcelosii*. The large Chichicastenango series permits an assessment of the variation present in this population of *Abronia*.

VARIATION IN THE CHICHICASTENANGO SERIES OF *ABRONIA*: The series comprises 40 specimens (38 adults, 2 juveniles), 36 of which were examined in detail (24 males, 12 females). The SVL of the largest male is 118 mm; that of the largest female 120 mm. Nine males (104–117 mm SVL; $\bar{x}$ = 111.7 mm) have head width/head lengths of 0.93 or

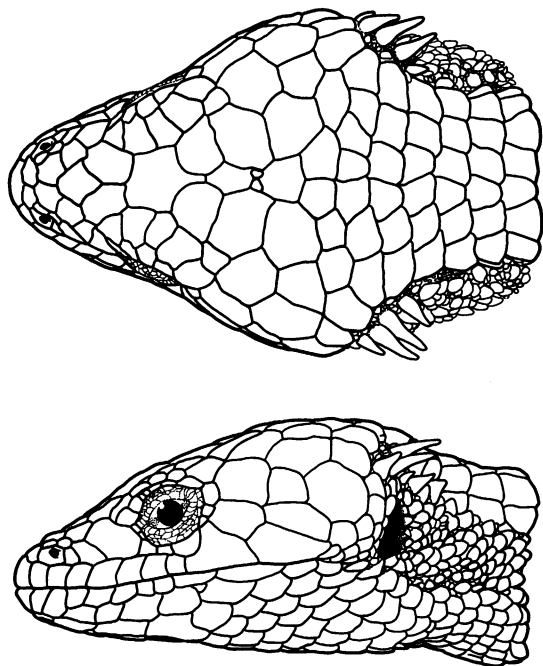


Fig. 3. *Abronia aurita*, dorsal and lateral aspects of head of male holotype (USNM 6769), head length 28.8 mm.

greater (0.93–0.99; $\bar{x}$ = 0.96). The head width/length ratio of the five largest females (105–120 mm SVL; $\bar{x}$ = 111.0 mm) is 0.83–0.88 ($\bar{x}$ = 0.85). Only eight specimens have unregenerated tails; the tail length is 1.45–1.65 ($\bar{x}$ = 1.55) of the body length and there are 84–94 ($\bar{x}$ = 88.1) caudal whorls.

The supracephalic scales possess well developed osteoderms and are convex. There is usually a single small supranasal on each side, but in three individuals two supranasals are present on one side, and one individual has two supranasals on each side. In seven specimens the supranasal (the anterior supranasal, if two are present) intervenes anteriorly at least on one side to contact the first supralabial, thus separating the nasal from the anterior internasal. Usually two postnasals occur on each side, but in six of 72 sides (8%) there is but a single postnasal owing to the fusion of the lower postnasal with the loreal. As in all species of *Abronia*, two pairs of internasals (anterior and posterior) are invariably present. A single canthal on each

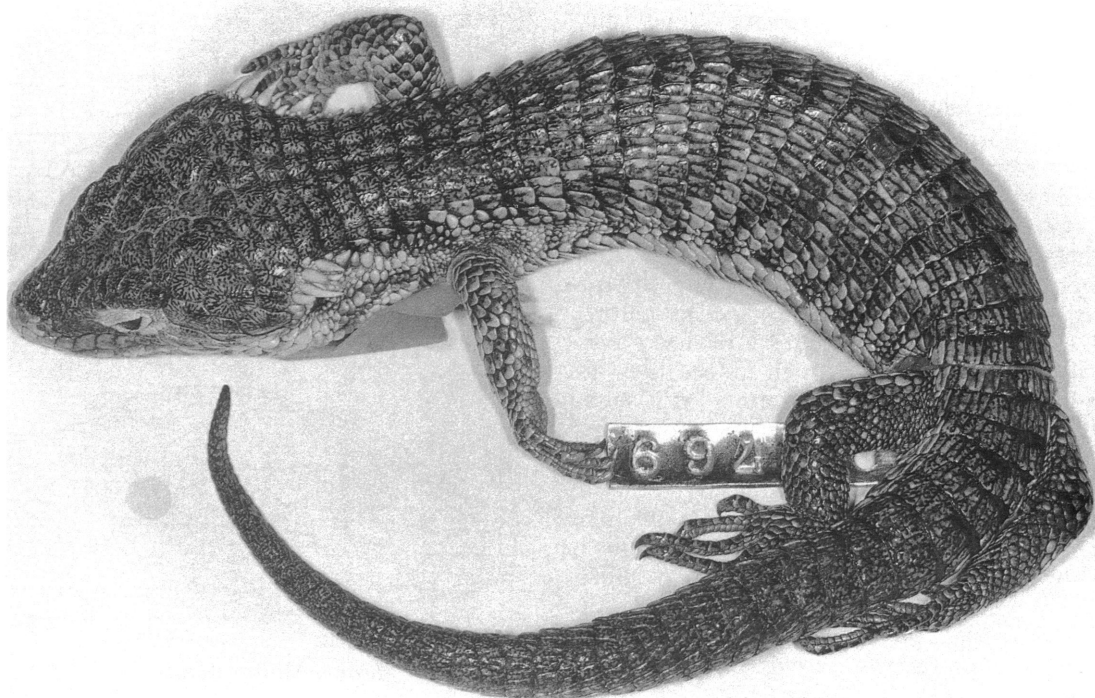


Fig. 4. *Abronia aurita*, male holotype (USNM 6769), 125 mm SVL, tail regenerated.

side is situated mostly on the dorsal surface of the head; canthals are never expanded to contact each other along the midline of the head. There is a single loreal and cantholorel on each side, and both of these scales are higher than long, with a few exceptions in specimens that have the posterior nasal fused with the loreal. A frontonasal is always present (divided in two in one specimen) and usually does not contact the frontal (32 of 37 specimens). There are almost always 5/5 median supraoculars (6 on one side in one spec-

imen) and 3/3 lateral supraoculars (2 on one side and 4 on four sides). There are 5 (4%), 6 (83%), or 7 (13%) superciliaries, the anteriormost always in contact with the cantholorel. A single large preocular is invariably present, followed by 2 (25%), or 3 (75%) suboculars, and 3 (42%) or 4 (58%) postoculars. The postocular series is arranged in an arc bordering the posterior margin of the orbit with the upper scale the largest and increasingly smaller scales ventrally; the ventralmost scales are often reduced to granules and

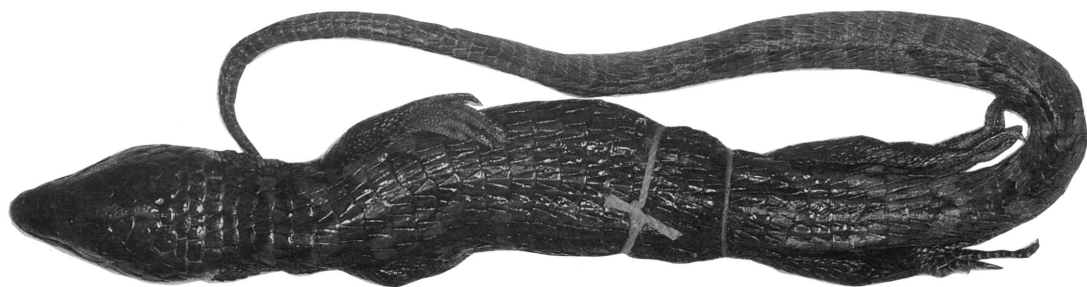


Fig. 5. *Abronia vasconcelosii*, juvenile female holotype (MNHN 2017), 54 mm SVL, 142 mm TL.

were not included in the counts. A large frontal contacts a narrow interparietal. Usually a single occipital is present (several additional scales are present anteriorly in two individuals), which is separated from the first transverse row of nuchals by 2 (61%) or 3 (39%) scales. Most frequently there are 3 primary temporals on a side (74%), but this number may be reduced to 2 (13%) in individuals lacking the upper primary temporal, or increased to 4 (13%) in specimens having two small upper temporals. The lower two temporals are invariably present and contact the postoculars. In many specimens (19 of 36) a small upper temporal contacts the frontoparietal, thus intervening between the parietal and median series of supraoculars so that these scales do not contact each other. However, the upper temporal does not reach the frontoparietal and the parietal contacts the median supraoculars, sometimes broadly, on one side in four individuals, and on both sides in 13 specimens. There are 9 (3%), 10 (44%), or 11 (53%) supralabials, with the penultimate being the last scale in the supralabial series to contact the orbit. There are 7 (10%), 8 (53%), 9 (32%), or 10 (5%) infralabials. The postmental is divided in ten individuals and undivided in 26. Three pairs of large chin shields are followed posteriorly by a smaller fourth pair that is about half the size of the preceding pair. The sublabial series usually has four scales on each side (89%), but may have 5 (10%), or rarely 3 (1%).

The minimum number of scales in a transverse nuchal row is usually 6 (34 specimens), but is 7 in two individuals. Supra-auricular scales are elongate and spinelike; there are usually 3 or 4 of these scales arranged in a dorsal series with 2–5 smaller pointed scales situated ventral to this series. There are 6–9 ($\bar{x} = 7.0$) very irregular rows of small, roundish scales between the lateral nuchals and the first large scales on the ventrolateral surface of the neck. Dorsal transverse scale rows number 27–31 ($\bar{x} = 28.6$), and there are 14 dorsal longitudinal scale rows, followed ventrolaterally by two rows of smaller platelike scales on each side (not included in our counts³). In most specimens, no more than

eight rows of dorsals are weakly keeled at midbody. The ventral transverse scale rows are arranged in 35–38 ($\bar{x} = 36.4$) rows, and there are 14 ventral longitudinal scale rows. Subdigital lamellae of the fourth toe number 17–23 ($\bar{x} = 19.9$).

The ground color in life of adults is pea-green, yellow-green, or pale turquoise (fig. 10A, B). Most of the supracephalic scales are finely vermiculated with black and the dorsal scales of the body are heavily mottled with black pigment, which is concentrated along the anterior portions of the scales, producing narrow, irregular crossbands. Black pigment is concentrated in rows of scales between some of these narrow crossbands producing 6–10 (between limb insertions) indistinct broad chevrons on the body. The region around the orbit, including the upper and lower eyelids and most of the postoculars and superciliaries is bright yellow. The supra-auricular spines are bright yellow. The gular region varies from pale whitish yellow to pale yellow-green, posteriorly becoming a darker shade of yellow-green to bluish green on the venter. Ventral surfaces of the hands and feet are yellowish. Regenerated portions of the tail tend to be dark, almost black.

Most of the scales on the top and sides of the head in large adult males have large orange spots, usually located posteriorly on the scales (fig. 10B). This orange coloration often extends posteriorly and is present on the distal portion of dorsal scales, especially laterally, becoming less intense posteriorly, but sometimes extending onto the tail. The margin of the lower jaw is usually orange from about the second or third infralabial to the last infralabial, except for the areas near scale sutures.

Juveniles are pale brown dorsally with 8–10 (between level of limb insertions) irregular

the nature of the scales just above the ventrolateral fold. Several of the ventralmost scales of a dorsal transverse series tend to be much reduced in size. For example, in *A. gaiophasma* there are 12 large scales in a dorsal transverse series, with a lower scale on each side generally about half the size of its dorsal neighbor, followed by another scale only about a fourth the size of most dorsal scales. Thus, the number of longitudinal rows might be counted variously as 12, 14, or 16. We have standardized by counting only enlarged scales.

³ The number of longitudinal rows of dorsal scales counted by different investigators often varies, owing to

black chevrons on the back (fig. 10C). The dorsal scales on the lateral surface of the body are dark brown. The tail has a series of irregular black dorsal markings. A wide postocular band is often present, extending from the postoculars to behind the corner of the mouth. Supra-auricular scales in juveniles are small and oval, somewhat protuberant, and enlarged over adjacent granular scales, but they are not spinelike.

In preservative, the coloration of individuals in this series agrees well with the description of the holotype of *A. aurita* (see below).

REDESCRIPTION OF THE HOLOTYPE OF *ABRONIA AURITA*: The holotype (USNM 6769) is an adult male of 125 mm SVL; the tail is regenerated (fig. 4). Head width/head length is 26.1 mm/28.8 mm = 0.91. There are a supranasal and two postnasals on each side. Two pairs of internasals are present, the posterior about twice the size of the anterior (fig. 3). A single canthal lies mostly on the dorsal surface of each side of the head; these are widely separated from each other by an intervening frontonasal. The single loreal and cantholoreal on each side are higher than long. A pair of prefrontals contact along the midline, precluding the frontonasal from contact with the frontal. There are 5/5 median and 3/3 lateral supraoculars. Superciliaries number 6/6, the anteriormost in contact with the cantholoreal. A single preocular is followed by 3/2 suboculars and 3/3 postoculars. The frontal is in narrow contact with the interparietal. Just posterior to the interparietal two small scales and a single large occipital are present. Three scales separate the occipital from the first transverse nuchal scale row. Three anterior temporals are present on each side; the lower two in contact with the postoculars, and the small upper anterior temporal contacts the frontoparietal, thus precluding contact of the median supraoculars by the parietal. There are 9/10 supralabials, the penultimate being the last to contact the orbit, and 7/9 infralabials. The postmental is divided, and there are three pairs of large chinshields followed by a smaller fourth pair which is about half the size of the preceding pair. There are 4/5 sublabials; the anterior scale does not reach the postmental.

About seven small very irregular scale rows

lie between the lateral nuchals and the first large scales on the ventrolateral surface of the neck. The large elongate and spinelike supra-auricular scales are arranged in a dorsal series of 3–4 scales. Minimally six scales compose a transverse nuchal row. There are 29 dorsal transverse scale rows, 14 dorsal longitudinal scale rows, 36 ventral transverse scale rows, and 14 ventral longitudinal scale rows. Subdigital lamellae of the fourth toe number 19.

This specimen still possesses a remarkable amount of color and pattern despite well over a century of preservation. The ground color is gray-green with black vermiculations on most of the supracephalic scales; heavy black mottling on the dorsal scales of the body, concentrated to “form indistinct Vs directed backwards on the middle of the back” as noted by Cope (“1868” [1869]). The circumorbital region and the superciliaries are immaculate pale yellow.

Comparison of the variation in the Chichicastenango series with characters exhibited by the holotype of *A. aurita* makes distinguishing *A. vasconcelosii* from *A. aurita* impossible. The two names, therefore, appear to represent the same taxon, with *A. aurita* having priority. An abbreviated synonymy for this species is:

- Gerrhonotus auritus* Cope, “1868” [1869]: 306.
Holotype: USNM 6769, according to Cochran, 1961: 114. Type locality: “vast forests of Vera Paz, in the neighborhood of the ancient cities of Peten and Coban.” Type locality stated as “Vera Paz, Guatemala” by Cochran, 1961; USNM catalogue lists “Guatemala, Vera Paz,” fide R. W. McDiarmid (personal commun.).
- Gerrhonotus vasconcelosii* Bocourt, 1871: 107.
Holotype: MNHN 2017, according to Guibé (1954) and Brygoo (1987). Type locality: “Argueta (Guatemala), à plus de 2,000 mètres d’altitude.”
- Gerrhonotus (Abronia) vasconcelosii*: Bocourt, 1878 [1870–1909]: 334, pl. 21A, figs. 8–8A; 1879 [1870–1909], pl. 21, fig. 3.
- Gerrhonotus auritus*: Hartweg and Tihen, 1946: 2.
Abronia aurita: Tihen, 1949a: 591; Tihen, 1954: 21.
- Abronia vasconcelosii*: Tihen, 1949a: 591; Tihen, 1954: 24.
- Abronia aurita*: Hidalgo, 1983: 10. [In part, Hidalgo’s allocated specimens included *A. aurita*, *A. fimbriata*, and *A. gaiophasma*.]
- Abronia vasconcelosii*: Hidalgo, 1983: 10. [In part,

TABLE 1
Selected Variations Observed in Species of *Abronia* Inhabiting Seasonally Dry Pine-Oak Forests in Nuclear Central America
Arranged in order of west-east distribution

Character	<i>A. lythrochila</i> (n = 7)	<i>A. aurita</i> (n = 57)
Canthals	variably fused with posterior internasals	discrete from posterior internasals
Lateral supraoculars	frequently 4 (36%)	rarely 4 (4%)
Parietals contact median supraoculars	variable	variable
Postmental	variable	variable
Adult color pattern	variable; usually brown, but may be yellowish with bold black markings	greenish with black mottling concentrated into indistinct crossbands
Coloration of orbital region	ambient color of head	bright yellow
Distribution	Meseta Central of Chiapas, Mexico	Plateau regions of Guatemala

Hidalgo's allocated specimens included *A. vasconcelosii* (= *A. aurita*), *A. anzuetoi*, and *A. matudai*.]

Abronia vasconcelosii: Good, 1988: 95. [In part, Good's allocated specimens included one specimen of *A. anzuetoi* and one of *A. aurita*, the holotype of *A. vasconcelosii*.]

DIAGNOSIS OF *ABRONIA AURITA* (see table 1): A species of *Abronia* having: (1) distinctive spinelike supra-auricular scales in subadults and adults; (2) unexpanded supranasals; (3) a median frontonasal scale, usually not contacting frontal; (4) posterior internasals not greatly enlarged; (5) discrete canthals; (6) 2–5 (usually 3) primary temporals, the lower two contacting the postoculars; (7) usually no parietal–median supraocular contact; (8) a single occipital; (9) posterolateral head scales not knoblike; (10) anterior superciliary contacting cantholorear, similar in length to other scales in series; (11) the posterior subocular broadly separated from the lower primary temporal by the penultimate supralabial, which is the posteriormost scale in this series to reach the orbit; (12) preauricular scales small, granular, elevated, usually disposed in 3–4 rows; (13) postmental variable, but most frequently single; (14) the posteriormost infralabial elongate, often about twice as long as preceding infralabials; (15) usually six longitudinal nuchal scale rows; (16) 27–31 dorsal transverse scale rows; (17) 14 dorsal longitudinal scale rows, these parallel to ven-

trolateral fold; (18) 14 ventral longitudinal scale rows; (19) adult greenish dorsal coloration with much black mottling concentrated into indistinct dorsal crossbands; (20) juvenile pattern of dark dorsal crossbands.

This species differs from all other species of *Abronia* that have protuberant supra-auricular scales, except *A. anzuetoi* (fig. 11C, D), *A. gaiophasma* (fig. 11A, B), some *A. matudai*, and *A. lythrochila* (fig. 11F), in having 14 longitudinal ventral scale rows. *Abronia aurita* differs from all other species of *Abronia* except *A. graminea*, *A. anzuetoi*, and *A. smithi* (fig. 11E) in having a distinctly yellow orbital region. *Abronia aurita* differs from *A. anzuetoi* in coloration (relatively pale green or yellow-green with yellow and/or orange markings versus dark emerald green or dark blue green), in having comparatively shorter posterior internasals, and being of a smaller size (maximum SVL 125 versus 135 mm). *Abronia aurita* differs from *A. gaiophasma* in having more numerous postoccipital rows between the occipital and first nuchal row (two or three versus one), having multiple rows of nonimbricate preauriculars (versus two or fewer subimbricate rows), having an expanded posterior infralabial, the parietal usually in contact with the median supraoculars (not so in *A. gaiophasma*), and features of color pattern. *Abronia aurita* differs from most specimens of *A. lythrochila* in having discrete canthals (versus canthals usu-

ally fused with posterior internasals) and in having a distinctly yellow circumorbital region.

DISTRIBUTION: Within this century this species was probably widespread in the Guatemalan highlands, including portions of the Huehuetenango, Quecchian, and Jalapa areas, and probably portions of the Sierran area (*sensu* Campbell and Vannini, 1989). The only known specimen from the north-eastern Guatemalan highlands (the holotype) lacks precise locality data. All definite locality records for this species are from pine-oak forest at elevations of 2000–2660 m (fig. 26), although the region surrounding Cobán (the indefinite type locality) is below 1500 m. Most of the original pine-oak forests have been destroyed and this species is restricted to a few enclaves either too steep for agriculture or in protected watersheds. The distributional pattern exhibited by *A. aurita* is shared by other terrestrial vertebrate species that are widespread in the pine-oak forests of the Guatemalan highlands, including *Hypopachus barberi*, *Rana maculata*, *Corytophanes percarinatus*, *Norops crassulus*, *Sibon fischeri*, and *Thamnophis fulvus*.

MATERIAL EXAMINED (57 specimens): **GUATEMALA:** *Alta Verapaz:* “vast forest of Vera Paz, in the neighborhood of the ancient cities of Peten and Coban,” according to Cope (“1868” [1869]: 306) (USNM 6769; holotype of *A. aurita*). *Huehuetenango:* Camino entre San Sebastián Huehuetenango y Chejoj, 2000 m (UVG R-1641; UTA slides 14893–96). *Jalapa:* Miramundo, near Torre de Guatel, 2300–2660 m (UTA R-30326–27, 31041–53). *Quiché:* 3.0 km SSE Chichicastenango, valley between Paxot and Camanibal, 2000–2100 m (AMNH 137787 [formerly UTA R-27249], 137788 [formerly UTA R-28914]; UTA R-16014, 19654–80, 19493, 22558–59, 26565–67, 27209–11, 27250–51); near Chichicastenango (AMNH 137789 [formerly UTA R-30279]). *Sololá:* Argueta, above 2000 m (MNHN 2017, holotype of *A. vasconcelosii*).

TAXONOMIC VALIDITY OF *ABRONIA FIMBRIATA*

Figures 6, 7, 10D–F

Based on three specimens, Bocourt (1878 [1870–1909]) described and figured (his pl.

21A, figs. 7–7a, and [1879 (1870–1909)] pl. 21, fig. 2) a species of *Abronia* from “Haute Vera Paz (République du Guatemala),” which he identified as *Gerrhonotus (Abronia) auritus* Cope and described as having “six scutelles inter-naso-rostrales disposés deux par deux” (i.e., two pairs of internasals plus a pair of expanded supranasals) and “bandes en forme de chevrons traversant les parties supérieures du corps.” It is apparent that Bocourt did not recognize the enlarged supranasals as such in that he stated “Pas de supéro-nasales,” a condition unknown in the genus *Abronia*. The illustration of the dorsal squamation of the head (his pl. 21A, fig. 7; our fig. 6) clearly depicts four pairs of scales, including the prefrontals, covering the snout; the frontonasal is absent. The brown transverse chevrons that Bocourt mentioned are evident in subadults (his pl. 21, fig. 2; our fig. 10E). The expanded supranasals, absence of a frontonasal, and presence of distinct brown dorsal chevrons in subadults and young adults are not characteristic of *A. aurita*. Subsequently, Cope (“1884” [1885]) recognized that Bocourt’s species was distinct from his *Gerrhonotus auritus*, and he described Bocourt’s species as *Barissia fimbriatus* (= *Abronia fimbriata*), diagnosing it as “having three pairs of supranasal plates” (actually two pairs of internasals and an expanded pair of supranasals that meet at the midline). Cope (“1884” [1885]) did not select a holotype and Guibé (1954) failed to list this species in the MNHN type holdings. Tihen (1954) stated that the museum number for the holotype of *Abronia fimbriata* was unknown. Subsequently, Stuart (1963) listed MNHN 1189 as the type, although this is clearly the lot number of the specimens, the three specimens being currently numbered 1189, 1189a, and 1189b (Brygoo, 1987). We designate the specimen bearing the tag 1189 as lectotype, rendering as paralectotypes those bearing the tags 1189a and 1189b.

Abronia fimbriata was recognized (as *Gerrhonotus fimbriatus*) by Günther (1885). However, Stuart (1948), placed this name into the synonymy of *A. aurita*, later (1963: 81) stating in a footnote “I find it difficult to believe that two species of *Abronia* exist sympatrically in Alta Verapaz.” This skepticism of the distinctiveness of the two species had also been voiced by Tihen (1954: 22), who

nevertheless recognized *A. fimbriata* and who regarded the question of its taxonomic status as one remaining to be resolved. However, Stuart's synonymy (1948, 1963) was continued, without question, by most subsequent authors (e.g., Hidalgo, 1983; Brygoo, 1987; Good, 1988), although no one compared type material before now. The only recent study to recognize *A. fimbriata* was that of Campbell and Vannini (1989). An abbreviated synonymy for this species is:

Gerrhonotus (Abronia) auritus: Bocourt, 1878 [1870–1909]: 337, pl. 21A, figs. 7–7a; 1879 [1870–1909], pl. 21, fig. 2.

Barissia fimbriata Cope, "1884" [1885]: 171. [Based on Bocourt's *Gerrhonotus auritus*.] Syn-types: MNHN 1189, 1189A, and 1189B, according to Brygoo (1987: 6), from "les forêts de pins de la haute Vera Paz (Guatemala oriental)" (Bocourt, 1878 [1870–1909]), here restricted to vicinity of Cáquiepec, Department of Alta Verapaz, Guatemala. MNHN 1189 here designated lectotype.

Gerrhonotus fimbriatus: Günther, 1885: 37.

Abronia fimbriata: Tihen, 1949a: 591; Tihen, 1954: 22.

Abronia aurita: Stuart, 1963: 81. [In part, Stuart's examined specimens included only *A. aurita*, although he considered *A. fimbriata* to be a synonym.]

Abronia aurita: Hidalgo, 1983: 10. [In part, Hidalgo's specimens included *A. fimbriata*, *A. aurita*, and *A. gaiophasma*.]

Abronia aurita: Good, 1988: 92. [In part, Good's allocated specimens included only *A. gaiophasma*, then unrecognized as distinct, although he retained the name *A. fimbriata* in synonymy.]

Abronia fimbriata: Campbell and Vannini, 1989: 9.

REDESCRIPTION OF THE LECTOTYPE OF *ABRONIA FIMBRIATA* (figs. 6, 7): The lectotype (MNHN 1189) is a small adult or subadult female with a SVL of 109 mm; the tail is entire and is 176 mm long. The head width/head length ratio is 16.2 mm/21.8 mm = 0.74. Two supranasals contact medially and separate the anterior pair of internasals from the posterior pair of internasals. Anterior internasals are about $\frac{2}{3}$ the size of the following supranasals, which are about $\frac{1}{3}$ the size of the following posterior internasals. Canthals are absent, apparently fused to the posterior internasals. The frontonasal scale is absent. The single loreal and cantholoreal on each side are higher than long. A pair of prefrontals

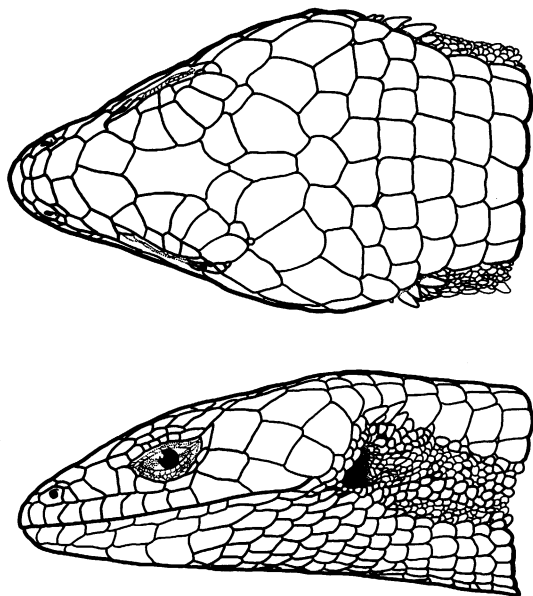


Fig. 6. *Abronia fimbriata*, dorsal and lateral aspects of head of female lectotype (MNHN 1189), head length 21.8 mm.

contact each other along the midline and, because the frontonasal scale is absent, contact broadly the posterior internasals. There are 5/5 median and 3/3 lateral supraoculars. There are 7/6 superciliaries, the anteriormost contacting the cantholoreal. A single preocular is followed by 3/2 suboculars and 3/3 postoculars. The frontal is in narrow contact with the interparietal. Just posterior to the interparietal a single large occipital is present. Two scales separate the occipital from the first transverse nuchal scale row. Anterior temporals 4/3, the uppermost anomalously divided transversely on the left side; the lower two anterior temporals contact the postoculars, and the small anterior temporal contacts the frontoparietal, thus precluding contact of the median supraoculars by the parietal. Supralabials number 10/10, the penultimate being the last to contact the orbit, and infralabials number 9/8. The postmental is single, and three pairs of large chinshields are followed by a smaller fourth pair which is less than half the size of the preceding pair. Sublabials number 5/4, the anteriormost not reaching the postmental.

About 11 small irregular scale rows lie between the lateral nuchals and the first large scales on the ventrolateral surface of the neck.

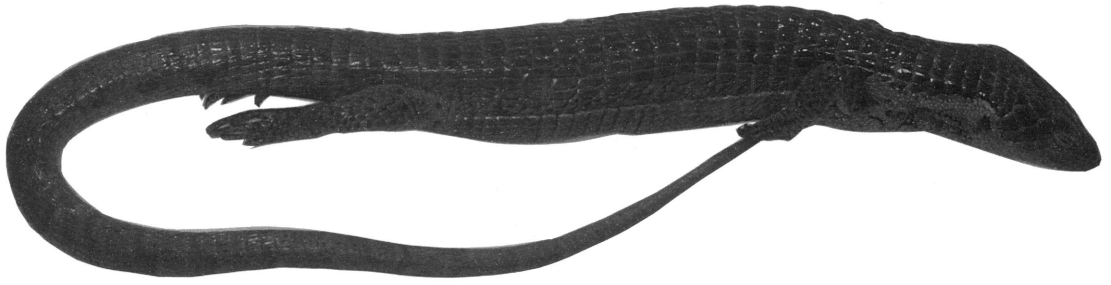


Fig. 7. *Abronia fimbriata*, female lectotype (MNHN 1189), 109 mm SVL, 176 mm TL.

The large elongate and spinelike supra-auricular scales are arranged in a dorsal series of four scales. Minimally, six scales are in a transverse nuchal row. There are 31 dorsal transverse scale rows, 14 dorsal longitudinal scale rows, 41 ventral transverse scale rows, and 14 ventral longitudinal scale rows. Subdigital lamellae of the fourth toe number 23.

The color pattern in life is still in evidence in spite of over 100 years in preservative. The ground color is brownish-gray with light posterior edges on the supracephalic scales and dorsal body scales. The granular scales on the sides of the neck are pale gray.

DIAGNOSIS OF *ABRONIA FIMBRIATA* (see fig. 6 and table 2): One of the most distinctive species of *Abronia*, having: (1) distinctive spinelike supra-auricular scales in subadults and adults; (2) expanded supranasals meeting at midline; (3) frontonasal absent; (4) posterior internasals relatively large through fusion with canthals; (5) no discrete canthals, these apparently fused with posterior internasals; (6) two or three (most frequently two [anomalous fourth on one side of the lectotype]) primary temporals, the lower two contacting postoculars; (7) parietals usually in contact with the median supraoculars; (8) a single occipital; (9) posterolateral head scales not knoblike; (10) anterior superciliary contacting cantholorear, similar in length to other scales in series; (11) posterior subocular in contact with the lower primary temporal or narrowly separated by the penultimate supralabial, which is the posteriormost scale in this series to reach the orbit; (12) preauricular scales small but not protuberant, disposed in 2–3 rows; (13) postmental single; (14) posterior infralabial not elongate; (15) six longitudinal nuchal scale rows; (16) 27–30 dorsal

transverse scale rows; (17) 14 dorsal longitudinal scale rows arranged parallel to ventrolateral fold; (18) usually 12 (infrequently 14) ventral longitudinal scale rows, lateral row expanded; (19) mature adult dorsal coloration brown with much black mottling (fine vermiculation) concentrated dorsally (fig. 10D); (20) juvenile pattern of a broad pale brown middorsal stripe; subadults and young adults with brown chevron-shaped crossbands (figs. 10E, F).

Abronia fimbriata consistently lacks the median frontonasal scale (figs. 6, 52); the only other species to do so (variably) are *A. oaxacae* (fig. 12F), in which a frontonasal is present in more than half of the known individuals, *A. taeniata*, in which a frontonasal is rarely absent, *A. lythrochila* (fig. 11F), in which one of eight specimens that we have examined lacks a frontonasal, and IBUNAM 340, which was previously identified as *Gerrhonotus fimbriatus* by Martín del Campo (1939) and as *Abronia ochoterenai* by Hartweg and Tihen (1946), Tihen (1954), and Casas-Andreu and Smith ("1990" [1991]). We have re-examined this specimen (IBUNAM 340) and find it to represent an undescribed species (see *A. leurolepis* account, following). The body of *A. fimbriata* (fig. 10D) is relatively elongate compared with *A. aurita* (fig. 10A), *A. anzuetoi* (fig. 11C), *A. ochoterenai* (fig. 14), *A. leurolepis* (fig. 17), and *A. lythrochila* (fig. 11F).

This species differs from all other *Abronia* having spinelike supra-auricular scales, except for *A. smithi*, *A. ochoterenai*, *A. leurolepis*, and some *A. matudai*, in usually having 12 longitudinal ventral scale rows, with the lateral rows expanded. *Abronia fimbriata* is distinctive from these species in lacking both a frontonasal and discrete canthal scales.

TABLE 2
Selected Variations Observed in Species of *Abronia* Inhabiting Atlantic Cloud Forests of Nuclear Central America
 Arranged in order of west-east distribution

Character	<i>A. ochoterenai</i> ^a (n = 2)	<i>A. leurolepis</i> ^a (n = 1)	<i>A. fimbriata</i> (n = 17)	<i>A. gaiophasmasma</i> (n = 7)
Supranasals	not expanded	not expanded	expanded, usually meeting at midline	not expanded
Frontonasals				
Canthals	present	absent	absent	present
	discrete from posterior inter-nasals	discrete from posterior inter-nasal on left	fused with posterior inter-nasals	discrete from posterior inter-nasals
Parietal contacting median supraoculars	no	variable side to side	usually yes	no
Number of postoccipital rows	2	1	usually 2	1
Postmental condition				
Lateral neck scales	variable	single	single	variable
Longitudinal ventral scale rows	8-11	8	9-12	11-12
	12	12	usually 12	14-16
Color pattern	Adults with about 8 darker crossbands (at least in females; not visible in single male)	Adult ground color unknown; with broken crossbands	Adults uniformly brownish; subadults banded; juveniles striped	Adults brownish with darker crossbands (indistinct in large adults)

^a We assume that these species are cloud-forest inhabitants (See The *Abronia ochoterenai* Problem).

Other than *A. fimbriata*, only *A. ornelasi* and *A. reidi* exhibit large expanded supranasals that meet at the midline. In some specimens of *A. matudai*, the only known specimen of *A. mitchelli*, and one example of *A. salvadorensis*, the supranasals are expanded part way across the dorsum of the snout, but do not meet at the midline. All of these species lack spinelike supra-auricular scales.

VARIATION: Our series for study of variation comprised 17 specimens (14 adults, 3 juveniles). The SVL of six adult males is 112–130 mm ($\bar{x}$ = 120.7 mm), that of two adult females is 93–110 mm ($\bar{x}$ = 101.5 mm). The head width/length ratio of six adult males is 0.75–0.81 ($\bar{x}$ = 0.78) and of two adult females is 0.69–0.72 ($\bar{x}$ = 0.71). Four adult specimens have entire, unregenerated, tails; the tail length is 1.41–1.74 ($\bar{x}$ = 1.64) times the body length and there are 86–104 ($\bar{x}$ = 97.3) caudal whorls.

Supracephalic scales are relatively flat and smooth, rather than convex. There is usually a single large supranasal on each side, expanded medially to the midline; in one specimen (AMNH 137786) the supranasals are enlarged but do not meet at the midline, allowing contact between the anterior and posterior pair of internasals. In all other individuals the supranasal intervenes to separate the small pair of anterior internasals from the large pair of posterior internasals (these latter fused with the canthals). Posterior to the posterior internasals is a pair of large prefrontals; the frontonasal is always absent. Usually two postnasals are on each side (88%), but occasionally a single postnasal is present (12%). A single loreal and cantholoreal are on each side. Invariably there are 5/5 median supraoculars and usually 3/3 lateral supraoculars (4 on one side in one specimen). There are 5 (12%), 6 (76%), or 7 (12%) superciliaries. A single large preocular is present, followed by 1 (12%), 2 (63%), or 3 (25%) suboculars, and 3 (94%) or 4 (6%) postoculars. A large frontal contacts an interparietal. A single occipital is present, which is separated from the first transverse row of nuchals by 1 (25%) or 2 (75%) scales. There are 2 (56%) or 3 (44%) anterior temporals on a side; the upper primary temporal, when present, is very small. Two lower temporals are invariably present and contact the postoculars. The posterior

subocular is in contact with, or barely separated from, the lower primary temporal. In all specimens, except the lectotype, the parietal contacts the median series of supraoculars. There are 9 (38%), 10 (50%), or 11 (12%) supralabials, with the penultimate being the last scale in the supralabial series to contact the orbit. There are 7 (31%), 8 (56%), or 9 (13%) infralabials. The postmental is undivided in all individuals. Three pairs of large chinshields are followed posteriorly by a smaller fourth pair that is about a third the size of the preceding pair. The sublabial series usually has four scales on each side (56%), but may have 5 (38%), or rarely 6 (6%).

The minimum number of scales in a transverse nuchal row is six. Supra-auricular scales are elongate and spinelike; there are usually 3–5 of these scales arranged in a dorsal series with about an equal number of smaller, pointed scales situated ventral and posterior to this series. There are 9–12 ($\bar{x}$ = 10.4) small subgranular scales between the lateral nuchals and the first large scales on the ventrolateral surface of the neck. Transverse dorsal scale rows number 27–30 ($\bar{x}$ = 28.9), with 14 dorsal longitudinal scale rows, followed ventrolaterally by one or two rows of smaller platelike scales on each side.³ In most specimens, no more than ten rows of dorsals are weakly keeled at midbody. Transverse ventral scale rows are arranged in 36–39 ($\bar{x}$ = 37.9) rows, and there are 12 (78%) or 14 (22%) longitudinal ventral scale rows. Fourth toes subdigital lamellae number 19–23 ($\bar{x}$ = 20.8).

The ground color of large adults in life is brown suffused with fine black vermiculations; laterally the body becomes paler brown. Most of the supracephalic scales are finely vermiculated with black and edged posteriorly with white, yellow, or yellow-orange. The small granular scales posterior to the auricular opening are white. Most of the superior margin of the lower jaw is orange, at least in large males. The color around the eye is not distinct from the rest of the head. The spine-like supra-auricular scales, lateral neck granules, and gular region are white. Some subadults (e.g., UTA R-30278 [SVL = 93 mm] and MNHN 1189b [SVL = 80 mm]) show development of approximately 8–10 darker crossbands or chevrons on the neck and back.

A newborn (UTA R-6647; 32 mm SVL)

has a broad pale brown middorsal stripe with dark brown sides of the body. A larger juvenile (UTA R-30199; 43 mm SVL) has the dorsum and sides uniformly dark brown. No dorsal crossbands or chevrons are apparent in either juvenile.

In preservative, the dorsal color of the body and dorsal surface of the forelimbs is most often greenish in adults, but sometimes brown, becoming mauve or gray laterally. The dorsum of the head is dark gray with the posterior edges of most supracephalic scales edged posteriorly with dingy white. The supra-auricular spines are white to pale yellow. The underside of the head is pinkish to yellowish white; the venter is pale gray to mauve, finely peppered with black specks.

DISTRIBUTION: Northeastern Guatemalan highlands; known with certainty from the cloud forests of the western portion of the Sierra de las Minas, Department of Baja Verapaz, at elevations of 1500–2100 m, and from the Sierra de Xucaneb (Montaña Ulpán), Department of Alta Verapaz, at elevations of 1400–2000 m (fig. 26). These localities are in the Quecchian Area and the Sierra de las Minas Sierran Subarea, as defined by Campbell and Vannini (1989). Bocourt (1878 [1870–1909]) reported specimens from “les forêts de pins de la haute Vera Paz.”

MATERIAL EXAMINED (17 specimens): **GUATEMALA:** *Alta Verapaz:* near Cáquiepec, 2000 m (UTA R-19642–44); Cáquiepec, 1400 m (AMNH 137786 [formerly UTA R-19645]); near Chirrubiquim, 2.0 km NNE (airline) Cáquiepec, 1830 m (UTA R-30199, R-30325); San Pedro Carcha, Aldea Chirukikim (near Cáquiepec) (AMNH 137790 [formerly UTA R-30278]); “haute Vera Paz” (MNHN 1189 [lectotype], 1189A, 1189B [paralectotypes]). *Baja Verapaz:* 7.7 km S Purulhá, 1560 m (UTA R-6492); Vuelta del Quetzal, Biotopo Mario Dary, 1600 m (UTA R-6495, 6647–48); vicinity of La Unión Barrios, 1700 m (UTA R-7789); between 0 and 2.4 mi SE Purulhá on Guatemala Hwy. CA-14, ca. 1500 m (UTA R-8856); W side Cerro Verde, 1676 m (KU 187243).

COMMENT: Atkinson (1907) reported several specimens of “*Gerrhonotus fimbriatus*” from Los Amates and Gualán, Guatemala. Both of these localities are in the Río Motagua Valley and lie at elevations below which

we would expect *Abronia* to occur. We have been unable to locate these specimens (they are not, as we had expected, in the Carnegie Museum—C. J. McCoy, personal commun.), but there is no reason to assume that Atkinson’s identifications were correct; many of the species reported in his paper are clearly misidentified.

DESCRIPTIONS OF TWO NEW SPECIES OF GUATEMALAN *ABRONIA* PREVIOUSLY CONFUSED WITH *A. AURITA* OR *A. VASCONCELOSII*

Explorations during the last several decades in the cloud forests of Baja Verapaz, Guatemala, have revealed the presence of another distinctive species of *Abronia*, in addition to *A. fimbriata*. This species has been previously misallocated to *A. aurita* by Campbell (1982), Hidalgo (1983), Good (1988), and Campbell and Vannini (1989). Resolution of the identity of *A. aurita* and *A. fimbriata* now clearly indicates that this other Baja Verapaz species is representative of neither and has never been formally named. We name it:

Abronia gaiophantasma, New Species Figures 8, 11A, B, 54A

Abronia aurita: Campbell, 1982: 361.

Abronia aurita: Hidalgo, 1983: 10. [In part, the specimens allocated by Hidalgo to this binominal included *A. gaiophantasma*, *A. aurita*, and *A. fimbriata*.]

Abronia aurita: Good, 1988: 92.

Abronia aurita: Campbell and Vannini, 1989: 9.

HOLOTYPE: The University of Texas at Arlington (UTA) R-19646 (field no. JAC 12430), an adult male obtained by the late Pantaleón Lucas and JAC on 17 December 1986, in cloud forest at 1600 m elevation on the west slope of Cerro Verde in the vicinity of La Unión Barrios, Baja Verapaz, Guatemala. This site is located at approximately 15°11'N, 90°12'W.

PARATYPES (6 specimens): **GUATEMALA:** *Baja Verapaz:* eastern Sierra de las Minas: east slope of Cerro Quisis, vicinity of La Unión Barrios, 1829 m, collected by the late P. Lucas on 4 October 1980 (KU 190851); West slope Cerro Verde, 1653 m, collected by J. A. Campbell on 16 July 1981 (KU

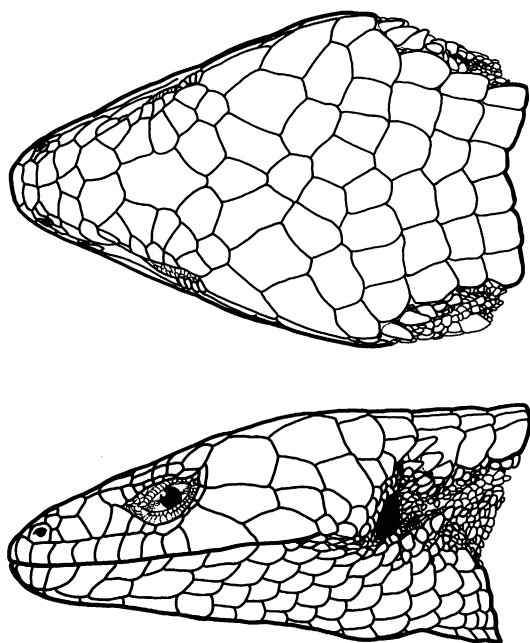


Fig. 8. *Abronia gaiophantasma*, dorsal and lateral aspects of head of male holotype (UTA R-19646), head length 23.2 mm.

192096); near Chilascó, collected by R. Fuentes, P. Elias, and J. Jackson in 1977–1978 (MVZ 143461); 4 km ENE Chilascó, 1829 m, collected by E. J. Koford on 22 April 1977 (MVZ 144537); Finca San Jorge, 5 km ENE Chilascó, 1829 m, collected by C. B. Koford on 17 April 1978 (MVZ 160608); Finca Miranda, 8 km ESE Chilascó, 1829–1981 m, collected by E. J. Koford et al. on 9 May 1978 (MVZ 160609).

ETYMOLOGY: The specific name is a noun in apposition, derived from the Greek, *gaio* (earth) + *phantasma* (spirit or phantom), in reference to the general overall coloration of this species and its similarity in hue to the reddish brown lateritic clays of the region the species inhabits, clays that are becoming increasingly evident as the forests are felled concomitant with human encroachment.

DIAGNOSIS (see fig. 8 and table 2): A species of *Abronia* having: (1) supra-auricular scales of subadults and adults spinelike; (2) supranasals relatively small and unexpanded, not in contact at the dorsal midline; (3) frontonasal scale present, not contacting frontal; (4) posterior internasals relatively small, only

slightly larger than the anterior internasals; (5) canthals discrete; (6) three or four anterior temporals per side, usually the lower two (rarely one) contacting the postoculars; (7) parietal not in contact with median supraoculars; (8) usually a single occipital; (9) posterolateral head scales not knoblike; (10) anterior superciliary contacting cantholoreal, similar in length to other scales in series; (11) posterior subocular broadly separated from the lower primary temporal by the penultimate supralabial, the posteriormost scale in this series to reach the orbit; (12) two or occasionally three incomplete rows of subimbricate preauricular scales; (13) postmental single or divided; (14) posteriormost infraorbital not elongate; (15) six longitudinal nuchal scale rows; (16) 28–30 dorsal transverse scale rows; (17) 12 dorsal longitudinal scale rows, arranged parallel to ventrolateral fold; (18) 14–16 ventral longitudinal scale rows; (19) adults tan, brown, gray-brown, or reddish brown (fig. 11A); (20) juveniles and subadults with dark brown crossbands (fig. 11B).

This species differs from other species of *Abronia* occurring east of the Isthmus of Tehuantepec in having 12 (versus 14 or more) dorsal longitudinal scale rows. *Abronia gaiophantasma* (fig. 11A, B) differs from all Nuclear Central American species, except *A. salvadorensis*, *A. matudai* females, and some individuals of *A. lythrochila* in having an essentially brown dorsal coloration, with or without dark crossbands. *Abronia gaiophantasma* differs from *A. salvadorensis* in lacking a fourth row of temporal scales, having distinct supra-auricular spines; from *A. matudai* in having unexpanded supranasals, in usually having 3–4 anterior temporals (versus usually 2), in having 14–16 ventral longitudinal scale rows (versus 12), in having distinct supra-auricular spinelike scales, and in lacking contact between the parietals and the median supraoculars; and from *A. lythrochila* in having smaller lateral neck scales, having larger scales in the temporal region, lacking multiple rows of granular preauriculars, and lacking red pigment on the upper edge of the infralabials.

DESCRIPTION OF THE HOLOTYPE: An adult male having a snout-vent length of 101 mm. Head from the rostral to the upper anterior edge of the auricular opening is 23.2 mm,

and the greatest head width is 18.7 mm (head width/length ratio = 0.81). The tail is complete (unregenerated), 191 mm long with 96 caudal whorls.

Supranasal scales are small, not expanded medially, and about the same size as the upper postnasal. An upper and lower postnasal are present on each side; the former is less than half the size of the nasals. Two pairs of internasals lie between the rostral, canthals, and frontonasal; the posterior internasals are about twice as large as the anterior internasals. A single canthal on each side is situated mostly on the dorsum of the snout; these scales are broader than long, and separate the posterior internasals from the prefrontals, loreal, and cantholoreale. The cantholoreale is higher than wide. The frontonasal is broadly separated from the frontal by a pair of large prefrontals and, at its broadest point, is slightly narrower than the canthals. There are 5/5 median supraoculars, 4/3 lateral supraoculars, and 7/7 superciliaries on the right and left sides, respectively. The first superciliary is in broad contact with the cantholoreale and preocular. There are 1/1 preoculars, 2/3 suboculars, and 4/4 postoculars. The frontal narrowly contacts the interparietal; the posterior end of the interparietal is in contact with a single large occipital which is bordered laterally by two large postparietals, which extend posteriorly well past the occipital. Two transverse rows of scales separate the occipital from the first transverse row of nuchals. Three primary temporals are on each side; the lower is horizontally elongate and is in broad contact with the next to the upper postocular and first two postorbital supralabials; the middle is about twice the size of the lower and is in contact with the upper postocular. The small upper (third) primary temporal separates the parietal from the median supraoculars and contacts the frontoparietal. The secondary temporal series consists of 3/4 scales. Supralabials number 10/10; the penultimate is the posteriormost to reach the orbit. Infralabials number 10/9. The postmental is divided and followed by three pairs of enlarged chinshields and a fourth posterior pair which is about half the size of the preceding pair. Scales of the sublabial series are 5/4, the anteriormost not in contact with the postmental.

The minimum number of nuchals in a transverse series is six. The 28 transverse and 12 longitudinal rows of dorsal scales³ are arranged in parallel horizontal rows on the sides; eight dorsal longitudinal rows are distinctly keeled. There are 36 transverse and 14 longitudinal rows of ventral scales.⁴ Osteoderms are well developed on the head, neck, trunk, and tail. Supra-auricular scales are relatively stout with about four spines per side. About 12 granular scales lie between the lateral nuchals and the first large scales on the ventrolateral surface of the neck; there are 12 antibrachials, counted from the insertion of the arm to the wrist. The ventrolateral fold has only 2–3 subgranular scales separating the small dorsal scales from the ventrals. Subdigital lamellae of the fourth toes number 22/23.

In preservative (ethanol after formalin) the top of the head and dorsum is medium coffee brown. Seven faint darker brown crossbands (about a scale row long) are on the body and about 24 bands or rings (2–3 caudal whorls long) on the unregenerated tail. The posterior temporal region, supra-auricular spines, lower jaw, gular region, anterior part of the chest, and ventral surfaces of the limbs are white. The cephalic portion of most of the scales on the venter of the body and tail are gray. The dorsal surface of the tongue is heavily suffused with black and the visceral peritoneum is black.

VARIATION: Five of the six paratypes are males with 95–105 mm SVL and head width/length ratios of 0.81–0.92 ($\bar{x}$ = 0.86). In large males the head is exceptionally broadly expanded in the temporal region. The single female paratype is 71 mm in SVL with a head width/length ratio of 0.70. The tail is complete (unregenerated) in three specimens and is 1.70–1.76 ($\bar{x}$ = 1.73) times the body length with 93–96 ($\bar{x}$ = 94.3) caudal whorls.

The frontonasal invariably is present and it fails to reach the frontal. In one specimen

⁴ The scales of the lateral longitudinal ventral scale rows tend to be the largest ventral scales on the body; the holotype appears to be anomalous in often having two scales in the place of one in this series, with 15 or 16 scales in transverse series at some places across the venter.

a small median scale separates the prefrontals. Three (67%) or 4 (33%) lateral supracoculars, 6–7 superciliaries, 2–4 suboculars, and 2–4 postoculars are present per side. The posteriormost subocular is broadly separated from the lower primary temporal by the penultimate supralabial. Except for the holotype, which has two, a single transverse row of scales separates the occipital from the first transverse row of nuchals in all specimens. Three (50%) or four (50%) primary temporals are on each side. The upper primary temporals separate the parietal from the median supracoculars and contact the frontoparietal. There are 9 (8%), 10 (75%), or 11 (17%) supralabials; 8 (42%) or 9 (58%) infralabials; 3 enlarged chinshields, except on one side where there are 4; and 4–6 sublabials per side. There are 28–30 ($\bar{x}$ = 29.0) transverse and 12 longitudinal rows of dorsal scales, and 35–38 ($\bar{x}$ = 36.2) transverse and usually 14 longitudinal rows of ventral scales (increased to 15 and 16 in one specimen each). About 11–12 small granular scales sit between the lateral nuchals and the first large scales on the ventrolateral surface of the neck. There are 20–22 ($\bar{x}$ = 20.6) subdigital lamellae on the fourth toes.

In life the dorsal coloration of this species may be reddish brown, pale gray-brown, or tan. Seven to nine dark brown dorsal crossbands are evident on the body, and the tail is similarly marked with a higher number of bands (proximally) or rings (distally), although large specimens tend to lose these markings and become uniformly brown dorsally. Most of the dorsal head scales (exclusive of the rostral and internasals) and scales of the temporal region are heavily vermiculate with black; this black vermiculation extends to the suprascapular region in some specimens. The lower temporal region and lower jaw are white, sometimes becoming yellow in the auricular region. The iris is copper-bronze.

DISTRIBUTION: Northeastern highlands of Guatemala (fig. 26); known only from the cloud forest and pine-oak forest of the western portion of the Sierra de las Minas in the Department of Baja Verapaz (the Sierra de las Minas Subarea of Campbell and Vannini, 1989).

MATERIAL EXAMINED (7 specimens): See type specimens.

Over 20 years ago, five specimens of a striking, uniformly bright green or bluish-green *Abronia* were collected on the southern slopes of the Volcán de Agua, Department of Escuintla, Guatemala. This material found its way into three different institutions in the United States where it has languished under the alias of *A. vasconcelosii*. Examination of these specimens reveals that they represent yet another undescribed taxon, which we name:

***Abronia anzuetoii*, New Species**

Figures 9, 11C, D

Abronia vasconcelosii: Hidalgo, 1983: 10. [In part, Hidalgo's allocated specimens included *A. anzuetoii*, *A. vasconcelosi* (= *A. aurita*), and *A. matudai*.]

Abronia vasconcelosii: Good, 1988: 95. [In part, Good's allocated specimens included one specimen of *A. aurita* (the holotype of *A. vasconcelosii*) and one specimen of *A. anzuetoii*.]

Abronia vasconcelosii: Campbell and Vannini, 1989: 9. [In part, allocated specimens included *A. aurita* and *A. anzuetoii*.]

HOLOTYPE: The University of Michigan Museum of Zoology (UMMZ) 129013, an adult male obtained by Roderico Anzueto on 15 August 1968 (preserved 9 January 1969) in cloud forest at 1219 m (4000 ft) elevation on the south slope of Volcán de Agua, Finca Rosario Vista Hermosa, Department of Escuintla, Guatemala. This site is about 12 km (airline) NNE Escuintla at approximately 14°25'N, 90°44'W.

PARATYPES (5 specimens): GUATEMALA: *Department of Escuintla*: south slope of Volcán de Agua: Finca Rosario Vista Hermosa: 15 km (airline) NNE [incorrectly cataloged as "4 mi. N" (fide R. Anzueto)] Escuintla, ca. 1829 m (6000 ft), collected on 5 December 1966 (AMNH 102177); 16 km (airline) NNE [incorrectly cataloged as "4 mi. N" (fide R. Anzueto)] Escuintla, ca. 2286 m (7500 ft), collected in March 1972 (AMNH 109053–54); (UTA R-4604; skeleton), collected in 1974; all specimens listed above secured by Roderico Anzueto. *Department Unknown*: UTA R-4482.

For many years UTA R-4482 was in the collection of the Jardín Botánico of the Universidad de San Carlos of Guatemala; it was presented to UTA by the late Lic. Mario Dary Rivera. Unfortunately, other than that the lizard is from Guatemala, no locality information is associated with the specimen, which is thought to have been collected in the 1940s.

ETYMOLOGY: This species name is a noun in the genitive case, formed in honor of the Guatemalan naturalist Roderico Anzueto, who has been responsible for the acquisition of most specimens of this species and is one of the few persons to have observed the species in nature.

DIAGNOSIS (see fig. 9 and table 3): A species of *Abronia* having: (1) distinctive spinelike supra-auricular scales in subadults and adults; (2) unexpanded supranasals; (3) a median frontonasal scale; (4) posterior internasals relatively small, although about twice the length of anterior internasals; (5) discrete canthals; (6) two or three primary temporals, the lower two contacting the postoculars; (7) usually no parietal–median supraocular contact; (8) a single occipital; (9) posterolateral head scales not knoblike; (10) anterior superciliary contacting cantholorear, similar in length to other scales in series; (11) posterior subocular broadly separated from the lower primary temporal by the penultimate supralabial, which is the posteriormost scale in this series to reach the orbit; (12) at least three rows of granular preauriculars; (13) postmental divided; (14) posterior infralabial elongate, often about twice as long as preceding infralabials; (15) six longitudinal nuchal scale rows; (16) 27–28 dorsal transverse scale rows; (17) 14 dorsal longitudinal scale rows arranged parallel to ventrolateral fold; (18) 14 ventral longitudinal scale rows; (19) adults dark green or dark blue-green (fig. 11C, D); and (20) juvenile pattern unknown.

This species differs from all other species of *Abronia* that have spinelike supra-auricular scales, except *A. aurita*, *A. gaiophasma*, *A. lythrochila*, and some *A. matudai*, in having 14 longitudinal ventral scale rows. *Abronia anzueto* differs from all other species of *Abronia*, except *A. aurita*, *A. graminea*, and *A. smithi*, in having a distinctly yellow circumorbital region. *Abronia anzueto*

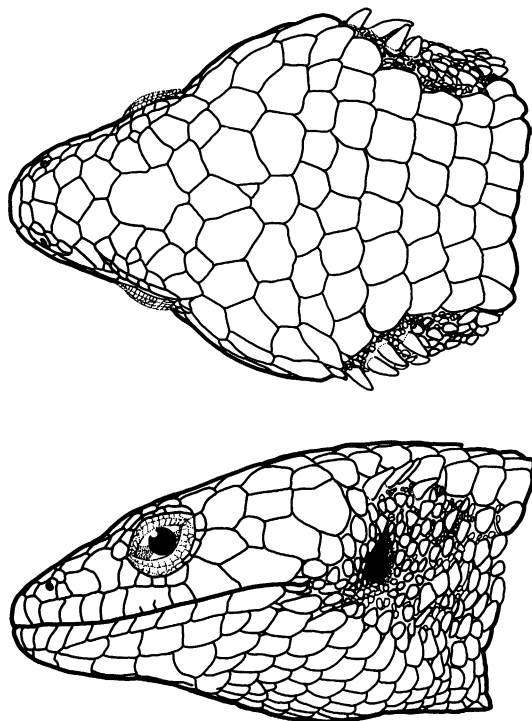


Fig. 9. *Abronia anzueto*, dorsal and lateral aspects of head of male holotype (UMMZ 129013), head length 28.3 mm.

differs from *A. aurita* in coloration (dark emerald green or dark blue green versus a paler green with yellow and/or orange markings), in having relatively longer posterior internasals, and possibly in being of a larger body size (maximum known SVL 135 mm versus 125 mm). *Abronia anzueto* differs from *A. gaiophasma* in having more numerous postoccipital rows between the occipital and first nuchal row (two or three versus one), expansion of the posterior infralabial, and in a green coloration with yellow eye region (versus a brown dorsum and circumorbital region not yellow), and from *A. lythrochila* in having a divided postmental (usually single in *A. lythrochila*), and in a green dorsal coloration with yellow orbit (color variable in *A. lythrochila*, but often brownish or with numerous black markings, never with yellow orbit).

DESCRIPTION OF THE HOLOTYPE: An adult male having a SVL of 124 mm. Head length

TABLE 3
Selected Variations Observed in Several Species of *Abronia* Inhabiting Pacific Versant Cloud Forests of Nuclear Central America
 Two species excluded, *Abronia ornelasi* and *A. bogerti*, probably occur on both Atlantic and Pacific watersheds of extreme southeastern Oaxaca; for these species see Campbell (1984). Arranged in west-east order of distribution.

Character	<i>A. smithi</i> (n = 11)	<i>A. matudai</i> (n = 4)	<i>A. anzuetoi</i> (n = 5)	<i>A. montecristoi</i> (n = 1)	<i>A. salvadorensis</i> (n = 4)
Supra-auricular spines in adults	well developed	poorly developed	well developed	absent	absent
Supranasals	not expanded	often partially expanded	not expanded	not expanded	slightly expanded in one specimen
Parietal contacting median supraoculars	no	yes	variable; usually no	no	no
Postmental	variable	variable	divided	single	single
Lateral neck scales	9-11	7-10	5-7	10	7-9
Transverse dorsal scale rows	27-30	33-37	27-28	28	31-32
Longitudinal dorsal scale rows	14	usually 16, rarely 14	14	14	14
Transverse ventral scale rows	34-39	36-37	35-38	37	??
Longitudinal ventral scale rows	12	usually 12, rarely 14	14	12-14	14
Adult male color pattern	uniformly green	greenish with dark lateral flecking	uniformly green	green with mosaic-like scale darkening?	fawn or pale brown with or without darker crossbands

from the rostral to the upper anterior edge of the auricular opening is 28.3 mm, and the greatest head width is 24.3 mm (head width/length ratio = 0.86). The tail is regenerated. Measurements taken by Charles M. Bogert before preservation are: 128 mm SVL, regenerated tail 208 mm.

Supranasals are small, not expanded medially, and about the same size as the upper postnasal. An upper and lower postnasal are present on each side; the former less than half the size of the nasal. Two pairs of internasals lie between the rostral, canthals, and the frontonasal; the posterior internasals are more than twice as long as the anterior internasals. A single canthal on each side is situated mostly on the dorsum of the snout; these scales are about as broad as long, and separate the posterior internasals from the prefrontals. The cantholoreale is about as high as wide. The frontonasal is broadly separated from the frontal by a pair of large prefrontals and, at its broadest point, is 1.3 times broader than a canthal. There are 5/5 median supraoculars, 3/3 lateral supraoculars with a fourth scale juxtaposed between the second and third median supraoculars, and 5/6 superciliaries on the right and left sides, respectively. The first superciliary is in broad contact with the cantholoreale and the preocular. There are 1/1 preoculars, 2/3 suboculars, and 3/4 postoculars. The frontal narrowly contacts the interparietal; the posterior end of the interparietal is in contact with a single large occipital (and a tiny asymmetrical scale), which is bordered laterally by two large postparietals extending posteriorly to about the same level as the occipital. Three transverse rows of scales separate the occipital from the first transverse row of nuchals. Three primary temporals sit on each side, with the uppermost separated from the rest of the series by contact of a secondary temporal with the median supraocular series. The lower primary temporal is horizontally elongate and is in contact with two postoculars; the middle is about the size of the lower, but higher than long, and is in contact with the upper postocular. The small upper (third) primary temporal separates the parietal from the median supraoculars and contacts the frontoparietal. Secondary temporal scales number 3/3. The postmental is divided transversely into an

anterior scale and a posterior segment which is longitudinally divided into two scales. Three pairs of enlarged chinshields are present and a fourth posterior pair is less than half the size of the preceding pair. Sublabial scales number 5/5, the anteriormost not in contact with the postmental.

The minimum number of nuchals in a transverse series is six. There are 28 transverse and 14 longitudinal rows of dorsal scales. These are arranged in parallel horizontal rows on the sides; eight longitudinal rows on the dorsum are distinctly keeled. There are 38 transverse and 14 longitudinal rows of ventral scales. Osteoderms are well developed on the head, neck, trunk, and tail; the supracephalic scales are knobby. Supraauricular scales are relatively stout with four dorsal spines per side and 4–6 smaller, pointed scales situated ventrally and posteriorly to these larger spines. About six small scales lie between the lateral nuchals and the first large scales on the ventrolateral surface of the neck; there are 11 antibrachials, counted from the insertion of the arm to the wrist. The ventrolateral fold has only 2–3 rows of subgranular scales separating the small dorsal scales from the ventrals. Fourth toe subdigital lamellae number 22/21.

In preservative (ethanol after formalin) the dorsum of the head and body is uniformly gray-green. The region around the eye, including the eyelids, lower postoculars, and most of the superciliaries, is yellow. The ventral surfaces of the head, body, hands, and feet are yellow.

VARIATION: Three of the four paratypes from the Volcán de Agua are females with a SVL of 98 to 102 mm and head width/length ratios of 0.69–0.79 ($\bar{x}$ = 0.74). The single male paratype is 119 mm in SVL with a head width/length ratio of 0.81. The tail is regenerated in all specimens.

The two posterior internasals are elongate in all specimens, ranging from 1.5 to 2.9 ($\bar{x}$ = 2.2) times the length of the anterior internasals. Three lateral supraoculars, 6–7 superciliaries, 2–3 suboculars, and 3–4 postoculars per side, with two (two specimens) or three (two specimens) transverse rows of scales separating the occipital from the first transverse row of nuchals. There are three primary temporals on each side except in one

specimen that lacks an upper primary temporal on one side. An upper primary temporal (except in the one instance where it is lacking) separates the parietal from the median supraoculars and contacts the frontoparietal. The lower scales of the primary and tertiary series are in contact, thus preventing supralabial contact by the secondary temporal series, half of the time (4 of 8 sides). Ten supralabials, 8 infralabials, 3 enlarged chinshields, and 4–5 sublabials are found per side. There are 27–28 ($\bar{x}$ = 27.8) transverse and 14 longitudinal rows of dorsal scales and 35–37 ($\bar{x}$ = 35.8) transverse and 14 longitudinal rows of ventral scales. About 5–6 small very irregular scale rows lie between the lateral nuchals and the first large scales on the ventrolateral surface of the neck. The fourth toes have 19–21 ($\bar{x}$ = 20.2) subdigital lamellae.

The scale characteristics of UTA R-4482 are typical for the species and all fall within the range of variation noted in the rest of the type series. It is, however, the largest specimen of *Abronia* known from Guatemala, with a SVL of 135 mm.

In life (color notes taken from UTA transparencies 14121–26 and two AMNH transparencies; all taken by C. M. Bogert), the adult dorsal coloration of AMNH 102177 was deep emerald green with the posterior borders of the dorsal scales edged with pale yellow-green. The small scales of the axillary region and ventrolateral fold were bluish green. The circumorbital region, the spinelike supra-auricular scales, and undersurfaces of the hands and feet were bright yellow. The lower temporal region and lower jaw were pale to yellowish green. The underside of the head and venter vary from yellowish white to yellowish green. Most of the dorsal head scales (exclusive of the rostral and internasals) and scales of the temporal region were heavily vermiculated with black; this black vermiculation extends to the suprascapular region in at least some specimens. The iris was copper-bronze.

DISTRIBUTION: South-central Guatemala (fig. 26): known only from the southern slopes of the Volcán de Agua, Department of Escuintla, in cloud forest at elevations of 1219–2286 m. These slopes lie within the eastern portion of the Fuego Area of Campbell and Vannini (1989). Specimens have been col-

lected in forest containing oak and cypress trees. We have received reports from inhabitants of the adjacent Volcán de Pacaya of a large, slow-moving, green arboreal lizard that may be of this species.

MATERIAL EXAMINED (6 specimens): See type specimens.

COMMENT: This is one of the largest species of *Abronia*; the holotype has a 124 mm SVL, and one of the paratypes of has a 135 mm SVL. The elongate, but relatively slender *A. fimbriata* reaches 130 mm SVL and one gigantic specimen of *A. mixteca* (MZFC 4420) is 148 mm SVL.

THE *ABRONIA OCHOTERENAI* PROBLEM

Abronia ochoterenai (figs. 13, 14, 53) was described, as *Gerrhonotus vasconcelosii ochoterenai*, by Martín del Campo (1939) from “Santa Rosa, Comitán,” Chiapas, Mexico. The exact whereabouts of this locality is uncertain, although Casas-Andreu and Smith (“1990” [1991]) have pinpointed two small towns of the name Santa Rosa to the north-northwest of Comitán. What is known with certainty about the type locality of *A. ochoterenai* is that it is in “la región de Comitán, cercana a Guatemala” and that *Bothrops nigroviridis aurifera* (= *Bothriechis aurifer*) and *Bothrops nummifera* (= *Porthidium nummifer mexicanum*) were collected at this locality during the same trip and by the same collector as for *A. ochoterenai* (fide Martín del Campo, 1938).

Moreover, a collection of birds also was assembled by this collector and subsequently reported by Berlioz (1939). Avian species listed from Santa Rosa included *Penelopina nigra* (Black Penelopina), *Aulacorhynchus prasinus* (Emerald Toucanet), and *Pharomacrus mocinno* (Resplendent Quetzal). These data, particularly the collection of *Bothriechis aurifer*, suggest that the stated type locality for *A. ochoterenai* is on the Atlantic versant of Chiapas and in, or at least very close to, cloud forest.

Hartweg and Tihen (1946) described *Gerrhonotus matudai* (= *Abronia matudai*) from the Pacific versant cloud forest (2000 m) on Volcán de Tacaná, Chiapas, and, in so doing, had occasion to reexamine and to provide a



Fig. 10. Species of *Abronia* photographed in life: A, *Abronia aurita*, male (AMNH 137788), 109.5 mm SVL; 3.0 km SSE Chichicastenango, valley between Paxot and Camanibal, 2100 m, Quiché, Guatemala. B, *Abronia aurita*, male (UTA R-19675), 113 mm SVL; locality data same as fig. 10A. [photo by D. G. Barker]. C, *Abronia aurita*, juvenile (UTA R-19662), 33 mm SVL; other data same as fig. 10A. D, *Abronia fimbriata*, male (UTA R-19644), 121 mm SVL; near Cáquiepec, Alta Verapaz, Guatemala, 2000 m [photo by W. W. Lamar]. E, *Abronia fimbriata*, subadult female (KU 187243), 93 mm SVL; West side of Cerro Verde, 1676 m, Baja Verapaz, Guatemala. F, *Abronia fimbriata*, juvenile (UTA R-6647), 33 mm SVL; Vuelta del Quetzal, "Biotopo Mario Dary Rivera," Baja Verapaz, Guatemala.

relatively complete description of the syntypes of *A. ochoterenai* (two adults, IBUN-AM 338–339).⁵ Additionally, they allocated

two other specimens from the Santa Rosa locality to *A. ochoterenai*, an adult specimen (IBUNAM 340), previously identified by

⁵ Hartweg and Tihen (1946) designated the adult male syntype, IBUNAM 339, as lectotype of *A. ochoterenai*. The tags on the specimens have them labeled backwards,

and Good (1988: 94), possibly for this reason, mistakenly reported IBUNAM 338, an adult female, as the holotype of the species.



Fig. 11. Species of *Abronia* photographed in life: **A**, *Abronia gaiophantasma*, male holotype (UTA R-19646), 101 mm SVL; W slope of Cerro Verde in vicinity of La Unión Barrios, 1600 m, Baja Verapaz, Guatemala. **B**, *Abronia gaiophantasma*, male paratype (KU 192096), 95 mm SVL; W slope Cerro Verde, 1653 m, Baja Verapaz, Guatemala [photo by W. W. Lamar]. **C**, *Abronia anzuetoii*, male paratype (AMNH 102177), 119 mm SVL; Finca Rosario Vista Hermosa, S slope Volcán de Agua, 1829 m, Escuintla, Guatemala; the unusual bifid tail is regenerated [photo by C. M. Bogert]. **D**, *Abronia anzuetoii*, data same as for fig. 11C. **E**, *Abronia smithi*, male (IHN), ca. 100 mm SVL; Paraje El Triunfo, Municipio de Mapastepec, Chiapas, Mexico [photo by W. W. Lamar, courtesy of A. Ramírez Velázquez]. **F**, *Abronia lythrochila*, male (UTA R-12137), 120 mm SVL; 12.1 km ESE Teopisca, Tulanca, 2073 m, Chiapas, Mexico [photo by W. W. Lamar].

Martín del Campo (1939) as *Gerrhonotus fimbriatus*, and a juvenile (IBUNAM 312), which was subsequently determined by Smith and Alvarez del Toro (1963) to be a specimen of *A. lythrochila*, undescribed at the time of

Hartweg and Tihen's report.⁶ At the time of the description of *A. matudai*, no other spe-

⁶ We regard as suspect, as did Casas-Andreu and Smith ("1990" [1991]), the subsequent association by Hartweg



Fig. 12. Species of *Abronia* photographed in life: **A**, *Abronia fuscolabialis*, male (UTA R-9899), 112 mm SVL; 3.1 mi [5.0 km] W Totontepec, Oaxaca, Mexico, 2158 m. **B**, *Abronia ornelasi*, male (UTA R-12499), 88 mm SVL; Colonia Rodolfo Figueroa, 1524 m, 19 km NW Rizo de Oro, Oaxaca, Mexico. **C**, *Abronia* species (undescribed member of the *A. bogerti* group), probably adult (IHN), Chiapas, Mexico [photo by A. Ramírez Velázquez]. **D**, *Abronia mixteca*, male (UTA R-12139), 109 mm SVL; El Tejocote, ca. 2200 m, Oaxaca, Mexico. **E**, *Abronia* species "Guerrero," female (UTA R-12136), 118 mm SVL; 0.8–1.6 km NE Puerto del Gallo, Guerrero, Mexico. **F**, *Abronia oaxacae*, male (AMNH 98003), 107 mm SVL; Loma Grand, 2500 m, Oaxaca, Mexico.

cies of *Abronia* was known from the Pacific highlands of Chiapas, Mexico.

and Tihen (1946) of IBUNAM 312 with the collection of *A. ochoterenai* made at Santa Rosa; this specimen was not noted in the report of the Santa Rosa specimens by Martín del Campo (1939).

Specimens of *A. lythrochila* (then undescribed) from the pine-oak forest of the Meseta Central of Chiapas continued to be confused with *A. ochoterenai* by Alvarez del Toro (1960) and Smith and Alvarez del Toro (1962). In the second edition of his book on the reptiles of Chiapas, however, Alvarez del

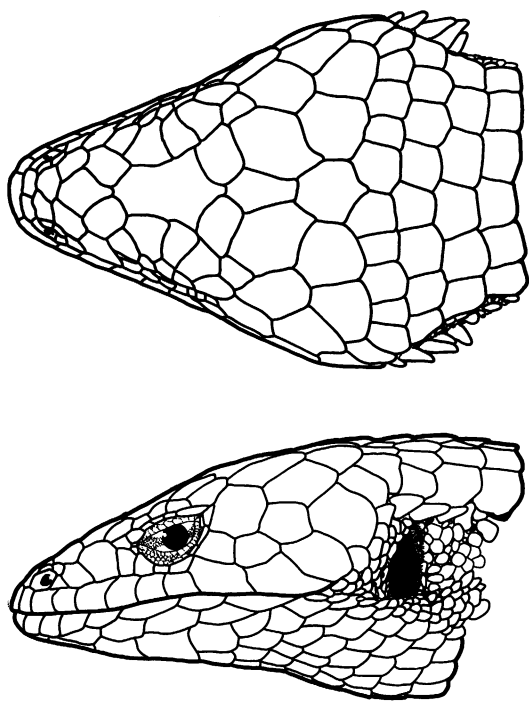


Fig. 13. *Abronia ochoterenai*, dorsal and lateral aspects of head of male lectotype (IBUNAM 339), head length 21.4 mm.

Toro (1973) corrected this error, having participated in the description of *A. lythrochila* (Smith and Alvarez del Toro, 1963), but he also reported for the first time *A. ochoterenai* from "la parte alta de la Sierra Madre" (i.e., the Pacific highlands of southern Chiapas) and he included a photograph of an adult male for which he described the dorsal coloration as "un hermoso verde azulado uniforme." Subsequently, a number of authors have followed Alvarez del Toro (1973) in assigning a Pacific versant population of *Abronia* to *A. ochoterenai* (Alvarez del Toro, 1982; Good, 1988; Johnson, 1989; Casas-Andreu and Smith, "1990" [1991]), an otherwise Atlantic versant species.

We regard as doubtful the purported distribution of putative *A. ochoterenai* in cloud forest on both the Pacific and Atlantic slopes of Chiapas. Besides a considerable expanse of seasonally-dry pine-oak forest on the Meseta Central of Chiapas, the barrier presented by the xeric Río Grijalva depression, which extends well into Guatemala, effectively and

completely isolates the cloud forests of the Atlantic and Pacific slopes. The herpetofaunal assemblages inhabiting the upper elevations of the Atlantic and Pacific versants of Chiapas share comparatively few species of reptiles and amphibians, other than forms that have wide elevational distributions. Although evidence from repeated phylogenetic patterns has not been accumulated, Johnson (1989) showed in a phenogram of faunal regions of Chiapas that the Atlantic versant highland forests (his "eastern highlands") and Pacific highlands (his "Sierra Madre") fall out as relatively distant branches. When "marginal" cloud forest species are excluded from the analysis, the faunal distinctiveness of these regions becomes even more trenchant, which makes questionable the likelihood of the two *Abronia* populations being conspecific.

Casas-Andreu and Smith ("1990" [1991]) noted this biogeographic anomaly and suggested that either the two disjunct Chiapan populations assigned to *A. ochoterenai* were perhaps continuous to the east of the Central Depression in Guatemala, or that perhaps the status of the Pacific versant population should be questioned. One of us has considerable field experience in Guatemala and can state categorically that no cloud forest corridor exists through western Guatemala between the Atlantic and Pacific versants. The suggestion by Casas-Andreu and Smith ("1990" [1991]) that the Pacific versant population of *Abronia* might represent an unnamed species seems the most sound and is a notion that had occurred to us also. A careful comparison of these specimens (11 specimens) with material from the Atlantic versant reveals the existence of three species, two from the Santa Rosa collection (not counting the specimen allocated to *A. lythrochila*), and one from the Pacific versant. The acquisition of additional material, along with information on *A. ochoterenai* from life, should provide yet more evidence clearly separating these populations. Because the Pacific versant population is distinctive and has never been named, we propose that it be known as:

***Abronia smithi*, New Species**

Figures 11E, 15, 53

Abronia ochoterenai: Alvarez del Toro, 1973: 129.

[In part, like other authors listed below, Alvarez

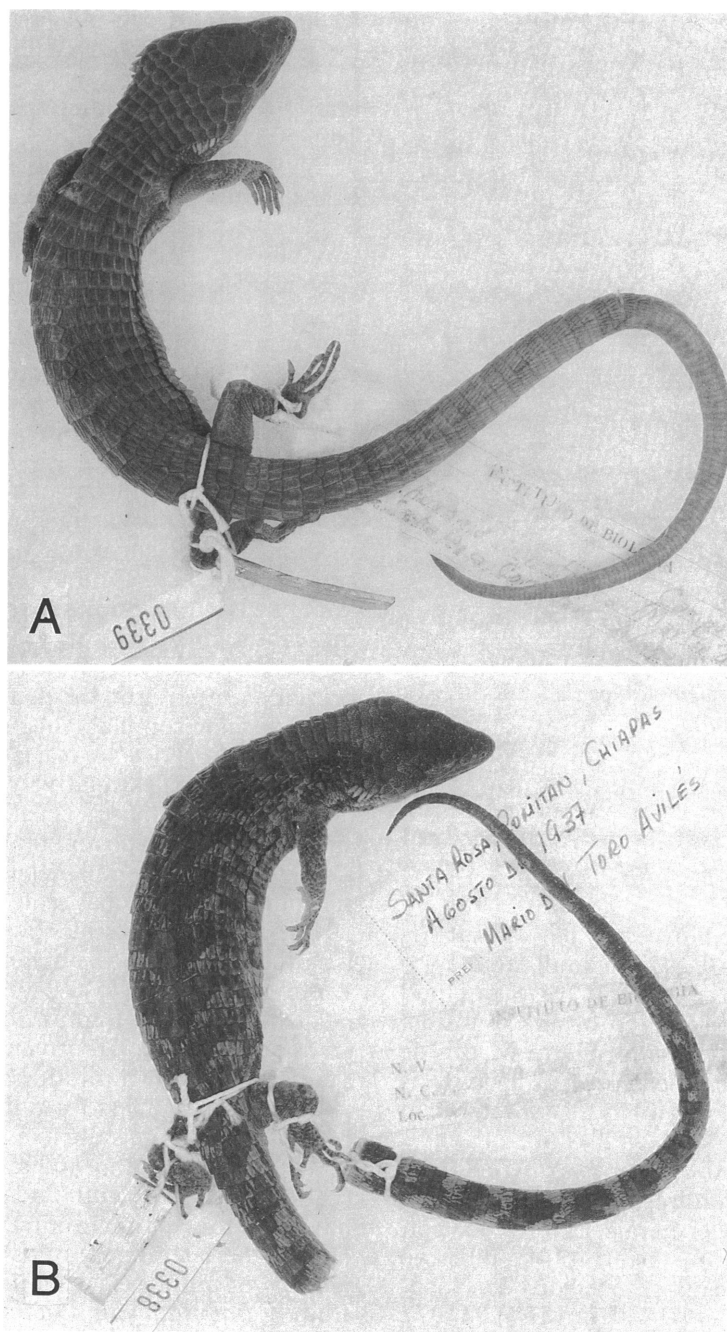


Fig. 14. *Abronia ochoterenai*. A, Male lectotype (IBUNAM 339), 93 mm SVL, 154 mm TL. B, Female paralectotype (IBUNAM 338), 97 mm SVL, 153 mm TL [photos by M. A. Donnelly].

del Toro's specimens included representatives of *A. smithi* and *A. ochoterenai*.]

Abronia ochoterenai: Alvarez del Toro, 1982: 95. [See comment above.]

Abronia ochoterenai: Good, 1988: 94. [Good's specimens included only *A. smithi*.]

Abronia ochoterenai: Johnson, 1989: 41, 63. [See comment above.]

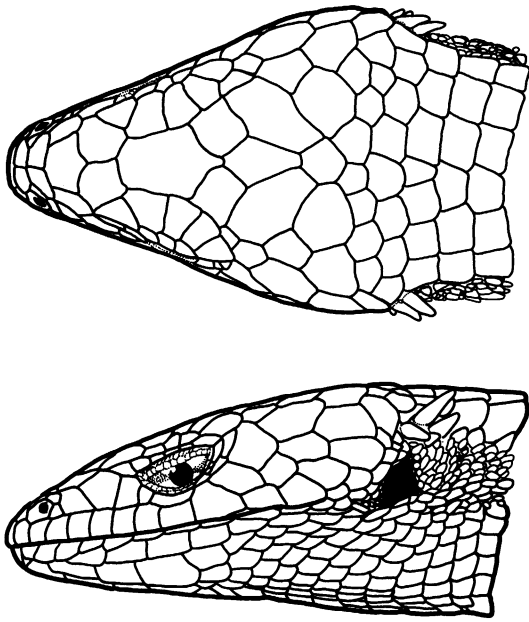


Fig. 15. *Abronia smithi*, dorsal and lateral aspects of head of female holotype (UTA R-30202), head length 18.5 mm.

Abronia ochoterenai: Casas-Andreu and Smith, "1990" [1991]: 318. [In part, their allocated specimens included *A. ochoterenai*, *A. smithi*, and *A. leurolepis*.]

HOLOTYPE: The University of Texas at Arlington (UTA) R-30202, an adult female obtained by a local collector in 1978 in cloud forest at 2020 m elevation on the southeast slope of Cerro El Triunfo, Sierra Madre de Chiapas, Chiapas, Mexico. This locality is about 13.1 km (airline) NNE Mapastepec at approximately 15°40'N, 92°48'W.

PARATYPES (10 specimens): **MEXICO**: **Chiapas**: Sierra Madre de Chiapas: Municipio de Mapastepec, Paraje El Triunfo, collected 21 March 1960 (IHN 643-44, plus two unnumbered juveniles); Región de Soconusco, collected 1944-1949 (UIMNH 34197); El Triunfo, on trail between Mapastepec and Angel Albino Corzo, collected by Alvarez del Toro on 7 May 1960 (UIMNH 52085-86); El Triunfo, 1950 m (see comment), collected on 21 March 1950 (UMMZ 197260); slopes of Cerro Mozotal, 7000-9000 ft [2134-2743 m], collected by D. E. Breedlove on 20 September 1976 (CAS 163888); SW slope Cerro

Male, on high ridge N Cerro Mozotal, Colonia Las Salivas, 5 km SW El Porvenir, 9200 ft [2804 m], collected by E. Palacios Martín and D. E. Breedlove on 31 May 1988 (CAS 169850).

ETYMOLOGY: This species name is a noun in the genitive case, honoring Dr. Hobart M. Smith, the most prolific student of the Mexican herpetofauna.

DIAGNOSIS (see fig. 15 and table 3): A species of *Abronia* having: (1) distinctive spine-like supra-auricular scales in subadults and adults; (2) unexpanded supranasals; (3) a median frontonasal scale, not contacting frontal; (4) posterior internasals not greatly enlarged; (5) discrete canthals; (6) usually four primary temporals, usually the lower two (rarely three) contacting the postoculars; (7) no parietal-median supraocular contact; (8) a single occipital; (9) posterolateral head scales not knoblike; (10) anterior superciliary contacting cantholoreal or not; (11) the posterior subocular broadly separated from the lower primary temporal by the penultimate or antepenultimate supralabial, the posteriormost scale in this series to reach the orbit; (12) preauricular scales relatively small, usually disposed in two rows, usually imbricate or subimbricate; (13) postmental divided or single; (14) posterior infralabial not elongate; (15) six longitudinal nuchal scale rows; (16) 27-30 dorsal transverse scale rows; (17) 14 dorsal longitudinal scale rows arranged parallel to ventrolateral fold; (18) 12 ventral longitudinal scale rows; (19) adult dorsal coloration greenish (fig. 11E); (20) juvenile pattern with a broad pale brown middorsal stripe.

This species differs from all other species of *Abronia* having spinelike supra-auricular scales, except for *A. ochoterenai*, *A. matudai* (variably), *A. leurolepis*, and *A. fimbriata*, in having 12 longitudinal ventral scale rows, and having the lateralmost rows wider than adjacent ventral rows. *Abronia smithi* differs from *A. fimbriata* and *A. leurolepis* in having a frontonasal scale, from *A. leurolepis* in having imbricate or subimbricate preauricular scales rather than multiple rows of protuberant scales, relatively short posteriormost infralabial, and definite keels on the body scales; from *A. fimbriata* in having unexpanded supranasals and discrete canthals; and from *A. matudai* in having four primary temporals

(usually two, rarely three or four in *A. matudai*), no parietal–median supraocular contact, and in lacking expanded supranasals. *Abronia smithi* appears to be most similar morphologically to *A. ochoterenai*, but differs from that species in having usually four or five, rather than three, primary temporals, usually having a fourth temporal scale row in evidence (clearly absent in *A. ochoterenai*), having the subocular separated from the lower primary temporal (broadly in contact in *A. ochoterenai*), usually having a divided rather than single postmental, having two or fewer rows of imbricate to subimbricate preauriculars rather than three rows of nonimbricate preauriculars, and in that adult females are yellow-green with darker spotting, rather than with dark transverse bands, and in having the circumorbital region bright yellow in *A. smithi*, not the ambient head color as in *A. ochoterenai*.

DESCRIPTION OF THE HOLOTYPE: An adult female having a snout-vent length of 95 mm. Head from the rostral to the upper anterior edge of the auricular opening is 18.5 mm, and greatest head width is 13.5 mm (head width/length ratio = 0.73). The tail is regenerated.

Supranasal scales are small, not expanded medially, and about the same size as the upper postnasals. An upper and lower postnasal are present on each side; the former is about a fourth the size of the nasal. Two pairs of internasals lie between the rostral, canthals, and the frontonasal; the posterior internasals are 1.3 times as long as the anterior internasals. A single canthal on each side is situated mostly on the dorsum of the snout; these scales are longer than broad, and separate the posterior internasals from the prefrontals. The cantholoreal is slightly longer than high. The frontonasal is broadly separated from the frontal by a pair of large prefrontals and, at its broadest point is 2.2 times broader than a canthal. There are 5/5 median supraoculars, 3/3 lateral supraoculars, and 7/6 superciliaries. The first superciliary is in broad contact with the cantholoreal and the preocular. There are 1/1 preoculars, 2/2 suboculars, and 3/3 postoculars. The frontal contacts the interparietal; the posterior end of the interparietal is in contact with a single large occipital, which is bordered laterally by

two large postparietals, which extend slightly posterior to the occipital. Two transverse rows of scales separate the occipital from the first transverse row of nuchals. Four primary temporals are on each side with the upper two scales on each side relatively small; the lower (first) is horizontally elongate and is in contact with the lower two postoculars; the next primary temporal (second) is more than twice the size of the lower, about as high as long, and contacts the middle and upper postocular. The small upper (third and fourth) primary temporals separate the parietal from the median supraoculars and the fourth contacts the frontoparietal. The secondary temporal series consists of 3/3 scales. The postmental is longitudinally divided into two scales. Three pairs of enlarged chinshields are present and a fourth posterior pair is less than half the size of the preceding pair. The scales of the sublabial series are 5/5; the anterior-most contact the postmental on one side.

The minimum number of nuchals in a transverse series is six. There are 29 transverse and 14 longitudinal rows of dorsal scales arranged in parallel horizontal rows on the sides; eight longitudinal rows on the dorsum are distinctly keeled. There are 37 transverse and 12 longitudinal rows of ventral scales, with the lateral rows widely expanded. Osteoderms appear to be well developed on the head, neck, trunk, and tail; the supracephalic scales are rugose but not knobby. Spinelike supra-auricular scales are present with two or three elongate dorsal spines per side and 3–4 smaller, pointed scales situated ventrally and posteriorly to these larger spines. About 10 small scales lie between the lateral nuchals and the first large scales on the ventrolateral surface of the neck; there are 13 antebrachials, counted from the insertion of the arm to the wrist. The ventrolateral fold has about three small flat scales separating the dorsal scales from the ventrals. Subdigital lamellae of the fourth toes number 22/22.

In preservative (ethanol after formalin) the dorsum of the head and body is uniformly blue-green; dorsal scales are mottled with black and edged posteriorly with turquoise. The region around the eye including the eyelids, lower postoculars, and most of the superciliaries is pale yellow or green. The ventral surface of the head is white, becoming

pale blue on the body. The ventral surfaces of the hands and feet are yellow.

VARIATION: Five of the paratypes are adult males with a SVL of 92 to 110 mm and head width/length ratios of 0.73–0.85 ($\bar{x}$ = 0.79). Three adult females, including two paratypes and the holotype, range in SVL from 95 to 103 mm and have head width/length ratios of 0.71–0.74 ($\bar{x}$ = 0.73). The tail is complete in two adult males and is 1.34–1.54 times longer than the SVL; there are 75 and 86 caudal whorls.

The posterior pair of internasals is 1.3–1.6 ($\bar{x}$ = 1.4) times the length of the anterior internasals. There are 3 lateral supraoculars, 5–8 superciliaries, 2–4 suboculars, and 3–4 postoculars per side. Two or three transverse rows of scales separate the occipital from the first transverse row of nuchals. In nine specimens there are four primary temporals on each side; one specimen has five scales on each side; and another specimen has three scales on each side, apparently resulting from the atypical fusion of the middle scale with an upper adjacent scale. Upper primary temporals separate the parietal from the median supraoculars and contact the frontoparietal. There are 9–11 supralabials, 7–10 infralabials, 3 enlarged chinshields, and 4–7 sublabials per side. There are 27–30 ($\bar{x}$ = 28.3) transverse and 14 longitudinal rows of dorsal scales and 34–39 ($\bar{x}$ = 36.3) transverse and 12 longitudinal rows of ventral scales. About 8–11 small scales lie between the lateral nuchals and the first large scales on the ventrolateral surface of the neck. The fourth toes have 18–25 ($\bar{x}$ = 20.9) subdigital lamellae.

In life (color notes taken, in part, from UTA transparencies 303-09, 14118–20) the adult dorsal coloration is yellow-green. Most of the dorsal scales on the body and tail are heavily mottled with black; this black mottling extends to the temporal region. The region around the orbit and undersurfaces of the hands and feet are pale yellow. The supra-auricular spines are usually pale green, but in some specimens the distal tips of the larger spines may be yellow. The lower jaw is often pale turquoise and white. Ventral surfaces of the head and body vary from yellowish white to yellowish green. The iris is copper-bronze.

Alvarez del Toro (1973, 1982) stated that adults of this species are sexually dimorphic

with the ground color of males being blue-green and that of females yellow-green.

DISTRIBUTION: Mexico: southeastern Chiapas; known only from cloud forest of the Sierra Madre de Chiapas (fig. 26). The elevational distribution is 1800–2500 m, according to Johnson (1989); our records range from 2020 to 2804 m.

MATERIAL EXAMINED (11 specimens): See type specimens.

COMMENT: One of the paratypes (UMMZ 197261) was taken from the stomach of a viper, *Cerrophidion godmani* (UMMZ 95151), 434 mm in total length, which also contained a rodent tail and hair and the hind feet of a hylid frog.

As noted earlier, we disagree with the allocation to *Abronia ochoterrenai* of the "*Gerrhonotus fimbriatus*" specimen (IBUNAM 340), reported by Martín del Campo (1939) from the type locality of *Abronia ochoterrenai* (Hartweg and Tihen, 1946; Tihen, 1954; Casas-Andreu and Smith, "1990" [1991]). Martín del Campo (1939) identified this specimen as *Gerrhonotus fimbriatus*, presumably because it lacked a frontonasal scale. Hartweg and Tihen (1946) subsequently referred it to *Gerrhonotus ochoterrenai*, noting (p. 2) that it differs from the syntypes of *G. ochoterrenai* (IBUNAM 338–339) and the juvenile (IBUNAM 312; subsequently referred to *A. lythrochila* by Smith and Alvarez del Toro, 1963) "in the absence of an azygous prefrontal [= frontonasal] and in the presence of obtusely rather than prominently keeled scales." In fact, the dorsal scales are almost without any trace of keeling, a condition quite different from that in *A. ochoterrenai*. We suggest that this specimen represents a distinctive and easily diagnosed species similar in general aspect to *A. gaiophasma*. We name this species:

***Abronia leurolepis*, New Species**
Figures 16, 17

Gerrhonotus fimbriatus: Martín del Campo, 1939: 359.

Gerrhonotus ochoterrenai: Hartweg and Tihen, 1946: 2. [In part, like other authors until 1963, Hartweg and Tihen's allocated specimens included *A. ochoterrenai*, *A. leurolepis*, and *A. lythrochila*.]

Abronia ochoterenai: Tihen, 1949a: 591, 1954: 22. [See comment above.]

Abronia ochoterenai: Smith and Alvarez del Toro, 1963: 100–105. [In part, Smith and Alvarez del Toro's specimens included only *A. smithi*, but they applied this name, which also had been applied to *A. leurolepis*, then undescribed.]

Abronia ochoterenai: Alvarez del Toro, 1973: 129, 1982: 95. [In part, like other authors listed below, Alvarez del Toro's specimens included only *A. smithi*.]

Abronia ochoterenai: Good, 1988: 94. [See comment above.]

Abronia aurita: Johnson, 1989: 40, 63. [Allocated here on the presumption that Johnson considered Martín del Campo's (1939) record of "*Gerhonorotus fimbriatus*" (= *Abronia leurolepis*) to be the same as *Barissia fimbriata* Cope, "1884" [1885] (which was regarded at the time of Johnson's writing to be a synonym of *Abronia aurita*).]

Abronia ochoterenai: Casas-Andreu and Smith, "1990" [1991]: 318. [In part, their specimens included *A. ochoterenai*, *A. leurolepis*, and *A. smithi*.]

HOLOTYPE: IBUNAM 340 from Santa Rosa, near Comitán, Chiapas, Mexico. Collected sometime from June to August, 1937, by Mario del Toro Aviles.

ETYMOLOGY: This species name is a noun in the nominative case, from the Greek, *leuros* (smooth, even) + *lepis* (scale), in reference to the strikingly flat dorsal body scales of the only known specimen.

DIAGNOSIS (see figs. 16, 17 and table 2): A species of *Abronia* having: (1) distinctive spinelike supra-auricular scales in adults; (2) unexpanded supranasals; (3) no median frontonasal scale; (4) posterior internasals not greatly enlarged, in the only known specimen the one on the right fused with the canthal; (5) canthals meeting at the midline, the left discrete, the right fused with the posterior internasal; (6) three primary temporals, the lower two contacting the postoculars; (7) narrow parietal–median supraocular contact on one side in the only known specimen; (8) a single large occipital; (9) posterolateral head scales not knoblike; (10) anterior superciliary contacting cantholoreal; (11) posterior subocular broadly separated from the lower primary temporal by the antepenultimate supralabial, the posteriormost scale in this series to reach the orbit; (12) preauricular scales

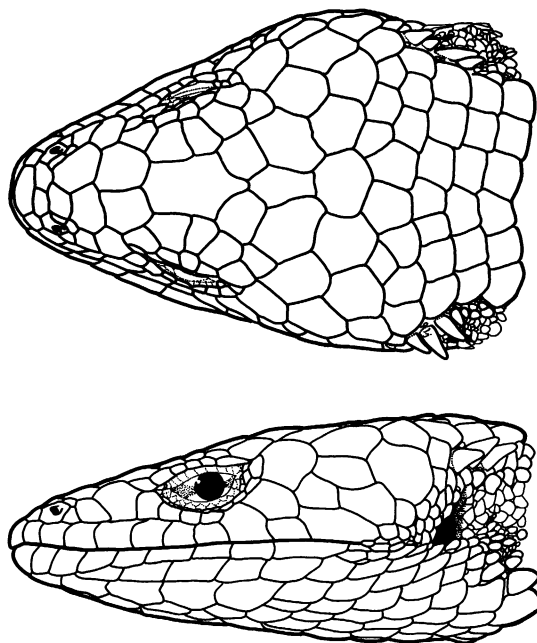


Fig. 16. *Abronia leurolepis*, dorsal and lateral aspects of head of female holotype (IBUNAM 340), head length 20.4 mm.

small, nonimbricate and in three rows; (13) postmental single; (14) posteriormost infra-labial elongate; (15) six longitudinal nuchal scale rows; (16) 31 dorsal transverse scale rows; (17) 14 dorsal longitudinal scale rows arranged parallel to ventrolateral fold; (18) 12 ventral longitudinal scale rows; (19) adult dorsal ground coloration unknown, but with dorsal crossbands; and (20) juvenile color pattern unknown.

This species differs from all other species of *Abronia* having spinelike supra-auricular scales, except for *A. smithi*, *A. ochoterenai*, and *A. fimbriata* (variably), in having 12 longitudinal ventral scale rows, with the lateral rows expanded compared with adjacent ventral rows. *Abronia leurolepis* differs from all members of the *Abronia aurita* group except *A. fimbriata* and *A. lythrochila* (variably) in lacking a frontonasal scale. *Abronia leurolepis* differs from *A. fimbriata* in lacking expanded supranasals that meet at the dorsal midline, in having more dorsal transverse scale rows (31 versus 27–30), and in being a stockier animal. *Abronia leurolepis* differs from *A. lythrochila* in lacking a frontonasal (usually

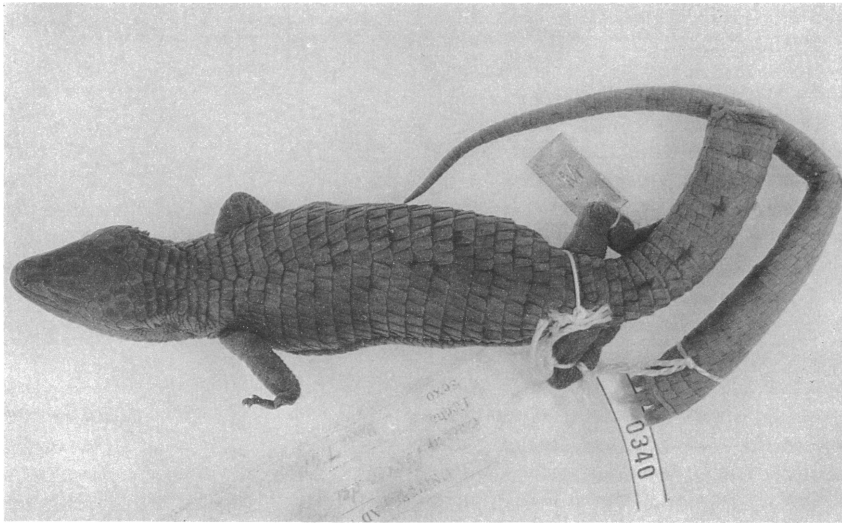


Fig. 17. *Abronia leurolepis*, female holotype (IBUNAM 340), 105 mm SVL, 268 mm TL [photo by M. A. Donnelly].

present in *A. lythrochila*), in having a single scale row between the occipital and first nuchal scale row, in having 12 versus 14 ventral longitudinal scale rows, and in having more (31 versus 28–30) dorsal transverse scale rows. *Abronia leurolepis* differs from *A. ochoterenai* in having a single (rather than two) postoccipital row between the occipital and first transverse nuchal scale row and in having no contact between the subocular and lower primary temporal (broad contact in *A. ochoterenai*). *Abronia leurolepis* differs from all members of the *A. aurita* group in having almost flat dorsal scales, with only slight traces of keeling on 3–4 scale rows on either side of the midline. The lateral longitudinal row of ventral scales are expanded in this species as they are in all members of the *A. aurita* group having 12 ventral longitudinal scale rows. However, the posterior (free) edges of the expanded scales in *A. leurolepis* are obtusely pointed, whereas in other species of the *A. aurita* group having 12 ventral longitudinal rows the posterior edges of these scales are rounded to truncate.

The occipital scale is large in *A. leurolepis* as are the scales immediately behind it; thus, only a single scale lies between the occipital and first transverse nuchal scale row, a character shared in the *A. aurita* group only with *A. gaiophasma*.

DESCRIPTION OF THE HOLOTYPE: An adult

female having a snout-vent length of 105 mm. Head length from the rostral to the upper anterior edge of the auricular opening is 20.4 mm, and the greatest head width is 16.5 mm (head width/length ratios = 0.73). Tail length is 163 mm.

Supranasal scales are small, not expanded medially, and slightly larger than the upper postnasal. An upper and lower postnasal are present on each side; the former is about a fourth the size of the nasal. A pair of anterior internasals lies posterior to the rostral and between the nasals; a single posterior internasal is present on the left side, on the right this scale is fused with the canthal. A single large canthal on each side is situated mostly on the top of the snout; the canthals are expanded and in broad contact along the dorsal midline. The cantholoreal is higher than long. The frontonasal is absent. There are 5/5 median supraoculars, 3/3 lateral supraoculars, and 6/6 superciliaries. The first superciliary is in broad contact with the cantholoreal and the preocular. There are 1/1 preoculars, 3/3 suboculars, and 3/4 postoculars (excluding small, almost granular scales). The frontal contacts the interparietal; the posterior end of the interparietal is in contact with a single large occipital, which is bordered laterally by two large postparietals. A single transverse row of scales separates the occipital from the first transverse row of nuchals. There are

11/10 supralabials, with the antepenultimate making contact with the orbit, and 7/8 infralabials. Three primary temporals are on each side with the upper scale being relatively small; the lower (first) is horizontally elongate and is in contact with two postoculars; the next primary temporal (second) is more than twice the size of the lower, about as high as long, and contacts the upper two postoculars. The small upper primary temporal separates the parietal from the median supraoculars on the left side, but the parietal is in narrow contact with this series on the right. The secondary temporal series consists of 4/4 scales. The postmental is single. Four pairs of enlarged chinshields are present, the fourth (posterior) pair is more than half the size of the preceding pair. Scales of the sublabial series number 4/5 and the anteriormost scale in the series does not contact the postmental.

The minimum number of nuchals in a transverse series is six. There are 31 transverse and 14 longitudinal rows of dorsal scales that are arranged in parallel horizontal rows on the sides. Dorsal body scales are almost flat with only vestigial keels on 3–4 rows to either side of the midline. There are 35 transverse and 12 longitudinal rows of ventral scales, with the lateral rows widely expanded. Osteoderms appear to be well developed on the head and anterior nuchals, but poorly developed on the body; the supracephalic scales are rugose (most prominently in the area from the frontal to the occipital and between the parietals) but not knobby in appearance. Supra-auricular scales are present with 4–5 elongate dorsal spines per side and 5–7 smaller, pointed scales situated ventrally and posteriorly to these larger spines. About 8 small scales lie between the lateral nuchals and the first large scales on the ventrolateral surface

of the neck; there are 11/12 antebrachials, counted from the insertion of the arm to the wrist. The ventrolateral fold has about 1–3 small flat scales separating the dorsal scales from the ventrals. There are 20/20 subdigital lamellae on the fourth toes.

In preservative (ethanol after formalin) the head and body are uniformly brown with a few faint darker spots on the dorsum. This specimen was described by Martín del Campo, (1939) shortly after preservation, as having an olive-gray dorsum with narrow dark crossbands, somewhat irregular in form and chevron-shaped; the tail had rounded dark spots along the midline; the ventral scales were pale with a darkening on the anterior part of each one.

DISTRIBUTION: Known only from the type locality in eastern Chiapas, Mexico (fig. 26).

MATERIAL EXAMINED: See holotype.

COMMENT: Martín del Campo (1939) gave the collection locality for the holotype of *Abronia leurolepis* as “Santa Rosa, Comitán, Chiapas,” Mexico. Casas-Andreu and Smith (“1990” [1991]) have pinpointed two localities in Chiapas, near Comitán called “Santa Rosa.” These villages lie at 1800 and 2300 m elevation. It is uncertain which, if either, is the actual type locality of *Abronia leurolepis* and *A. ochoterenai*. We suggest that *A. leurolepis* and *A. ochoterenai* are cloud forest inhabitants. This conjecture is based on (1) our previously stated incredulity regarding the association of one specimen of *A. lyth-rochila* (otherwise a pine-oak species) from “Santa Rosa” in the face of evidence that this locality is in cloud forest, and (2) because all regions of known or suspected syntopy among species of *Abronia* are in cloud forest, rather than in seasonally dry pine-oak woodland.

NOTES ON *ABRONIA* TAXONOMY

Below we provide an account of a poorly known species of southern Guatemala and adjacent Chiapas, Mexico, in order to document its distinctiveness. Also, we address two minor problems in *Abronia* taxonomy and geography. The first of these regards the status of *Abronia kalaina*. The second regards the status of putative *Abronia montecristoi*

specimens reported from Honduras (Wilson et al., 1986).

ABRONIA MATUDAI

Figures 18, 19

Gerrhonotus matudai Hartweg and Tihen, 1946:
3. Holotype: UMMZ 88831. Type locality: Volcán Tacaná, Chiapas, Mexico, 2000 m.

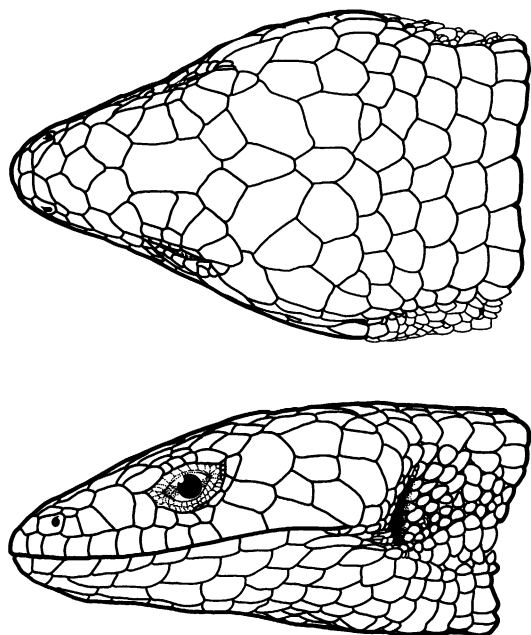


Fig. 18. *Abronia matudai*, dorsal and lateral aspects of head of female holotype (UMMZ 88331), head length 16.2 mm.

Abronia matudai: Tihen, 1949a: 591; Good, 1988. *Abronia vasconcelosii*: Hidalgo, 1983: 10. [In part, Hidalgo's specimens allocated to this name included *A. vasconcelosii* (= *A. aurita*), *A. anzuetoi*, and *A. matudai*.]

Abronia matudai is a species of the Pacific versant of southeastern Mexico and southwestern Guatemala. Its geographical distribution is not known to overlap that of *A. smithi* to the west or *A. anzuetoi* to the east. We include an account of this species to document its distinctiveness from its geographically nearest neighbors, *A. smithi* and *A. anzuetoi*.

DIAGNOSIS (see figs. 18, 19 and table 3): A species of *Abronia* having: (1) supra-auricular scales of adults and subadults protuberant, but not spinelike; (2) supranasals large and often expanded, extending partially across the top of the snout, but not contacting each other at the dorsal midline; (3) a relatively large frontonasal scale, not contacting frontal; (4) posterior internasals relatively small, nearly the same size as the anterior internasals (except on one side of the holotype); (5) discrete canthals; (6) usually two anterior temporals

per side, occasionally three or four; (7) parietal contacting median supraoculars; (8) a single occipital scale; (9) posterolateral head scales not knoblike; (10) anterior superciliary contacting cantholorear, longer than other scales in series; (11) the posterior subocular separated from the lower primary temporal by the antepenultimate or occasionally the penultimate supralabial, the posteriormost scale in this series to reach the orbit; (12) two rows of subimbricate to granular preauricular scales; (13) postmental single or divided; (14) posteriormost infralabial not elongate; (15) six longitudinal nuchal scale rows; (16) 33–37 dorsal transverse scale rows; (17) 14–16 dorsal longitudinal scale rows, arranged parallel to ventrolateral fold; (18) 12–14 ventral longitudinal scale rows; (19) adult males green, females brown; (20) juvenile pattern unknown.

This species differs from all species of *Abronia* east of the Isthmus of Tehuantepec, except *A. ornelasi*, *A. bogerti*, *A. montecristoi*, and *A. salvadorensis*, in lacking distinctive spinelike supra-auriculars, although adults have relatively short but protuberant supra-auricular scales. *Abronia matudai* differs from all Nuclear Central American species, except *A. fimbriata*, *A. bogerti*, and some individuals of *A. aurita*, in having the parietal contact the median supraoculars. *Abronia matudai* differs from *A. ornelasi* in having supranasals that do not contact each other at the dorsal midline and in having a frontonasal that does not contact the frontal; from *A. montecristoi* and *A. salvadorensis* in having more (33–37 versus 28 and 31–32 respectively) dorsal transverse scale rows; from *A. fimbriata* in having supranasals that do not meet at the dorsal midline and in having a frontonasal; from *A. bogerti* in usually having a minimum of six (versus eight) nuchals across the nape and 33–37 (versus 40) dorsal transverse scale rows; and from *A. aurita* in having more dorsal transverse scale rows (33–37 versus 27–31) and in lacking distinctive spinelike supra-auricular scales.

VARIATION: Our series comprises four specimens, two males and two females. The SVL of the largest male is 83 mm; that of the largest female is 96. The head width/length ratios of males are 0.73–0.76 ($\bar{x}$ = 0.75) and females are 0.75–0.77 ($\bar{x}$ = 0.76). Two spec-

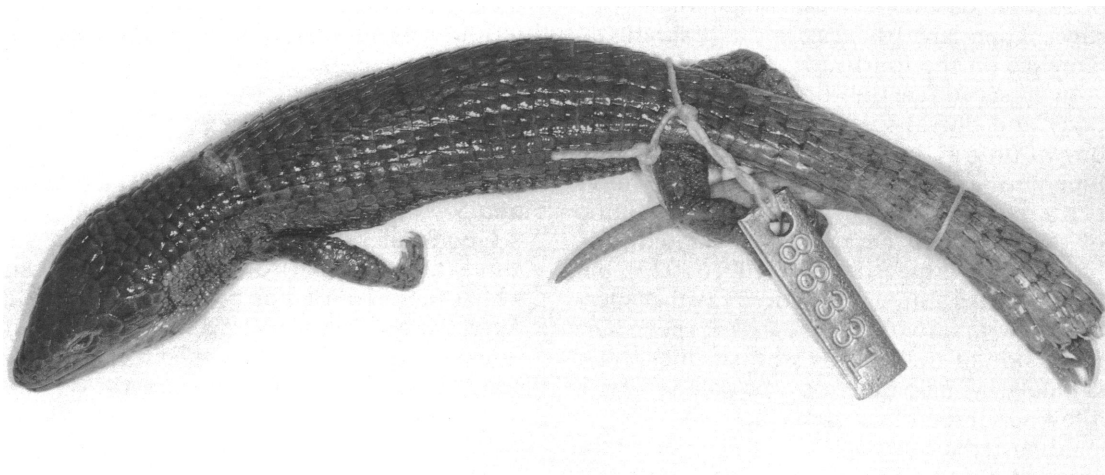


Fig. 19. *Abronia matudai*, female holotype (UMMZ 88331), 80 mm SVL, broken tail regenerated.

imens have complete, original, tails; the tail lengths are 1.57 and 1.70 ($\bar{x} = 1.64$) times the body length and there are, respectively, 96 and 97 ($\bar{x} = 96.5$) caudal whorls.

Supracephalic scales are relatively flat and smooth, rather than knobby. Usually there is a single supranasal on each side; in three specimens this scale is slightly to moderately expanded medially across the snout; in one specimen (holotype; UMMZ 88331) the supranasals almost meet at the midline. A pair of anterior internasals and a pair of posterior internasals is usually present, but in the holotype the posterior internasal and canthal are fused on the left side. Posterior to the posterior internasals is a pair of large prefrontals; the frontonasal is present and fails to contact the frontal. There are two postnasals, a loreal, and a cantholoreal on each side. Invariably there are 5/5 median supraoculars and 2 (38%), 3 (25%), or 4 (38%) lateral supraoculars. There are 4 (12%), 5 (38%), 6 (38%), or 7 (12%) superciliaries. A single large preocular is present, followed by 2 (63%), 3 (25%), or 4 (12%) suboculars, and 3 (88%) or 4 (12%) postoculars. The large frontal contacts the interparietal. A single occipital is present except on LACM 75514, which possesses irregular scales in this region. Scales posterior to the occipital region are highly variable in size and the occipital is separated from the first transverse row of nuchals by 1

(one specimen), 2 (2 specimens), or 3 (one specimen) scales. There are 2 (63%), 3 (25%), or 4 (12%) anterior temporals on a side. The lower two temporals invariably contact the postoculars. The posterior subocular is separated from the lower primary temporal by the penultimate or antepenultimate supralabial. In all specimens, the parietal contacts the median series of supraoculars. There are 9 (38%), 10 (50%), or 11 (12%) supralabials. There are 7 (25%), 8 (25%), 9 (12%), or 10 (38%) infralabials. The postmental is undivided in three individuals, divided in one. Three pairs of large chinshields are followed posteriorly by a smaller fourth pair that is about a third the size of the preceding pair. The sublabial series usually has four scales on a side (63%), but may have 5 (25%), or rarely 6 (12%).

The minimum number of scales in a transverse nuchal row is six. Supra-auricular scales in adults are protuberant, not spinelike. There are 7–10 ($\bar{x} = 8.5$) small subgranular scales between the lateral nuchals and the first large scales on the ventrolateral surface of the neck. Dorsal transverse scale rows number 33–37 ($\bar{x} = 35.5$), and there are 16 dorsal longitudinal scale rows, except in one specimen which has 14. Six to 10 rows of dorsals are weakly keeled at midbody. Ventral transverse scale rows are arranged in 36–38 ($\bar{x} = 36.8$) rows, and there are 12 (three specimens)

or 14 (one specimen) ventral longitudinal scale rows. There are 19–22 ($\bar{x}$ = 20.7) subdigital lamellae on the fourth toe.

In preservative, the dorsal coloration of the body and dorsal surface of the forelimbs is brown or gray-brown, sometimes becoming blue-gray laterally. Most specimens have scattered dark dots on the dorsum. The top of the head and neck is vermiculated with black in one large female (MVZ 161022), but more-or-less uniformly colored in other specimens, with or without a few dark spots. The underside of the head is whitish; the venter is pale gray, pale blue-gray, or pale tan, with a few scattered black spots laterally.

Alvarez del Toro (1972, 1982) reported the color of living adults as pale green with numerous dark crossbands.

DISTRIBUTION: Southwestern Guatemala and southeastern Chiapas, Mexico (fig. 26): known in Guatemala only from two localities on the Pacific versant near San Marcos, Department of San Marcos, at elevations of 2300–2630 m, which is near the boundary of the pine-oak and pine-cypress zones (as delimited by Stuart, 1951). The Guatemalan localities lie near the border defined for the western portion of the Fuegan Area and the Chimaltenangan Subarea (Campbell and Vannini, 1989). In Mexico, this species is known only from Volcán Tacaná, Chiapas.

MATERIAL EXAMINED (4 specimens): GUATEMALA: *San Marcos*: 5.5 km W, 1 km S (airline) San Marcos, 2630 m (LACM 75514); Finca Insula, less than 4 km WSW El Rincón, El Rincón transect no. 1, 2300 m (MVZ 161022). MEXICO: *Chiapas*: Volcán Tacaná, in cloud forest on trail above Colonia Talquian, 1950 m (MVZ 161793); Volcán Tacaná, 2000 m (UMMZ 88331: Holotype).

THE TAXONOMIC STATUS OF *ABRONIA KALAINA*

Abronia fuscolabialis was described from two specimens (holotype and paratype) collected on "Mt. Zempoaltepec, Oaxaca," Mexico (Tihen, 1944). This species was placed in the *A. deppii* group by Tihen (1944). Although the diagnosis given in the original description is inadequate to distinguish the species from many of its congeners (several of which were described subsequently from the

state of Oaxaca), a reasonably complete description and illustration of the holotype was provided. We have examined the holotype (AMNH 85634), which is in good condition, and two nearly topotypic specimens in life, including an adult male (UTA R-9899; 112 mm SVL) and a juvenile (UTA R-14147; 37 mm SVL).

Good and Schwenk (1985) described *A. kalaina* (figs. 20, 21) from a single specimen, which they reported as being an adult male. Actually, at 82 mm SVL (given as 86 mm in original description), this specimen is probably a subadult; unfortunately, the viscera have been removed, making it impossible for us to examine the gonads.

In their diagnosis, Good and Schwenk (1985) distinguished *A. kalaina* from other members of the *A. deppii* group by it having: (1) contact of the frontoparietals along the midline of the head; (2) midline contact of the second pair of large chin shields; and (3) "virtual" fusion of the frontoparietals with the frontal. Scale irregularities are common in the genus *Abronia* and examination of the holotype of *A. kalaina* reveals that this specimen possesses several aberrant dorsal head scales including the partial fusion of the frontoparietals with the posterior portion of the frontal with attendant irregular sutures extending forward on the frontal. Two of the features purported to be diagnostic ("1" and "3" above) by Good and Schwenk (1985) are clearly related to this aberrancy and are likely of no diagnostic value.

The only remaining character in the diagnosis of *Abronia kalaina*, that of midline contact by the second pair of large chin shields, is not compelling. The second pair of chin shields of all species of *Abronia* typically are separated by only a single midventral scale. While we have not attempted a comprehensive survey, we have noted midline contact by the second pair of chin shields in five additional species of *Abronia*: *A. aurita* (UTA R-19661), *A. bogerti* (holotype, AMNH 68887), *A. fimbriata* (UTA R-19644–45), *A. matudai* (holotype, UMMZ 88331), and *A. oaxacae* (AMNH 102656). This feature, therefore, is likely indicative of individual variation and not diagnostic.

Other features suggested by Good and Schwenk (1985) as possibly distinguishing *A.*

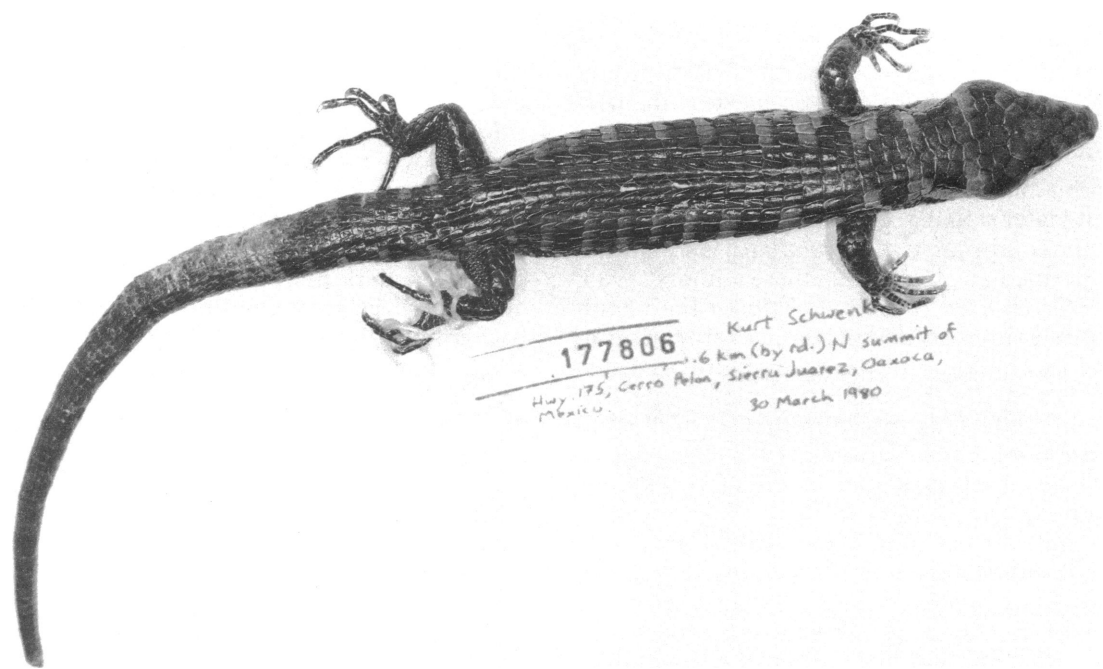


Fig. 20. *Abronia kalaina*, male holotype (MVZ 177806) [= *A. fuscolabialis*], 82 mm SVL.



Fig. 21. Lateral view of head and neck of holotype of *Abronia kalaina* (MVZ 177806), above, and *A. fuscolabialis* (UTA R-9899), below, showing similar distinctive dark lateral markings.

kalaina from *A. fuscolabialis* do not survive scrutiny. Good and Schwenk (1985: 138) reported that in both of these species "the posterior supralabials have expanded sufficiently for there to be only two scales between the orbit and the posterior margin of the mouth" and later stated, somewhat ambiguously, that "the condition in *A. fuscolabialis* is somewhat intermediate." Although these authors (1985: 136) reported that in *A. kalaina* the penultimate supralabial is in contact with the orbit, an examination of the holotype reveals that it is actually the antepenultimate scale that is in contact, as shown in their own illustration (Good and Schwenk, 1985: their fig. 2). Their view is explained by Good's (1988: 25) subsequent statement, that "the posterior margin of the mouth has shifted anteriorly half way along the posteriormost supralabial in *A. fuscolabialis* and to the next scale forward in *A. kalaina*." We have compared the external and internal corner of the mouth in these two species with other species of *Abronia* and have found that the distinction between the condition in *A. kalaina* and other species of *Abronia* is exceedingly slight, so slight that it would surprise us if individual variation did not obviate its diagnostic value.

The holotype of *A. kalaina* was reported in life to be "brilliant turquoise" (Good and Schwenk, 1985) in contrast to *A. fuscolabialis* adults which are green. We find this unconvincing evidence for recognition of *A. kalaina* because the ontogenetic changes in *A. fuscolabialis* coloration are dramatic. Live juveniles (UTA R-14147) are beige with dark brown to black crossbands, whereas adults (UTA R-9899) are bright green dorsally, becoming yellow-green on the flanks, with dark dorsal bands. A number of scales, especially those on the dorsum and those interspersed among the dark dorsal bands, are blue-green to turquoise (fig. 12A). The holotype of *A. kalaina* is small and possibly the turquoise coloration is representative of its size. Also, this species, as well as other green species of *Abronia* (e.g., *A. aurita*, *A. smithi*) can undergo a rapid change from green to turquoise in captivity and under some conditions in nature this hue may be attained. Although the holotype of *A. kalaina* was turquoise in the field (D. A. Good, personal commun.), an *A. fuscolabialis* adult (UTA R-9899),

mostly green on capture, turned to mostly turquoise within about two months in captivity.

More striking than any purported differences between *A. kalaina* and *A. fuscolabialis* are similarities of color and pattern that are not seen in other species. Both have a pale "arrowhead" marking on top of the head, distinctive dark markings on the side of the head and neck that stand out against a pale background (fig. 21; also illustrated by Tihen, 1944, his fig. 1), vertical rows of pale scales on the flanks (these extend across the middorsum on UTA R-9899; the holotype of *A. kalaina* has a darker middorsum with pale bars separated by 5–6 dorsal scales), rings extending ventrally across the tail, and a blue-gray ground coloration in preservative.

Abronia kalaina is putatively distinguished from *A. fuscolabialis* in having reduced osteoderm development on the dorsum (Good and Schwenk, 1985: 136, 140; Good, 1988: 28). However, because the unique specimen of *A. kalaina* is a subadult, osteoderm development, not surprisingly, is relatively slight compared with that of adult specimens of *A. fuscolabialis*.

Abronia fuscolabialis and *A. kalaina* occur in cloud forest of the Atlantic versant of Oaxaca in the Sierra Juárez and Sierra Mixe (Cerro Zempoaltepec region), respectively. The major entrenchment between these mountain ranges is the valley of the Río Cajones, although a cloud forest corridor extends along its headwaters between the Sierra Juárez and Sierra Mixe. Because the cloud forest is continuous between these two peaks it is not surprising that many highland species of amphibians and reptiles are shared among them, including *Pseudoeurycea juarezi*, *Hyla chaneque*, and *Exiliboa placata*.

Viewed against the background of known variability within *Abronia*, not a single compelling character distinguishes *A. kalaina* from *A. fuscolabialis*. In addition, the occurrence of the latter in the Sierra Juárez is expected. Therefore, we relegate *A. kalaina* to the synonymy of *A. fuscolabialis*. The synonymy for this species is:

Gerrhonotus fuscolabialis Tihen, 1944: 112. Holotype: AMNH 85634 [originally 400 in the personal collection of R. T. Moore]. Type locality: "Mt. Zempoaltepec, Oaxaca," Mexico.

Abronia fuscolabialis: Tihen, 1949a: 591.

Abronia kalaina Good and Schwenk, 1985: 135.

Holotype: MVZ 177806. Type locality: "16.6 km (by road) N summit on Hwy. 175, Cerro Pelón, Oaxaca, Mexico, ca 2300 m." NEW SYNONYMY.

DIAGNOSIS: A species of *Abronia* having: (1) supra-auricular scales of adults not protuberant; (2) supranasals small, not expanded; (3) relatively large frontonasal scale, not contacting frontal; (4) posterior internasals relatively small; (5) discrete canthals; (6) four anterior temporals per side, the lower two contacting the postoculars; (7) parietal not contacting median supraoculars; (8) a single occipital; (9) knobby posterolateral head scales; (10) anterior superciliary contacting cantholoreal, similar in length to other scales in series; (11) the posterior subocular separated or not from the lower primary temporal by the antepenultimate supralabial, the posteriormost scale in this series to reach the orbit; (12) a single row of preauricular scales; (13) postmental divided; (14) posteriormost infralabial scale not elongate; (15) four to six longitudinal nuchal scale rows; (16) 28–32 dorsal transverse scale rows; (17) 11–14 dorsal longitudinal scale rows, arranged parallel to ventrolateral fold; (18) 14 ventral longitudinal scale rows, lateral row not expanded; (19) adults with green to turquoise ground color and dark crossbands, orbital coloration not distinct from surrounding region (fig. 12A); (20) juveniles with dark dorsal crossbands.

This species differs from all species of *Abronia*, except *A. deppii*, *A. graminea*, *A. taeniata*, *A. mixteca* (fig. 12D), *Abronia* species "Guerrero" (fig. 12E), and *A. oaxacae* in having pronounced knoblike posterolateral head scales in adults (fig. 60); it differs from *A. mixteca*, *A. species* "Guerrero," *A. deppii*, and *A. oaxacae* (fig. 12F) in having dorsal longitudinal scale rows on the flanks arranged parallel rather than oblique to the ventrolateral fold (fig. 57). *Abronia fuscolabialis* may be distinguished from *A. graminea* and *A. taeniata* in having a canthal discrete from the posterior internasal, a nasal not in contact with the third supranasal, and in having a distinctive dark marking on the sides of the neck (fig. 21).

MATERIAL EXAMINED (4 specimens): MEX-

ICO: Oaxaca: Mt. Zempoaltepec (holotype, *A. fuscolabialis*, AMNH 85634); Sierra Juárez, 16.6 km (by road) N summit on Hwy. 175, Cerro Pelón, ca. 2300 m (holotype, *A. kalaina*; MVZ 177806); Sierra Mixe, 3.1 mi [5.0 km] W Totontepec, 2158 m (UTA R-9899); Sierra Mixe, 16.1 km SW Totontepec, 2438 m (UTA R-14147).

STATUS OF HONDURAN SPECIMENS REPORTED AS *ABRONIA MONTECRISTOI*

Wilson et al. (1986: 4–5) reported two specimens of *Abronia montecristoi* from the departments of La Paz and Intibucá, Honduras, near the type locality in El Salvador of *A. salvadorensis* and far east of the type locality of *A. montecristoi*. We have examined both specimens (KU 195560–61) reported by Wilson et al. as *Abronia montecristoi* and find them to be representatives of *A. salvadorensis* (figs. 22, 23, 58B), rather than *A. montecristoi* (figs. 24, 25, 58C). These species differ strongly in general appearance and color pattern, although this is difficult to appreciate from the descriptions and diagnoses supplied by Hidalgo (1983). The color description given by Wilson et al. (and repeated by Good, 1988: 94) adequately describes the animals in question and agrees well with the holotype of *A. salvadorensis*, not the holotype of *A. montecristoi* (which appears to have been patterned very similarly to *A. ornelasi*, fig. 12B). The Wilson et al. specimen, KU 195560 (as well as UTA R-26108), has 12 transverse ventral scale rows as does the holotype of *A. montecristoi*. Their other specimen (KU 195561) has 14 transverse ventral scale rows like the holotype of *A. salvadorensis*. The Wilson et al. material also shows broad contact between the anterior superciliaries and the cantholoreal (also in UTA R-26108) like the holotype of *A. montecristoi*; there is no contact in the holotype of *A. salvadorensis*. However, as in the holotype of *A. salvadorensis*, there are two primary temporals in contact with the postocular row (not three as in *A. montecristoi*). Hidalgo (1983: 4) reported only two temporals in contact with the orbit (= in contact with the postoculars) in the holotype of *A. montecristoi*; our examination of this specimen shows three temporals in con-

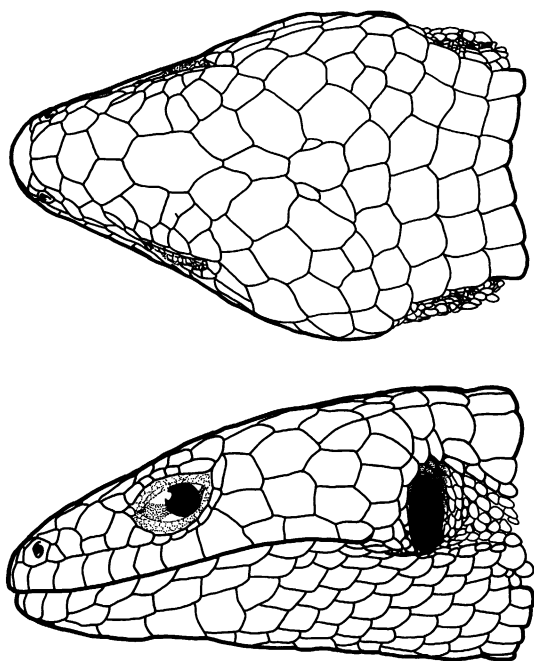


Fig. 22. *Abronia salvadorensis*, male (KU 195561), dorsal and lateral aspects of head, head length 20.5.

tact with the postoculars, the uppermost in narrow contact. Hidalgo (1983: 5) reported five enlarged chinshields on the holotype of *A. salvadorensis* and four on the holotype of *A. montecristoi*, whereas we count four and three, respectively; apparently he was also

counting the postmental in this series. The Wilson et al. material and UTA R-26108 have three enlarged chinshields with the next scale posteriorly clearly enlarged, but not as large as the previous three. This condition is closer to that in *A. salvadorensis* rather than that in *A. montecristoi*.

With this reidentification of Wilson et al.'s Honduran material, the purportedly anomalous distribution of Honduran "*Abronia montecristoi*," found within a few kilometers of the type locality of *A. salvadorensis* and 85–95 km ESE of the type locality of *A. montecristoi*, is resolved. *Abronia montecristoi* is still known only from the unique holotype from northwestern El Salvador, and *A. salvadorensis* is known only from the uplifts of the Sierra de Opalaca in Honduras and the Sierra de Montecillos in Honduras and adjacent El Salvador (Tegucigalpa Quadrangle, Central America 1:1,000,000 map, American Geographical Society, 1937).

MATERIAL EXAMINED: *Abronia montecristoi*: EL SALVADOR: *Santa Ana*: Cordillera de Alotepeque-Metapán, Metapán, Hacienda Montecristo, 2250 m (KU 184046, holotype). *Abronia salvadorensis*: EL SALVADOR: *Morazán*: Cordillera de Nahuaterique, 10 km NE Perquín, Cantón Palo Blanco, 1900 m (KU 184047, holotype). HONDURAS: no other data (UTA R-26108); *Intibucá*: Zacate Blanco, 2125 m (KU 195560); *La Paz*: 5 km S Santa Elena, 2020 m (KU 195561).

NOTES ON THE NATURAL HISTORY OF *ABRONIA*

HABITAT AND SYMPATRY

Species of the genus *Abronia* occur from southern Tamaulipas, Mexico (Martin, 1958), to northeastern El Salvador (Hidalgo, 1983) and southern Honduras (Wilson et al., 1986) (figs. 1, 26). In Mexico west and north of the Isthmus of Tehuantepec, the distribution of the genus is disjunct, with populations occurring in portions of the Sierra Madre Oriental, the southern escarpment of the Mesa Central, the Sierra Madre del Sur and associated ranges of southern Mexico, and the Sierra de Los Tuxtlas of southern Veracruz. East and south of the Isthmus of Tehuantepec

in Chiapas, Mexico, and Guatemala, all of the major highland areas in Nuclear Central America are inhabited by one or more species of *Abronia*, and several mountain ranges are inhabited in Honduras and El Salvador.

As far as is known, members of the genus *Abronia* usually have allopatric distributions (Stebbins, 1958; Bogert and Porter, 1967; Good, 1988). Possible regions of sympatry are relatively few and are usually in areas that have been poorly surveyed by collectors. Beyond this, most species of *Abronia* are known from so few localities that we cannot discuss how broad, or how narrow, the ecological limits of species might be. Smith and Alvarez

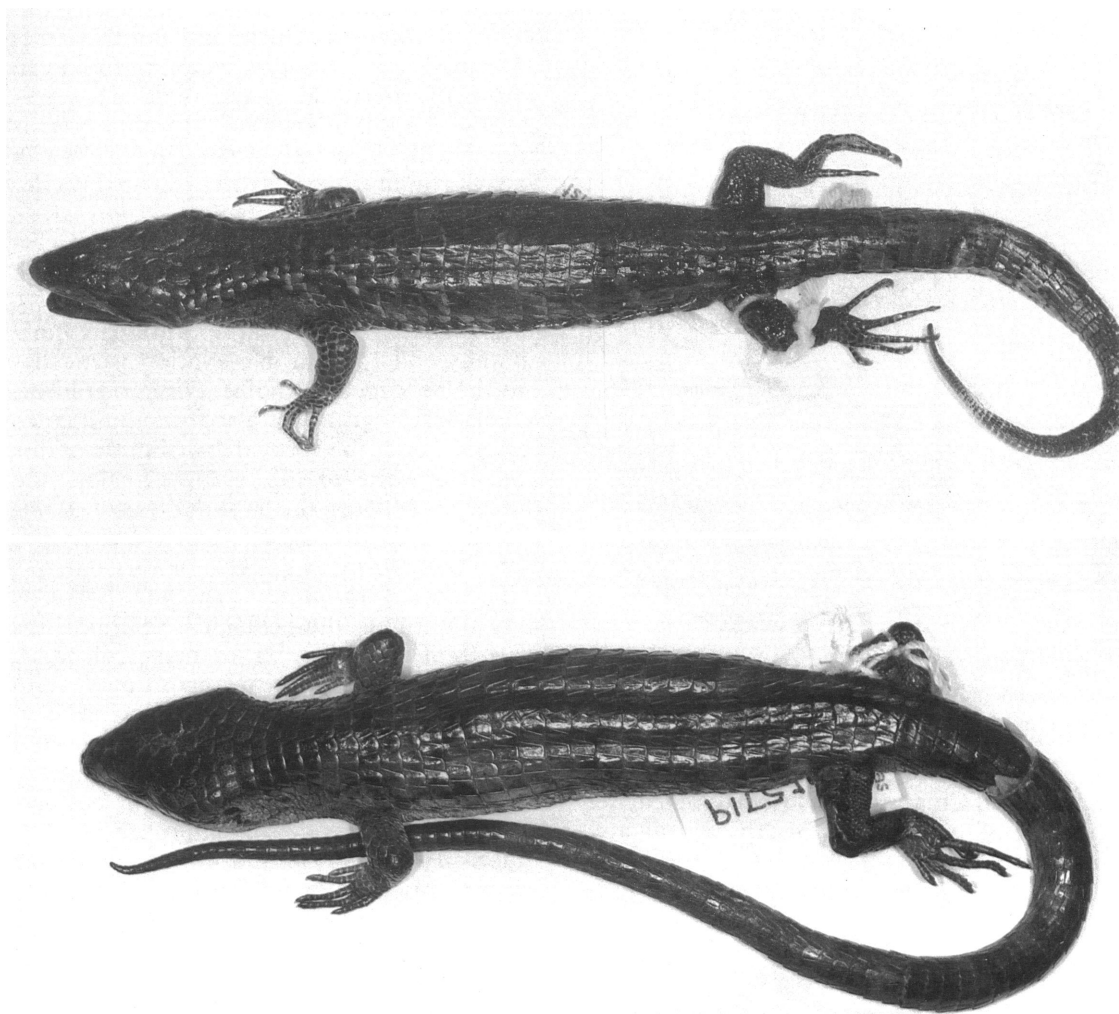


Fig. 23. *Abronia salvadorensis*, (above) female holotype (KU 184047) and (below) an adult male specimen from Honduras (KU 195561), 94 mm SVL.

del Toro (1963) suggested that *A. lythrochila* and *A. ochoterenai* might be sympatric on the basis of four specimens representing both species purportedly collected at "Santa Rosa" near Comitán, Chiapas, Mexico. As we have noted previously, this series of four specimens actually represents three species (*A. ochoterenai*, *A. lythrochila*, and *A. leurolepis*), and the collection containing these specimens was assembled by a collector who visited many sites in the region (Berlioz, 1939), some

of which were in pine-oak forest and others in cloud forest. Smith and Alvarez del Toro (1963) made a distinction between the habitat of *A. ochoterenai* and *A. lythrochila*, with the former presumably inhabiting humid cloud forest and the latter definitely occurring in drier pine-oak forest. The habitat of *Abronia leurolepis* we suspect is cloud forest; our reasons for this conjecture are summarized under the "Comment" in the *A. leurolepis* account. Subsequent investigations in the

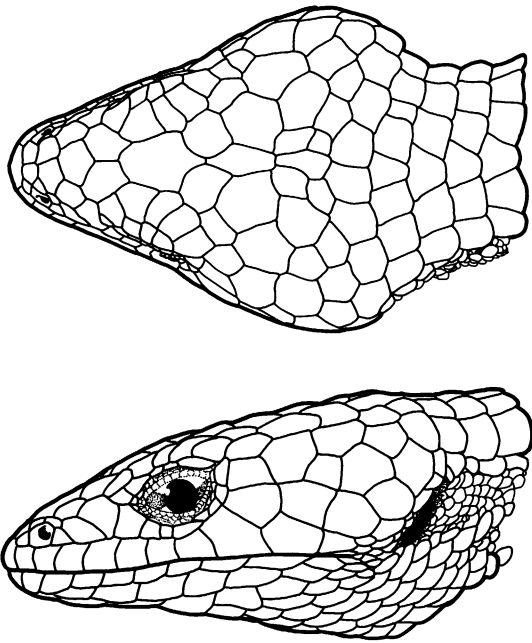


Fig. 24. *Abronia montecristoi*, dorsal and lateral aspects of head of male holotype (KU 184046), head length 22.3 mm.

highlands of Chiapas have failed to reveal the presence of two species of *Abronia* at any single site.

Although both *Abronia reidi* and *A. chisz-*

ari occur in the Sierra de los Tuxtlas region, Veracruz, Mexico, Smith and Smith (1981: 55) stated that "It does appear . . . that even within the Sierra de Tuxtla there is a segregation of *Abronia* species." *Abronia reidi* is known only from the crater rim of Volcán San Martín in cloud forest at 1637 m (Werler and Shannon, 1961), whereas *A. chiszari* is known only from 2.5 mi [4 km] east of Cuetzalapan in rain forest at 360 m (Smith and Smith, 1981). The type localities of *A. reidi* and *A. chiszari* are about 20 km apart horizontally and 1300 m in elevation vertically, but the new specimen of *A. chiszari* (Flores-Villela and Vogt, 1992), also from the Tuxtlas region extends the vertical distribution of this species upwards to 800 m. Nevertheless, the difference between the habitat types of *A. reidi* and *A. chiszari* suggests that sympatry between these forms is unlikely or very narrow.

The case of *Abronia ornelasi* and *A. bogerti* may illuminate the ecological relationships of *A. reidi* and *A. chiszari*, inasmuch as *A. ornelasi* is the likely sister taxon of *A. reidi* and *A. bogerti* is the likely sister taxon of *A. chiszari*. Campbell (1984: 379) stated "Whether the two species [*A. ornelasi* and *A. bogerti*] are sympatric is unknown, but certainly their ranges closely approach one another." However, *Abronia ornelasi* remains known only from cloud forest in the vicinity

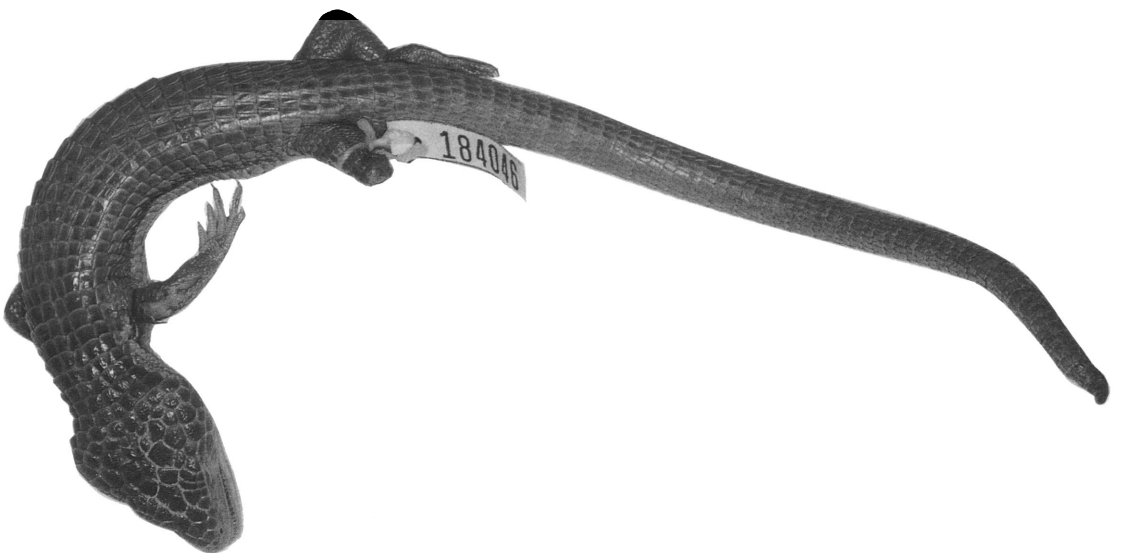


Fig. 25. *Abronia montecristoi*, male holotype (KU 184046), SVL 93 mm, tip of tail regenerated.

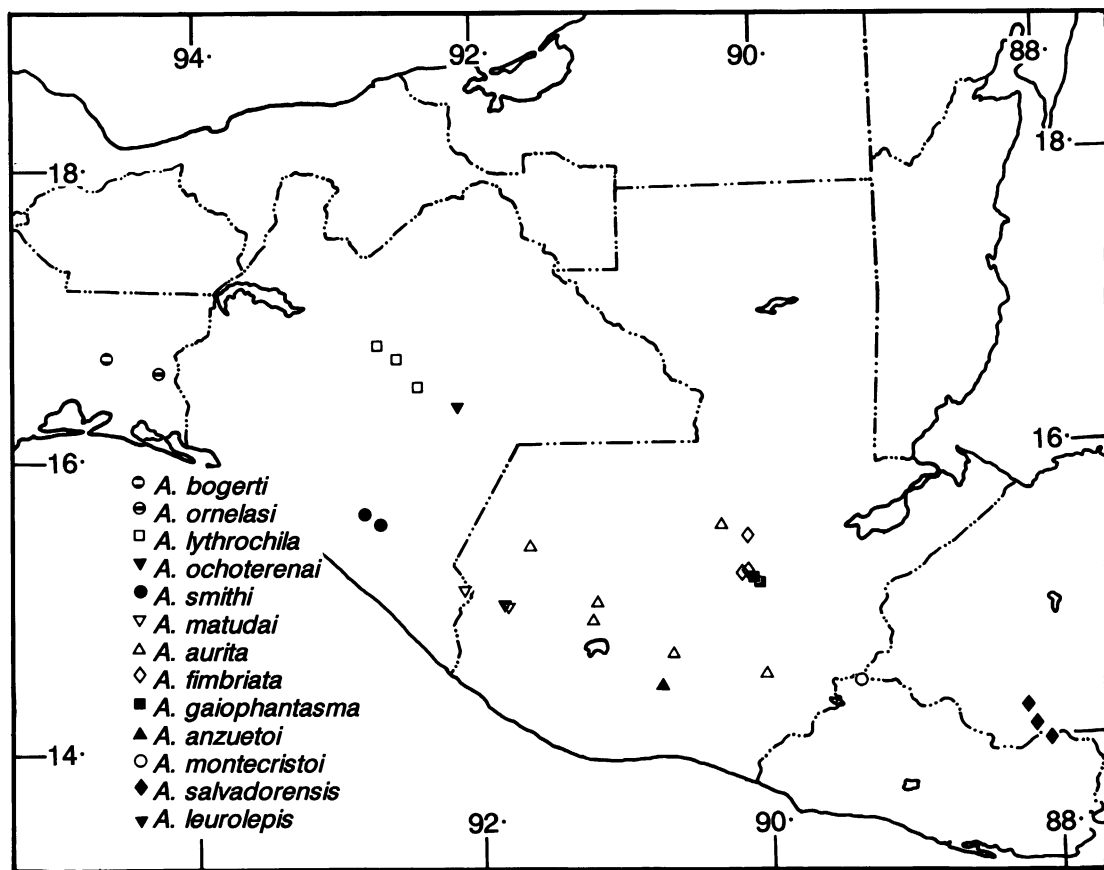


Fig. 26. Distribution of members of the genus *Abronia* occurring in Nuclear Central America. *Abronia ochoterenai* and *A. leurolepis* are known only from the same type locality.

of Cerro Baúl, Oaxaca, Mexico, at elevations of 1500–1600 m. The unique specimen of *A. bogerti* is from the Pacific versant of the same highland region about 35 km away and was reportedly from an elevation between 762 and 1372 m, most likely in rain forest. The apparently ecological distinctiveness of *A. ornelasi* + *A. reidi* (cloud forest) from *A. chiszari* + *A. bogerti* (rain forest) may mean that they are not syntopic anywhere, even though they approach each other closely geographically.

Good and Schwenk (1985: 135), in discussing the distributions of *A. mitchelli* and *A. kalaina* (= *A. fuscolabialis*), stated “While we cannot unequivocally document sympatry because of the difference in elevation of the type localities [2700 versus 2300 m, respectively], the two species occupy similar

habitat on Cerro Pelón.” This statement rests on the assumption that the forest covering the northern escarpment of the Sierra Juárez provides “similar habitat” at these different elevations and they may have underestimated the ecological narrowness of the preferred habitat of either of these species. Along with differences in temperature and humidity, the floral composition and stature of the forest may vary dramatically over relatively short distances in the Sierra Juárez, as discussed by Bogert (1968). Most of the herpetofaunal species inhabiting the higher elevations (> 1200 m) of the Sierra Juárez are restricted to narrow elevational zones, although they may be relatively abundant within these zones. The unique specimen of *Abronia mitchelli* was taken near the crest of Mexican Highway 175 near Cerro Pelón at an elevation of 2700

m where the forest consisted of a few pines and many hardwood trees, mostly oaks, of short and somewhat gnarled stature, presumably owing to the effects of strong prevailing winds. The holotype of *A. kalaina* (= *A. fuscolabialis*) was taken lower (2300 m) in the cloud forest 16.6 km (by road) north of the summit of Mex. Hwy. 175. We are familiar with this site, which is considerably wetter than the *A. mitchelli* locality and which is dominated by huge hardwood trees of many species and tree ferns. Other specimens of *A. fuscolabialis* (UTA R-9899, R-14147) were taken in very similar habitat in the Sierra Mixe at 2158 m and 2438 m, respectively. Both of these localities are at lower elevations, and in "lower" habitat types than the type locality of *A. mitchelli*. So, although it remains possible that *A. mitchelli* and *A. fuscolabialis* occur syntopically, it may be that they occur in such narrow ecological zones that they do not occur together.

Stuart (1963: 81) synonymized *A. fimbriata* with *A. aurita* because he thought "it difficult to believe two species of *Abronia* exist sympatrically in Alta Verapaz," Guatemala. Although these two species are valid and do occur in Alta Verapaz, they appear to inhabit different habitats and are not known to be sympatric.

We know of only one unquestionable instance of sympatry in the genus *Abronia*. Both *A. gaiophasma* and *A. fimbriata* coexist microsympatrically in the wet cloud forest of the western portion of the Sierra de las Minas of Guatemala. We have observed multiple specimens of both species in a small tract (~4–5 ha) within the "Biotopo Mario Dary Rivera" Preserve. On one occasion JAC observed an individual of each species in a patch of sunlight on adjacent buttressed roots of the same tree. *Abronia gaiophasma* also occurs farther to the east in the region near Chilascó, which is drier and covered mostly with pine-oak forest; *A. fimbriata* has not been seen in that region. *Abronia fimbriata* ranges to the north in cloud forest in Alta Verapaz, a region where *A. gaiophasma* is unknown.

As a generalization, many species of *Abronia* appear to be restricted to cloud forest (*A. mitchelli*, *A. fuscolabialis*, *A. ornelasi*, *A. reidi*, *A. smithi*, *A. ochoterenai*, *A. leurolepis*, *A.*

matudai, *A. anzuetoi*, *A. fimbriata*, and *A. montecristoi*) or seasonally dry pine-oak forests (*A. deppii*, *A. species* "Guerrero," *A. mixteca*, *A. oaxacae*, *A. lythrochila*, *A. aurita*), whereas other species are more widely distributed and occur in both cloud forest and pine-oak forest (*A. taeniata*, *A. graminea*, *A. gaiophasma*) (table 4). The range of several species extends to high elevations (> 2500 m) into forests dominated by firs (*A. matudai* near San Marcos, Guatemala, and *A. species* "Guerrero" near Puerto del Gallo, Guerrero, Mexico). Two species (*A. chiszari* and *A. bogerti*) occur at relatively low elevations and apparently enter or are restricted to rain forest.

BEHAVIOR

Members of the genus *Abronia* are generally arboreal and many species apparently live most of their lives among epiphytes. We have taken *A. gaiophasma*, *A. aurita*, and *A. mixteca* from large tank bromeliads and "Spanish moss" growing on oak trees. *Abronia taeniata* has been found in bromeliads growing on pines (Martin, 1955b). *Abronia smithi* (referred to as *A. ochoterenai*) hides in bromeliads or tree holes (Alvarez del Toro, 1960, 1973). Near Acultzingo, Smith (1941) "secured many [*A. graminea*] in . . . bromeliads, where they were hibernating, half covered with ice-cold water." In the same region Smith (1941) reported seeing "these lizards sunning themselves on the outer branches of low, bushy trees." The holotype and paratype of *A. reidi* were discovered "under thick layers of moss growing on the trunks of stunted trees . . . at a height of twelve to fifteen feet above the ground" (Werler and Shannon, 1961). Smith and Alvarez del Toro (1963) reported that *A. lythrochila* lives in the largest trees and suggested that this species may climb to heights in excess of 40 m; they reported a specimen as falling from limbs at this height.

We have encountered *A. mixteca*, *A. gaiophasma*, *A. fimbriata*, and *A. lythrochila* on tree trunks 1–4 m from the ground. Most of these specimens were on hardwood trees; however, an *A. lythrochila* (UTA R-3354) was on a large pine. An *Abronia* species "Guerrero" (reported as *A. deppii*) from near Om-

ilteme, Guerrero, was found on a tree trunk (Davis and Dixon, 1961).

Members of this genus are predominantly arboreal. Nevertheless, because of the non-arboreal habits of *Homo sapiens* it is fortunate that specimens of *Abronia* do descend to the ground. Sumichrast (1882) reported that *A. graminea* lives beneath rotten logs and loose bark. JAC encountered a juvenile *A. fuscolabialis* (UTA R-14147) beneath a large rock in a cleared area. JAC observed *A. ornelasi*, *A. mixteca*, *A. lythrochila*, *A. fimbriata*, and *A. gaiophasma* in leaf litter in primary forest. Bogert and Porter (1967) reported an individual of *A. oaxacae* on the ground in a moist ravine in association with recently felled trees; a juvenile *A. oaxacae* was also reported by these authors as discovered in a bromeliad growing in an oak. Only one of a series of 11 specimens of *A. taeniata* was found on a tree (Martin, 1955b).

In our experience lizards of the genus *Abronia* are strictly diurnal. Alvarez del Toro (1973, 1982) stated that *A. lythrochila* does not become active until the sun has warmed its tree. *Abronia smithi* (given as *A. ochoterrenai*) is found most often near natural breaks or artificial clearings in the cloud forest, and it is active only during the relatively infrequent sunny, warm days in the region (Alvarez del Toro, 1973). *Abronia lythrochila* occasionally comes down from trees to the ground, but when threatened escapes by rapidly ascending a tree trunk (Alvarez del Toro, 1960).

One of the most remarkable field observations of *Abronia* was relayed to us by the late Mario Dary Rivera, Rector of the Universidad de San Carlos, Guatemala, who observed a specimen of *A. fimbriata* (UTA R-6495) swimming in a small pool of a cascading mountain stream flowing in cloud forest. This lizard made no attempt to leave the water and repeatedly dived to the bottom to a depth of about 40 cm. This specimen subsequently was found to be a gravid female.

A notable aspect of *Abronia* behavior is relative tameness. Of the 10 species we have observed in life, nine of these usually become docile shortly after capture and feed readily on orthopterans offered to them by hand. Only one species, currently undescribed (Brodie and Savage, 1993) is known to be consistently

aggressive. Gadow (1905) remarked that specimens of *A. graminea* "lose their shyness in a few hours after having been caught and handled." Alvarez del Toro (1960) stated that *A. lythrochila* (given as *A. ochoterrenai*) is not wary.

Formanowicz et al. (1990) examined intraspecific interaction in *A. vasconcelosii* (= *A. aurita*) under laboratory conditions. Males were more aggressive toward other males than they were to females. When male aggression escalated to biting, the majority of the attacks were directed at the proximal portion of the tail, injuries in this region possibly resulting in decreased mating opportunities. Females were less aggressive to other females than to males and, when it occurred, it was more frequently directed at the head or trunk. Also, because the tail of *Abronia* is prehensile, its loss may severely impair mobility and security in an arboreal habitat. Regenerated tails are shorter and "less effective" (Martin, 1955b).

Behavior patterns have not been studied in other species of *Abronia*, and may vary significantly from those of *A. aurita*. Martin (1955b) reported that two adult male *A. taeniata* were encountered by Charles F. Walker near Rancho del Cielo, Tamaulipas, "lying quietly along a forest path" with their jaws interlocked.

REPRODUCTION AND YOUNG

All species of *Abronia* for which reproductive data are available bear live young. Werler (1951) reported four young born to a specimen of *A. graminea* on 12 April. Martin (1955b) reported *A. taeniata* also had four young. Smith and Williams (1963) reported that a specimen of *A. oaxacae*, presumably held captive for an extended period, gave birth to a single young in May 1960 and again in May 1961. An *Abronia* species "Guerrero" (UTA R-5653) collected in August, from the highlands of Guerrero, gave birth to two young (UTA R-5553, 5654) 30 mm SVL on 31 December. *Abronia smithi* (reported as *A. ochoterrenai*) produces three or four young (Alvarez del Toro, 1973). An *A. fimbriata* (UTA R-6495) gave birth on about 15 June to four young (two of which are UTA R-6647-48) having SVL's of 33 mm. *Abronia lyth-*

TABLE 4
Vegetational Associations and Elevations Inhabited by Members of the Genus *Abronia*

<i>Abronia</i> Species	Vegetation	Elevation
<i>anzuetoi</i>	cloud forest (this paper)	1219–2286 m (this paper)
<i>aurita</i>	pine-oak forest (this paper)	2000–2660 m (Bocourt, 1871; this paper)
<i>bogerti</i>	rainforest or lower cloud forest, by inference	Probably between 762 and 1372 m (2500 and 4500 ft) (Tihen, 1954)
<i>chiszari</i>	rainforest ^a (Smith and Smith, 1981)	360–800 m (Smith and Smith, 1981; Flores-Villela and Vogt, 1992)
<i>deppii</i>	ash-oak or pine-oak forest with epiphytes (Sanchez-Herrera and López-Formont, 1980; Castro Franco, 1987; Flores-Villela and Hernández-García, 1989)	2000–2600, by inference (Sánchez-Herrera and López-Formont, 1980; Castro Franco, 1987)
<i>finbriata</i>	cloud forest (this paper)	1400–2100 m (this paper)
<i>fuscolabialis</i>	cloud forest (Good and Schwenk, 1985; this paper)	2158–2438 m (Good and Schwenk, 1985; this paper)
<i>gaiophantasma</i>	cloud forest and pine-oak forest (this paper)	1600 to about 2000 m (this paper)
<i>graminea</i>	pine-oak and cloud forest (Sumichrast, 1873; Gadown, 1905; Smith, 1941; by inference ^b)	2000–2743 m (Gadow, 1905; Smith, 1941; by inference)
<i>leurolepis</i>	cloud forest (Smith and Alvarez del Toro, 1963; by inference)	Probably between 1800–2300 m (Casas-Andreu and Smith, “1990” [1991])
<i>lythrochila</i>	pine-oak forest (Alvarez del Toro, 1973, 1982; Smith and Alvarez del Toro, 1963)	2000–3000 m (Alvarez del Toro, 1960; Johnson, 1989)
<i>matudai</i>	cloud forest (Alvarez del Toro, 1973, 1982); near boundary of pine-cypress zone (this paper)	1950–2630 m (Hartweg and Tihen, 1946; this paper)
<i>mittchelli</i>	cloud forest (Campbell, 1982)	2750 m (Campbell, 1982)
<i>mixteca</i>	pine-oak forest (Bogert and Porter, 1967)	2134–2400 m (Bogert and Porter, 1967)

TABLE 4—(Continued)

<i>Abronia</i> Species	Vegetation	Elevation
<i>montecristoi</i>	cloud forest (subtropical lower montane wet forest (Hidalgo, 1983)	2250 m (Hidalgo, 1983)
<i>oaxacae</i>	pine-oak forest (Bogert and Porter, 1967; Gehlbach and Collette, 1957)	2100–2743 m (Bogert and Porter, 1967; Gehlbach and Collette, 1957)
<i>ochoterenai</i>	cloud forest (Smith and Alvarez del Toro, 1963; by inference)	Probably between 1800–2300 m (Casas-Andreu and Smith, "1990" [1991])
<i>ornelasi</i>	cloud forest (Campbell, 1984)	1500–1600 m (Campbell, 1984)
<i>reidi</i>	cloud forest (Werler and Shannon, 1961)	1637 m (5370 ft) Werler and Shannon, 1961
<i>salvadorensis</i>	cloud forest (subtropical montane wet forest)	1900–2250 m (Hidalgo, 1983; Wilson et al., 1986)
<i>smithi</i>	cloud forest (Alvarez del Toro, 1983; Johnson, 1989; this paper)	2020–2804 (this paper)
<i>taeniata</i>	humid montane forest (Martin, 1955a); cloud forest and humid pine-oak forest (Martin, 1958); pine-oak, sweetgum, and walnut (Dixon et al., 1972); forêts de pins et de chênes (Sumichrast, 1873)	1000–2000 m (Martin, 1955b, 1958)
species "Guerrero"	pine-oak cloud forest (Davis and Dixon, 1961; Muñoz-Alonso, 1988)	2100–2804 m (Davis and Dixon, 1961; Muñoz-Alonso, 1988; UTA specimens, this paper)

^a Because the holotype of *A. chisari* was taken from the bumper of a car (Smith and Smith, 1981), the possibility that the specimen originated from somewhere other than the type locality cannot be discounted. However, it was unlikely that the provenance of the holotype was from a higher elevation because on the day of capture the car had been driven only from the town of Catemaco to Tebanca and had remained at approximately the same elevation (W. F. Pyburn, personal commun.).

^b Cope (1887) recorded *A. graminea* from 3000 m on Orizaba, an elevation that may be a rough approximation rather than an exact figure.



Fig. 27. Mating pair of *Abronia lythrochila*. Photograph taken 10.3 km ESE of Teopisca, Chiapas, Mexico, at an elevation of 2050 m on 2 August 1976. These specimens had a more-or-less uniformly brown dorsum; this species has a highly variable color pattern (see fig. 11F).

rochila has been reported to give birth to four or five young between June and August, with parturition sometimes extending over several days to several weeks (Alvarez del Toro, 1973, 1982). A female *A. aurita* (UTA R-31041), kept in captivity and well fed, gave birth to 12 young on 26–28 January 1992 (UTA R-31042–53). Smith and Alvarez del Toro (1962) reported that a specimen of *A. lythrochila* (given as *A. ochoterena*) gave birth to a single young on 15 July. JAC observed a mating pair of *A. lythrochila* in nature on 2 August 1976 at a locality 10.3 km ESE Teopisca, Chiapas, Mexico, 2050 m (fig. 27). These specimens were in leaf litter beneath a large epiphyte-laden oak tree. The male was straddled across the back of the female and had the back of her head firmly gripped in his mouth and his tail loosely intertwined with hers. The pair was observed for about

45 minutes, during which time they continued to lie quietly on the ground.

The smallest juvenile *Abronia taeniata* collected by Martin (1955b) was 82 mm SVL. It was collected 1 August which suggests that young in that region may be born during the early rainy season (mid-May to mid-June in that region). In July and August we collected juvenile *A. mixteca* (UTA R-25771–72) having SVL's of 40–42 mm, suggesting that they were born within a few months of capture.

The color pattern of juvenile *Abronia* is variable, but usually consists of a series of dark dorsal crossbands: *A. taeniata* (Martin, 1955b), *A. graminea* (Werler, 1951; P. W. Smith et al., 1952), *Abronia* species "Guerrero," *A. mixteca*, *A. fuscolabialis*, *A. oaxacae* (Smith and Williams, 1963), *A. chiszari* (Smith and Smith, 1981), *A. aurita*, and *A. gaiophasma*. The juvenile pattern con-

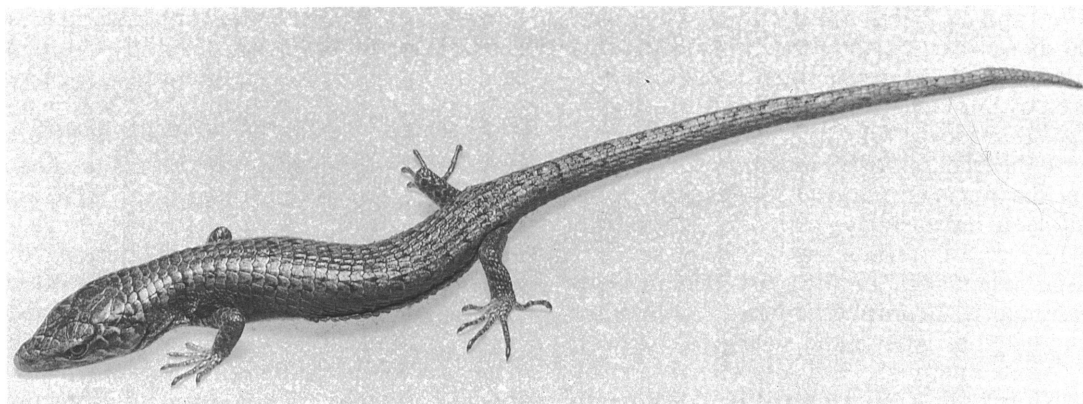


Fig. 28. *Abronia reidi*, juvenile paratype (UIMNH 73732), 41.9 mm SVL, 91.9 mm TL. Crater rim of Volcán San Martín, 1642 m, Veracruz, Mexico. [Photograph courtesy of J. Werler. Previously published by Werler and Shannon (1961)].

sists of middorsally narrowly incomplete weak bands in *A. reidi*⁷ (fig. 28) (Werler and Shannon, 1961; personal obs.), and *A. lythrochila* (Smith and Alvarez del Toro, 1962; Alvarez del Toro, 1973, 1982). *Abronia smithi* (Alvarez del Toro, 1973; personal obs.) and *A.*

fimbriata show a broad middorsal stripe that is paler than the sides of the body (fig. 10F). *Abronia aurita* shows an intermediate condition in which the sides are dark, the broad middorsal stripe being crossed by 8–10 dark bands (fig. 10C).

CONSERVATION BIOLOGY

Although *Abronia* represents more than half of gerrhonotine anguid lizard species diversity (approximately 25 out of 45 species), restricted distributions and habitats disturbed or destroyed by human development have made most species of the genus among the most endangered lizards in the world. Moreover, because cloud forest species tend to be restricted to single or adjacent cloud forests, several undescribed species of *Abronia* likely have already become extinct with the human

destruction of cloud forests on several of the volcanoes of southern Guatemala and adjacent El Salvador. As an example of this habitat destruction, the ranges of *A. mitchelli* (known from a single specimen) and *A. fuscolabialis* (known from only five specimens) in Oaxaca, Mexico, are currently being clear-cut, much of it apparently illegally. This destruction is irreversible and inexorable; there is ample evidence that officials who stand in the way of the cutting of Oaxacan forests are at risk of assassination by logging interests (Katz, 1992).

⁷ Werler and Shannon (1961) said about the dorsal markings of the juvenile paratype: "Although difficult to count, there are perhaps 10 or 11 indistinct dark transverse bands on the body; interrupted middorsally and extending four scale rows on either side of the middorsal line." Actually, each transverse scale row contains a transverse stripe, this stripe becoming with increasing age the dark scale centers of adult *A. reidi*. The median interruption noted by Werler and Shannon is due to the transverse scale rows being offset along the dorsal midline.

Our decision to address the issue of imminent extinction of *Abronia* was not taken lightly. Systematic biologists have been slow learners when it comes to the political realities of "biological conservation," and it has become very clear that the usual consequence of biologists supplying information on endangerment of species is the regulation of biologists (and therefore of information acqui-

sition) and not habitat protection (Hedges and Thomas, 1992; personal obs.). As the world fauna and flora become increasingly endangered by human overpopulation (the primary manifestation of which is habitat degradation), the freedom of biologists to survey rapidly disappearing natural faunas and floras has been increasingly restricted. Regardless of this counterproductive effect of species-based regulation, in the past two decades many species of amphibians and reptiles have been listed by federal and state governments, or, more onerously and less effectively, by the Convention on International Trade in Endangered Species of Flora and Fauna (CITES). Particularly in tropical countries, this regulation has had negligible influence on habitat destruction and, with the exception of a few large and/or photogenic mammals and birds, extirpation of species.

Once species are legally protected, study by biologists usually requires expensive and/or difficult-to-obtain permits. In effect, legislation limits access to regulated animals to those most able to pay (i.e., commercial interests) or to those whose activities indirectly extirpate species (e.g., subsistence woodcutters). For example, at the time of this writing, scientific collecting permits for non-nationals in Mexico are \$1000/permit, clearly far above their administrative overhead cost, and obviously aimed at restricting access of non-Mexican scientists to that rapidly disappearing fauna. There appears to us to be no effective limitation of habitat destruction in that country. The extinction of the frog *Rana tlaloci* (O. Flores-Villela, personal commun.) within 10 years of its discovery (Hillis and Frost, 1985), due entirely to the effects of urbanization of central Mexico, is an example of this regulatory asymmetry. That is, it would have cost a non-Mexican biologist \$1000 to legally collect a single specimen of *Rana tlaloci* from the canals of Xochimilco, even as the unregulated effects of urbanization were driving this species of frog extinct. Although we note regulatory conditions in Mexico, where many *Abronia* occur, regulatory conditions in other countries (including the United States⁸) and internation-

ally are frequently the same or worse, so these are widespread problems. With respect to international regulation, in recent years we have witnessed the CITES listing of dendrobatid frogs on the basis of no evidence of endangerment whatsoever (C. W. Myers, personal commun.; see also Mrosovsky, 1988, and Bringsøe, 1992), as well as the U.S. delegation to the 1987 CITES convention vote against the delisting of an Australian mammal, even though there was no evidence of trade in the species, Australia initiated the proposal for delisting, and Australian laws were considered adequate for its protection (DRF, personal obs.). In other instances, conservation legislation such as CITES listing or the Endangered Species Act appears to be largely irreversible and in some instances continues to protect some species for which a secure future has been won (Enderson, 1992), thus wasting valuable funding and effort that might be allotted to those species and habitats in critical need of protection.

At a more local administrative level, U.S. state wildlife agencies often deny biologists access to "endangered" species (e.g., *Batrachoseps wrighti* in old-growth forests in Oregon) while other regulatory agencies may be promoting destructive development or logging in the same areas, although this development causes many deaths of these protected organisms. The state of California protects the sand dune-restricted lizard species *Uma inornata*, but allows access of all-terrain vehicles in their habitat with murderous results⁹ (Brattstrom and Bondello, 1983; Brattstrom, 1988). It is obvious to us, and many others (Hedges and Thomas, 1992; Gans, 1992), that the only viable approach to maintaining self-renewing natural populations of many organisms, including *Abronia*, is to protect blocks of natural environments, not individual organisms or particular species, the regulatory approach often taken by state and federal governments, and fre-

impossible for Mexican nationals (as well as other non-U.S. citizens) to pursue collecting-based research in the United States.

⁹ Indeed, the state of California has opened state parks to off-road vehicles, providing that they remain on pre-existing trails, a restriction of dubious practical value.

⁸ The plethora of overlapping U.S. state and federal wildlife laws, as well as visa policies, make it effectively

quently promoted by conservation organizations.

Further, if individual populations are to be protected adequately, they must be discovered and recognized while still viable. Ingram (1991) reported that a single specimen of the Australian gastric-brooding frog (*Rheobatrachus silus*) was collected possibly as early as 1915, yet this species was not described until 1973. Now thought to be extinct, *Rheobatrachus silus* and its habitat might have received sufficient protection to ensure its survival had it been described 57 years earlier. This observation, plus the fact that even some of the most thoroughly explored parts of the earth (e.g., California) still hold undiscovered vertebrates (Greene and Losos, 1988), suggests to us the need for expanded, rather than restricted, scientific collecting on a global basis.

What the counterproductive aspect of wildlife regulation demonstrates, of course, is that biologists, besides being the smallest among those groups interested in wildlife issues, are the least vocal and politically weakest group among logging, construction, and recreational interests, the leather industry, and animal importers and exporters. All of these other interests can afford legal aid (e.g., Pet Industry Joint Advisory Council) against disorganized, underinformed, and heavily bureaucratized international (e.g., CITES), federal (e.g., U.S. Fish and Wildlife Service [USFWS]), and state agencies. The result is that scientists, the segment of the "consuming" public that is the smallest and the least punitive to natural populations and one of the most important for rational habitat regulation, are also the most regulated. As an example of the resources of commercial compared with research interests, recently, in response to USFWS discussion of increased regulation of bird importation, the Pet Industry Joint Advisory Council was able to make a direct mailing to 1,000,000 households (Anon., 1992). This kind of effort is beyond the capability of any research organization.

Currently, the *documented* (Busack, 1974; W. King in Dodd, 1986; Bräutigam, 1991; Fitzgerald et al., 1991) commercial trade in amphibians and reptiles and their products is responsible for more than five times as much collecting *per year* than scientific col-

lecting has accomplished in total for its *entire* history (data from Wake et al., 1975, plus estimates of non-U.S. collection holdings). This translates to scientific collecting being responsible for less than 1% of the annual regulated take of amphibians and reptiles. Further, the undocumented effects of human overpopulation and urban development are surely directly responsible for several orders of magnitude more deaths of amphibians and reptiles per year than either commercial or scientific collecting. Given that annual takes of amphibians and reptiles for commercial purposes are multiples of the number of specimens ever deposited in scientific collections, one must wonder if regulation of scientific collection is worth the administrative effort, particularly because few biologists have any interest in commercially valuable or truly endangered species. Nevertheless, if the failure of the United Nations Conference on Environment and Development (UNCED, Rio de Janeiro) to distinguish between scientific and commercial activities is any indication (Barton, 1992), we likely can look forward to the continuation of biodiversity research (i.e., systematics) being restricted by misguided "biodiversity" regulations. Although we agree that governments and international treaty organizations have the right to regulate scientific collecting, it does seem that a more rational and expedient means could be found to insure the protection of species that are truly endangered rather than the unworkable and detrimental arrangement now in place.

Regardless of our hopes, we expect that our comments presented here will have no effect on reducing habitat destruction where *Abronia* occur. We expect that we will live to see *A. mitchelli*, *A. fuscolabialis*, *A. fimbriata*, *A. anzueto*, *A. ornelasi*, *A. reidi*, *A. matudai*, *A. smithi*, *A. ochoterenai*, *A. leurolepis*, *A. montecristoi*, *A. bogerti*, and *A. chiszari* extinct, or found only in such small tracts as to be biologically nonviable. *Abronia montecristoi* may already be extinct inasmuch as its only known locality is one of the best known in Central America and no additional specimen has been collected in over 30 years.¹⁰ Species

¹⁰ The conclusion that this one specimen was the "last of its species," killed off by a scientific collector, would be almost certainly incorrect. El Salvador is well-known

inhabiting pine-oak woodlands (*A. aurita*, *A. lythrochila*, *A. deppii*, *A. species* "Guerrero," *A. gaiophantasma*, *A. graminea*, *A. mixteca*, *A. oaxacae*, and *A. taeniata*) may survive somewhat longer because of their more extensive habitats, even though this habitat is generally more accessible to humans. Nevertheless, we doubt seriously if any of these species (representing half of gerrhonotine anguid diversity) will survive the 21st century, with little possibility of any additional understanding of these animals because of legal restrictions that are part and parcel of these species' destruction. We also expect that our comments here will have the undesirable effect of making it more difficult to obtain collecting permits and export licenses from the pertinent countries, with no effective improvement of habitat conservation. After all, permit officials are human, and they do not

enjoy being told that their policies and actions are counterproductive.

In short, most species of *Abronia* have already had their habitats severely disturbed and many species face extinction in our lifetimes. Our messages are: (1) protect their remaining habitats; (2) if this cannot be done effectively, let anyone have access to these organisms without permit—at least herpetoculturists will keep some of them going into the next century and they will be available for their nontrivial aesthetic value. If the effect of our statements is to make others press for legal restrictions in the taking of these animals, without serious protection of their habitats, then we can only lament that these people will have failed what is, in effect, a conservation biology IQ test. They will have put a new roof on a burning house.

A PHYLOGENETIC ANALYSIS OF *ABRONIA*

Good (1988) presented a discussion of external characteristics and a phylogenetic scenario for *Abronia* within a larger study of gerrhonotine anguid lizards. However, in that study a priori and a posteriori reasoning in the formulation of transformation series were confounded, and unpolarized and unordered (= nonadditive) transformations were treated as if the same. Also, Good appears to have posited transformational pattern based upon a posteriori notions of likelihood (e.g., see the "a priori" hypotheses of secondary miniaturization in his Character Transformation 91 and "secondary" loss of scale keeling in his Character Transformation 73) or possibly on unwarranted notions of process (e.g., assuming that paedomorphosis is common and/or recognizable without a covering phylogenetic hypothesis). Beyond our disagreement with a number of his hypotheses of transformation, we disagree with several of his observations, we have found that some of his terminal taxa (e.g., his *A. aurita* and *A. vasconcelosii*) were based, at least in part, on

misidentified specimens, and we have added taxa that he did not have (see above).

We originally wanted to integrate the osteological information published for *Abronia* by Gauthier (1982) and Good (1987) in order to include all previously published evidence in our phylogenetic analysis. However, because of unavailability of specimens, the species sampled by those authors for osteological study of *Abronia* were limited to *A. species* "Guerrero" (as *A. deppii*), *A. taeniata*, *A. mixteca*, and *A. oaxacae*. On the basis of external morphological data (see Good, 1988, and Results), this represents a subsidiary monophyletic group patristically removed from the "base" of the *Abronia* cladogram. Therefore, that selection of species of *Abronia* cannot provide compelling evidence for the monophyly of *Abronia*.¹¹ Analysis of osteo-

¹¹ The small number of species of gerrhonotines that Good (1987) had available for osteological study (4 of the 19 species of *Abronia* recognized in his paper, all of them in the phenotypically compact *A. deppii* group; 3 of 7 *Elgaria*; 0 of 1 *Coloptychon*; 1 of 2 *Gerrhonotus*; and 4 of 5 *Mesaspis*) makes several of his generic diagnoses arguable. Moreover, the same a posteriori approach to character analysis that marked his analysis of squamation (Good, 1988) is evidenced in the osteolog-

for its leadership in habitat destruction in Central America, an ongoing process well advanced in the region of the Hacienda Monte Cristo.

logical data across a larger selection of species will have to wait for increased availability of specimens, or, barring that eventuality, application of nondestructive imaging techniques (e.g., CT scans).

MONOPHYLY OF *ABRONIA*

Although the weight of evidence suggests that *Abronia* is monophyletic, when examined critically, this evidence is not extensive. As noted above, none of the suggested osteological synapomorphies of *Abronia* (Gauthier, 1982; Good, 1987) can be placed with confidence at that level of universality, because they may be synapomorphies of the

ical work, both in the formulation of transformation series, and in the noninclusion of unpolarized transformations. For examples, see the "a priori" arrangement of the first two transformations in his 1987 paper: (1) premaxillary bridge extends laterally from nasal process of the premaxilla to isolate the medial ethmoidal foramen from the naris (*Gerrhonotus liocephalus*, *Barisia imbricata*, *Mesaspis gadovii*, *M. monticola*, *M. moreleti*, and *M. viridiflava*); (2) premaxillary spur extends between the medial ethmoidal foramen and the naris, but does not isolate the premaxilla from the naris (*Abronia deppii*, *A. mixteca*, *A. oaxacae*, and *A. taeniata*). The presence of a lateral spur on the premaxilla in his Character Transformation #1 and Character Transformation #2 are a priori treated as nonhomologs, based only on their degree of development, that is, whether they isolate the naris or not. We suggest that it is more parsimonious to assume that outgrowths from the premaxilla in the same place, but merely of different length, are homologs at some level of universality. Therefore, we would have coded this as lateral spur absent $\rightarrow$ (spur present; isolates naris $\rightarrow$ spur present; does not isolate naris). Because Good (1987: 288) stated that the premaxillary bridge in *Mesaspis* is similar to that of *Abronia* in its narrowness, it may be that he missed a synapomorphy uniting these genera. In practical effect, the osteological characters hypothesized by Good (1987, 1988) to be synapomorphies of the gerrhonotine genera are arguably apomorphies of the *Abronia deppii* group rather than *Abronia*, *Barisia imbricata* rather than *Barisia*, and *Gerrhonotus liocephalus* rather than *Gerrhonotus* (or possibly even *Gerrhonotus* + *Coloptychon*). The evidence supporting several hypotheses of generic interrelationships are also questionable for this reason. Nevertheless, in the subsequent squamation study, Good (1988: 35) did not supply a phylogenetic analysis based on external morphology for the entire Gerrhonotinae. Instead he assumed monophyly of the genera based on the earlier (1987) limited osteological data, and upon an intergeneric analysis of squamation that was never presented explicitly.

subset of *Abronia* available to these authors. Additionally, some features, like reduction of body osteoderms and expanded interpterygoid vacuity can be rejected as synapomorphies on the basis of radiographic examination of species that these authors did not see. For example, *A. salvadorensis* (which was not discovered until after Gauthier's work) has well-developed osteoderms. Good (1988: 87–88) did suggest a number of external features in support of the hypothesis of monophyly of *Abronia*: (1) loss of the fifth temporal row of cephalic scales; (2) reduction of the number of transverse dorsal scale rows to fewer than 40; (3) reduction from eight to six or fewer nuchal scale rows; (4) loss of the lateral fold between the ear and the forelimbs; (5) long, well-clawed limbs; (6) a widened and depressed head; (7) and *usually* [italics ours] a characteristic dorsal banding pattern, at least in juvenile specimens.

Loss of the fifth temporal scale row (#1), reduction of the depth of the lateral fold between the ear and limb (#4), and the "long, well-clawed limbs" (#5) appear to be synapomorphies of *Abronia*, although one of the four known specimens of *A. salvadorensis* (KU 195560) has a partial fifth row of temporals on one side, perhaps anomalously. The number of transverse dorsal (#2) and nuchal (#3) scale rows, however, are likely manifestations of a single transformation and cannot be taken a priori as synapomorphies. Because evidence for the monophyly of a group cannot rest on a priori notions of phylogenetic structure within that group, but must rest on a broader evaluation of taxa, putative synapomorphies of *Abronia* must be unique within the Gerrhonotinae, or at least with reference to the first two outgroups, *Mesaspis* and *Barisia*. Dorsal and nuchal counts do not meet this criterion; the number of transverse dorsal scale rows (#2) is known to exceed 40 in *A. chiszari* (47 in UNAM-LT 3151) and probably does also in *A. bogerti* (39 in the unique holotype; 39 and 40 in photographs of two other specimens of unnamed species in the *A. bogerti* group; see figure 12D for one of these), thus placing this character within the range of variation of most other gerrhonotines. *Abronia bogerti* and *A. chiszari* (Good, 1988: 28), as well as the undescribed species in this group, also have eight longitudinal

nuchal rows, rendering without force the a priori consideration that six or fewer nuchal scale rows is a synapomorphy for *Abronia*. The widened and depressed head (#6) also must be rejected as an a priori synapomorphy because of interspecific variation. It cannot be considered a synapomorphy of *Abronia* even a posteriori, because those species paritistically most basal by Good's reckoning (*A. ornelasi*, *A. reidi*, and *A. mitchelli*) either have heads as narrow or narrower than those in *Mesaspis*, or the specimens available for observation are inappropriate for comparison. That is, this feature is best developed in adult males and the only available specimens are subadults or females. The widening and flattening of the head in many *Abronia* is likely the transformation for which several of the characters of cranial osteology (Gauthier, 1982; Good, 1987) are dependent. Lastly, citation of the "characteristic" dorsal banding pattern of *Abronia* (#7), suggested by Good, appears to us to be mistaken because interspecific variation in dorsal color pattern (see below) is as wide as variation across the entire Gerrhonotinae. Further, *Abronia mitchelli*, *A. ornelasi*, and *A. reidi*, the species considered most primitive by Good (1988), are either patternless (*A. mitchelli*) or have a juvenile pattern of one transverse band/transverse scale row (fig. 28) turning into a pattern of one dark spot/dorsal scale in the adults (*A. ornelasi* and *A. reidi*) (figs. 12B, 56). Therefore, the "characteristic" banding pattern suggested by Good (1988) to be synapomorphic for the genus cannot be considered so, either a priori or a posteriori.

METHODS AND MATERIALS

The general approach used herein to attempt to recover the evolutionary history of *Abronia* is a parsimony analysis (Kluge and Farris, 1969; Farris, 1983; Farris and Kluge, 1985, 1986), with the corollary that the weight of all available evidence must be followed (Miyamoto, 1985; Kluge, 1989). We have employed outgroup comparison as the most general means of deciding the polarity of character transformations (e.g., Kluge and Farris, 1969; Stevens, 1980; Arnold, 1981; Farris, 1982; Kluge, 1985; Kluge and Strauss, 1985; Mabee, 1989), although justification

for at least one of our additive multicharacter transformations is implicitly ontogenetic. Because at least two outgroups are required for recovering the evidence supporting the basal stem of any ingroup (Maddison et al., 1984), we have followed Good (1987, 1988) in accepting *Mesaspis* and *Barisia*, respectively, as the first and second taxonomic outgroups of *Abronia*. Although we have reservations about the gerrhonotine revisions by Good (1987, 1988) on methodological and observational grounds, it does seem clear that this outgroup structure is the most parsimonious for the available data, at least as currently understood.

The transformation series have been arranged (see below) into data matrices that were analyzed using the PAUP (Phylogenetic Analysis Using Parsimony, version 3.0s) program of Swofford (1991a). Because the number of terminal taxa is too large to permit exact methods (e.g., evaluating all trees or employing the branch-and-bound method of Hendy and Penny, 1982), only heuristic methods were used to analyze the data. We reject bootstrapping (Felsenstein, 1985, 1988) as an objective means of evaluating confidence in support for clades because use of bootstrapping within historically interconnected groups clearly violates a number of the underlying assumptions of the technique (Sanderson, 1989; Carpenter, 1992; Kluge and Wolf, 1993) and, moreover, it is sensitive to the amount of data supporting clades even when these data are not incongruent with other evidence (Sanderson and Donoghue, 1989; Carpenter, 1992). That is, if a stem is supported by fewer than three characters, even when these are not incongruent with other lines of evidence, that stem will be rejected as not significantly supported. Additionally, bootstrapping is sensitive to character optimization choices. A stem supported under accelerated transformation optimization (ACCTRAN) by many features might be considered to be statistically significant, but the same stem under delayed transformation optimization (DELTRAN) might be rejected. Further, unless we are willing to make a number of unwarranted process assumptions and also knowingly violate assumptions of historical connections (although this must be done to some degree to treat taxa and homo-

logs as sets), we must be satisfied with progress in systematics being derived from a form of argumentation much closer to dialectics than the discovery methods (e.g., parametric statistics) used in other fields of evolutionary biology.

In this study the hypothesized character transformations fall into three categories: (1) polarized and additive—ancestral condition and transformational pathway hypothesized; (2) unpolarized and additive—ancestral condition not hypothesized but relative transformational pathway between two or more characters hypothesized; (3) nonadditive—ancestral condition hypothesized but relative transformational pathway not. Although stems with a *maximum* length of zero under all character optimization schemes can be collapsed as an option within the PAUP program, trees that include stems of a *minimum* length of zero (that is, these stems have a length of zero under at least one character optimization, but not others) are still included in our counts of trees. This means that tree counts may include topologies that are dependent on a particular character optimization method. Because of the number of trees to be evaluated, we have made no attempt to apprehend these artifactually resolved cladograms.

MULTICHARACTER TRANSFORMATIONS: Not counting the coding necessities of dealing with intraspecifically variable characters (see below), we have employed four multicharacter transformations, two of these considered as nonadditive sets (i.e., #14 and 24). Like unpolarized transformations, nonadditive transformations must be included in the character analysis because the objective of any analysis, beyond recovering historical patterns, is to summarize observations in the most parsimonious fashion. Both additive but unpolarized and nonadditive transformations have substantial roles to play in the development of the most parsimonious unrooted tree of terminal taxa, because all character matches (hypotheses of homology) must count in any kind of overall solution. Two of the multicharacter transformations that we employed (#14, number of occipital scales, and #24, condition of lateral neck scales) cannot be posited as additive on grounds of ontogeny or adjacency and/or intermediacy.

Two others (#16, supra-auricular scale condition, and #23, number of nuchal scale rows) can be defended as additive either on the basis of ontogeny and intermediacy (#16) or intermediacy and within-species variation (#23). Appreciating the effects of assuming multicharacter transformations is not as simple as comparing the results of an “all unordered” program option with the results derived from analyzing ordered multicharacter transformations, as was suggested by Hauser and Presch (1991), because not all multicharacter transformation series are legitimately reduced to single sets of particulate character matches. For instance, if the transformation, (0) no antlers → (1) small antlers → (2) large antlers, is considered nonadditive, the implicit tree-building hypothesis, (0) antlers absent → (1) antlers present, is lost, simply because the worker who wanted to reduce the “assumptions” built into someone else’s data matrix made an unforeseen mistake. Nevertheless, the only justifications that we accept for multicharacter transformations are intermediacy ($\approx$ adjacency—Pogue and Mickevich, 1990) and ontogeny, even though empirical evidence is growing that they can yield erroneous conclusions (Mabee, 1989; Wheeler, 1990; but see Kraus, 1988), or, at least, conclusions not congruent with those based on outgroup comparisons of binary transformations. Morphological intermediacy as a justification of a priori multicharacter transformations may merely be the assumption of orthogenesis in another guise, rather than an implicit assumption of ontogeny, and, therefore, we think that additive multicharacter transformations should be used cautiously. We have, therefore, comparatively treated character transformations #16 and #23 as: (1) additive multicharacter transformations; (2) “simplified” transformations in which the 1 and 2 conditions have been combined. Partially additive sets (i.e., $0 \rightarrow [1 \leftrightarrow 2]$),¹² which would allow the apo-

¹² This is accomplished by having one transformation for presence/absence, which is polarized, and one non-additive character set for “condition of presence,” in which cells for taxa that do not have “presence,” as well as the ancestral line, are coded as “unknown.” This coding prevents the appearance of “presence” being weighted twice by the addition of a transformation from absence to a condition of presence in the second column.

morphic characters (i.e., 1's and 2's) to be polarized by congruence with other transformations, without dispensing with legitimate character matches, would have been appropriate in two of our analytical approaches (the "baseline" and "any instance" approaches). However, in two others (the "unscaled" and "scaled" analyses, explained below) attempting this resulted in daunting coding problems and for this reason this "partial additivity" approach has been forgone. Nevertheless, the effects of this coding could have affected topologies beyond the "simplified" coding only in the *A. deppii* group because at least Character Transformation 16 has one of its two apomorphic conditions restricted to a single species (*A. matudai*).

It would be inappropriate to treat as non-additive the multicharacter transformations produced by the coding method used for intraspecifically variable characters in the "unscaled" and "scaled" analyses. This would introduce (in fact, it would invent) considerable unwarranted homoplasy (see below for further discussion).

NONFIXED CHARACTERS: Specimens of *Abronia* are rare, but variation in their squamation is not. We have not entered lightly into the treatment of variable characteristics as bearers of phylogenetic signal because of the number of difficult philosophical and practical issues involved. Also, to foreshadow our results, it is clear that the rarity of specimens of *Abronia* makes a study of this taxon to be a marginally appropriate vehicle on which to approach the issue of evidential content of intraspecifically variable characters; sampling errors may overshadow conclusions drawn from this "class" of characters. Nevertheless, the last revisor of this group (Good, 1988) used intraspecifically variable attributes to infer phylogenetic relationships, and claims have been made by others (e.g., Nixon and Wheeler, 1990) about the lack of a legitimate role for intraspecifically variable features in phylogenetic studies. We regard both to be good reasons for serious discussion of this class of attributes. In order to promote this discussion we have tried to discover the evidential limits of intraspecifically variable characteristics. By "intraspecifically variable" we mean only those features that vary within a semapho-

ront-class, not among them. That is, characters that vary ontogenetically or by gender are specifically excluded from our class of characters that we consider "variable." If we did not exclude features such as these, then *all* multicellular features would be considered variable because of ontogeny. We suggest that characters that are not "fixed," such as the condition of mental scale (divided/entire), may provide evidence of history if we assume that organismal characteristics, regardless of frequency, have ancestor-descendant connections. We also suggest that the appearance of "fixation" of an organismal character within a population is a function of sample size, although this opens a methodological and philosophical Pandora's Box into which we are hesitant to peer too deeply.¹³ Although we claim that identification of a character as "fixed" is dependent on sample size, characterization, and semaphoront choice, for the purposes of this analysis we take the practical position that a character is "fixed" if it appears to be "fixed" at one condition within our sample of a terminal taxon and it is "variable" if it is variable among the organisms within our sample of a terminal taxon. In other words, because we regard the distinction between "fixed" and "unfixed" characters to be artificial, we doubt that a satisfying theoretical justification can be found for treating them differently. Nevertheless, there is no doubt that for practical purposes they do fall into separate categories and we think that some attempt must be made to address the question, which most taxonomists have had to deal with at one time or another.

Because the claim has been made (Nixon and Wheeler, 1990; Wheeler and Nixon, 1990) that only intraspecifically "fixed" characters are of interest to systematists,¹⁴ a com-

¹³ We hope to evaluate the results of the analytical technique of Donoghue (1985) and Vrana and Wheeler (1992), in which organisms are treated as terminal taxa, thereby rejecting any a priori notions of supraorganismal entities. However, because we became interested in the philosophical and operational aspects of this approach late in the development of this manuscript, it is not included.

¹⁴ One can define two classes of intraspecifically variable characters: (1) those that were phylogenetically "fixed" in the past and have become subsequently variable though character reversal; (2) those features that

ment is required. The epistemology of cladistic analysis is: (1) taxa are treated methodologically as sets of organisms; (2) apomorphic characters of organisms, judged on the basis of similarity to be homologs, are taken to be set definers; (3) these delimited sets are reconciled to minimize the number of ad hoc explanations required for character origination (that is, the incongruent "synapomorphies" are taken to represent the result of homoplasy and possibly supplying additional information); and (4) this reconciled tree of nested sets is taken to represent the result of evolution; i.e., the nested sets are taken to be taxa. Although we can think of no better method of discovery, when the ontology of taxa is taken into consideration two limitations become clear: (1) taxa do not have characters, organisms do; (2) all characters must vary at least to some degree in time and space among parts of taxa (i.e., organisms), because taxa are really entities rather than classes, although the amplitude of this variability itself varies enormously among attributes.

Methodologically, systematists deal primarily with attributes of organisms that are "fixed" in the semaphoront of interest, not because "fixed" characters are necessarily always more informative, but because they are less difficult to deal with than intraspecifically variable attributes because of coding ambiguities, analytical procedures, and, most importantly, having to discriminate among additional sources of variation (e.g., composite "species," mutation, teratology, semaphoront choice, environmental effects). Nevertheless, the decision to use only "fixed" characters in analysis rests on social pact rather than on theoretical justifications. Fortunately, with respect to alternative explanations for character variability, most species of *Abronia* have such small distributions that mixed samples treated as single terminal taxa are, we hope, not a serious problem. Al-

though only genetically mediated characters (rather than those that are epigenetically or environmentally induced) are relevant to analyses of relationship, the distinction is not always readily clear. In the absence of clear evidence of teratology or environmental effects we have had to assume that all "polymorphic" conditions, including alternative conditions shown in bilateral asymmetry, are phylogenetically meaningful.

The criticism that many characters (both those that are intraspecifically variable as well as many that are "fixed") are really continuously varying attributes reified through the language of description (Stevens, 1991) also cannot be ignored, although if descent with modification is a fact, all individuation of characters must be of imposed distinction, if not "helped along" by extinction providing gaps (which is nothing more than having a technique that improves with increasing ignorance). Further, regardless of the attribute under discussion, deciding how similar conditions among organisms must be to be considered a "match" requires the imposition of discontinuous definitions. This must be true for all features that undergo ontogeny. For this reason, and because almost all of our characters have conditions that are readily recognized, we have not entered into the discussion of treatment of morphometrically continuous variables in phylogenetic analysis (e.g., Archie, 1985; Farris, 1990). The characters that we treat as "variable" are not "polymorphic" in the sense of allozymic alleles, and the reification inherent in treating a continuously varying characteristic, such as the position of a suture between two scales with respect to a third scale, as a particulate character match contains the risk that we are merely injecting noise into our analysis. Nevertheless, the important issue as we see it is not that definitions are imposed on continuously variable features, but whether morphologies are idealized to fit these definitions. It is true that the characters we have addressed that are intrapopulationally (and sometimes intraorganismally) variable have sometimes presented us with characterization difficulties. We have therefore attempted to evaluate the effects of characterization problems, among other causes, on the use of intraspecifically variable characters by means

have never been "fixed," i.e., they have remained variable from ancestral lineages to daughter lineages. Nevertheless, without inferring from a preexisting tree these are indistinguishable. Cladistic analysis can only deal with the operational aspects of intraspecific variability, i.e., whether or not all organisms in a particular sample show a particular feature.

of examining the amount of differential a priori weighting on "fixed" versus "variable" characters it takes to approach a result dependent only on "fixed" characters. Without a "true" tree for comparison, it will be difficult, if not impossible, to distinguish the effects of sample size, although congruence (or lack thereof) with evidence discovered in the future should prove illuminating.

SAMPLING ERROR: Most species of *Abronia* are among the rarest lizards in scientific collections, with eight of the 23 species that we treat known from fewer than five specimens. The result of this is that distinguishing intraspecifically "variable" from "fixed" characters in these animals is not always possible. When a terminal taxon is known only from a unique specimen (e.g., *A. montecristoi*, *A. bogerti*, *A. leurolepis*, and *A. mitchelli*), unless it is intraorganismally variable, any of the features of the animal will be coded as "fixed." Although we think that this is the most serious problem to overcome in our analysis, we restrict discussion of this to Results for the reason that our suspicions of sampling error can only allow us to accept less resolution than the data offer, not more resolved solutions unsupported by evidence.

ANALYTICAL TECHNIQUES USED: As explained above, for better or worse, like Good (1988), we have attempted to deal with the information content of intraspecifically variable characters. Deciding what is an anomaly (an atavism or convergence) and what is homologous, excepting clear cases of damage or teratology, is a priori insoluble. Good dealt with this problem by arbitrarily fixing the threshold for recognizing a feature as informative for it to be present in 10% of his sample, claiming (1988: 5) that placing the threshold below this level "completely swamped the analysis with homoplasies." A threshold has been used by other authors in an attempt to "squench" noise in the phylogenetic signal caused by mutation (particularly in electrophoretic data—Mickevich and Johnson, 1976; Miyamoto, 1981). However, beyond the theoretical problem of deciding what threshold should be selected (an example of Kluge's "slippery slope"), one problem with this approach is that it requires large numbers of specimens/species (a serious problem in *Abronia* where most samples [14

of 19 species recognized in Good's study and 8 of 23 species in our study] consist of fewer than five specimens) to make a claim for this being a legitimate method for partitioning homoplasies from homologies. That is, without sufficient sample sizes one cannot argue whether "rare" conditions are truly rare or whether "common" conditions really are common. And even then, "rarity" in and of itself is not evidence of nonhomology. Regardless, computer-assisted reanalysis of Good's data set does not support his assertion of homoplasy obscuring results; considering a priori all instances of features to be homologs (i.e., setting the threshold for his data not at $\geq 10\%$ as Good did, but at $> 0\%$) had no effect on his results. Because we lack the sample sizes to legitimately partition rare from common conditions and because we lack confidence that this procedure is appropriate for a priori partitioning of homology from analogy, we have avoided the use of thresholds. Similarly, we have also avoided using character frequencies as evidence. Swofford and Berlocher (1987) have argued for the legitimacy of these data, at least in electrophoretic studies, and Crother (1990) has argued against their use. We find the issue of the consideration of frequencies as evidence to warrant continued serious discussion because conceptually this controversy is the same as that surrounding scaling of morphometric data as well as the more fundamental issue of what constitutes evidence in recovering phylogenetic signal. Nevertheless, sample size limitations prevent us from attempting to use these data.

Although we do have preferences, based on philosophical principles, regarding the analysis of intraspecifically variable characters, we have used comparatively five analytical techniques. One of these excludes all character transformations in which one or more of the terminal taxa are variable. Four other techniques, which incorporate intraspecifically variable characters, but differ in underlying assumptions of coding, are compared in an attempt to illuminate the effects of these underlying assumptions on data analysis:

Reference Analysis. "Fixed" Characters Only: As a reference, we analyzed the data, excluding those character transformations

that contained any polymorphic cells in the data matrix (i.e., excluding Character Transformations 1–7, 9–11, 17–19, 23 [1 → 2 only], 26, and 27). This rendered a set of results that can be said to rest on only intraspecifically “fixed” characters. Because we are interested in the effects of a priori multicharacter transformations, we ran a second analysis in which Character Transformation 16 (supra-auricular scale development) was collapsed to a binary transformation (i.e., 0 → 1 → 2 became 0 → [1 or 2]).

Baseline Analysis of All Data: As a baseline study of intraspecifically variable character analysis we analyzed the data matrix, including intraspecific polymorphisms, as allowed in PAUP even though in the PAUP program

‘Polymorphism’ refers only to variability within a [supraspecific] ‘terminal taxon.’ Multistate taxa do not provide a mechanism for dealing with characters that are polymorphic in a population-genetic sense. In particular, there is no provision for polymorphism in hypothetical ancestral taxa (internal nodes). If a taxon is coded as having multiple states, it is assumed that this taxon represents a monophyletic collection of subtaxa, each of which are themselves monomorphic. [Swofford, 1991a: 73–74.]

That is, no provision is made in the analytical algorithm for polymorphism surviving speciation (under any definition of that term). Operationally this means that character variability is not allowed on internal stems of the resultant cladograms. In this analysis “variable” cells are optimized as if they were coded as “unknowns” (within the constraints of the possible characters assigned to a single cell). Therefore, a comparison with the Reference Analysis (#1) will illustrate whether “variable” characters are tending toward congruence with “fixed” characters; differences between Analysis #1 and #2 will be due to the information content of nonpolymorphic cells in the data matrix, even when the column in the matrix (the “character” of other authors) contains polymorphic cells.

“Any Instance” Analysis: As an alternative method of analyzing intraspecifically variable characters, we considered any frequency of the apomorphy in a sample to count as an “instance,” much as was done by Good (1988) in his gerrhonotine analysis (differing only in the frequency threshold used) and Hillis et

al. (1983) in their allozyme analysis of leopard frogs. That is, for any character for any terminal taxon, if an apomorphic condition is present at *any* frequency, the cell in the data matrix for that taxon is coded for that apomorphy only. The drawback of this methodology is that informative character reversal may be rendered invisible, allowing some characters to be “unconnected” in the final cladogram with no cost to parsimony. Because Character Transformations 2, 3, and 19 contain polymorphisms and are also unpolarized it cannot be decided a priori for which direction of transformation the “instance” should be coded. For this reason the technique requires a posteriori optimization of these kinds of transformations. That is, an analysis must be performed first that excludes these features, then the unpolarized polymorphic transformations can be optimized on the resultant tree(s) in order to accelerate transformation to the character determined in the previous analysis to be apomorphic in that region of the topology. In one sense, this is traditional coding for morphological characters inasmuch as most morphological systematists implicitly idealize coded morphologies (i.e., they exclude organismal data that does not fit their global hypotheses of character transformation) in order to reduce the variability with which they must deal.

Unscaled Analysis: Our preferred technique is to code polymorphisms as characters intermediate between the “fixed” characters (a morphological equivalent of the “minimum allele turnover” coding method of Mickevich and Mitter, 1983) (subsequently referred to as the “unscaled analysis”). That is, in the case where we hypothesize 0 → 0/1 → 1, this would be recoded as 0 → 1 → 2. The appearance of one character, at any frequency, is regarded to be one step, and the loss of the plesiomorphic character is also regarded as one step. This particular approach to data analysis is most powerful at maximizing the “connectedness” of hypothesized homologs and, as far as this aspect of character analysis is concerned, is equivalent to traditional “fixed” character analysis. That is, no evolutionary steps are hypothesized that are not observed somewhere and all hypothesized steps are, at least for the first analytical pass through the data, considered to be of

equivalent length (= weight). The disadvantage of this coding is that transformations with inherent characterization problems (intraorganismal variation) are weighted equally (at least initially) with transformations containing characters whose heritability is less suspect.

Although this recoding of nonfixed characters results in a number of additive multicharacter transformations, considering these to be nonadditive is not legitimate because it serves only to create "technical" homoplasy that would have nothing to do with legitimate character transformation. That is, if the transformation $0 \leftrightarrow 0/1 \leftrightarrow 1$ were not considered additive, there would be no parsimony cost to "getting" the appearance of 1's independently in the 0/1 and 1 conditions. In other words, $0/1 \leftarrow 0 \rightarrow 1$, which would derive the condition "1" twice, would be equally parsimonious with $0 \rightarrow 0/1 \rightarrow 1$. We continue in this analysis, and that following, to investigate the effects of "simplified" coding of Character Transformations 16 and 23.

Scaled Analysis: The fourth technique used for coding intraspecifically variable characters, referred to here as the "scaled" approach, is a modification of the "unscaled" approach in which the transformational length from "fixation" to "fixation" in a nonintraspecifically variable character is scaled to the same length as from "fixation" through "variability" to "fixation" in a "variable" character. Although, at one level, the criticism of Mickevich and Farris (1981) and Farris (1990), that this confuses weight with steps can be made, our approach here is somewhat different than scaling all multicharacter transformation series (presumably all containing "fixed" characters) to the same total transformational diameter, as was recommended by Colless (1980) and Chappill (1989). In this case, rather than assuming that the total length of all transformation series must be the same, regardless of the number of steps hypothesized in them, we assume merely that "polymorphism" is evidence of an "incomplete" step. The underlying assumption is that all transformation from one "fixed" condition in a population to another "fixed" condition in the same population requires a transitional polymorphic step, a rea-

sonable assumption if cladograms are taken to be diagrams of recovered history rather than metaphors of character generality. This technique also has the effect of "buffering" the affects of rare (assumed to be convergent) conditions by giving their appearance half the weight of transformations from "fixation" to "fixation." That is, it adds a weighting function in favor of what we have called "fixed" characters (i.e., character transformations in which no polymorphisms are recognized). Nevertheless, this technique suffers from the serious theoretical drawbacks that (1) unobserved steps are hypothesized and (2) the homologous appearance of a feature that persists as a polymorphism among taxa is treated necessarily as if it carries less information than features that are fixed. In other words, the "connectedness" of hypothesized homologs is not maximized by this approach.

For analytical reasons, Character 23 (number of longitudinal nuchal rows) had to be coded in additive binary fashion because the original transformation was $0 \rightarrow 1 \rightarrow 1/2 \rightarrow 2$, in other words, there was no 0/1, making the $0 \rightarrow 1$ interval unsymmetrical with the $1 \rightarrow 2$ interval. Also, like the "unscaled" analysis, attributes with inherent characterization problems may easily overwhelm more easily defined characteristics.

The results of these five techniques are compared in the Results and Discussion.

"Unknown" Matrix Entries: A number of "unknown" conditions were coded into the matrices in all approaches to data analysis. The unknowns are due to: (1) absence of appropriate material, that is, due to specimen damage or lack of appropriate specimens the observation is lacking (e.g., lip color in *Abroonia leurolepis*); or (2) because of the logical necessities of coding, such as coding scale contact in a species in which that scale is lacking (e.g., evaluating frontonasal-frontal contact in *A. leurolepis* and *A. fimbriata*, both of which lack frontonasals). We have tracked these particular problems to avoid conclusions based on absence of data.

DIFFERENTIAL CHARACTER WEIGHTING: The literature of a priori and a posteriori differential character weighting is becoming extensive (e.g., Wheeler, 1986; Neff, 1986; Carpenter, 1988). Nevertheless, it is not our purpose here to compare all of the various

suggested techniques. What we have done is investigate the effects of successive approximations as the currently most popular form of differential weighting, as well as the effect of differential a priori weighting on "fixed" characters over "variable" ones because of controversies about characterization and legitimacy (see above).

Successive character approximation is a method of differential character weighting on the basis of "cladistic reliability" (Farris, 1969; Farris, 1983; Carpenter, 1988; Platnick et al., 1991), a controversial method that *may* pay for increased precision (i.e., reduced numbers of trees under consideration) at the expense of accuracy (i.e., inadvertently rejecting the true tree). Additionally, the measure of character reliability is estimated solely from the ingroup taxa rather than from the universe of occurrences. Because members of a set of homoplasies are united by analogy (definition) and not homology (historical connection), there is no logical reason to restrict evaluation of the frequency of analogous transformation to just the ingroup. This is because we are attempting to make generalizations about historically unconnected members of a class. Therefore, in order to make use of a measure of homoplasy we must assume that the measure of character transformation "reliability" is based on some significant sample of taxa to insure that the ingroup-only measure is not affected by sampling error. Likely of more practical concern (M. Novacek, personal commun.) is the observation that successive approximations may differentially weight transformation series that contain missing data, because missing data decrease the possibility of homoplasy within any particular transformation series. However, missing data pose the same problem for parsimony analysis so it is unclear that this criticism can be restricted to successive approximations (G. Gould, personal commun.). Also, the choice among weighting functions (e.g., bounded or unbounded, mean rescaled consistency index, best rescaled consistency index, worst rescaled consistency index, retention index, or consistency index) is directed by only weak theoretical considerations. We have chosen the maximum rescaled consistency index over the average rescaled consistency index as our weighting

function because it makes the most robust hypothesis of the value of any particular character match. We see no justification for using the smallest value, and using the average is sensitive to the frequency of occurrence of particular topologies, analogous to consensus by majority rule.

Carpenter et al. (1993) have suggested that any data matrix that produces novel trees under successive approximation is inherently suspect in its ability to accurately predict the history of evolution. However, although we find this idea seductive, we question whether this can be taken as a test of data "reliability"; it seems that if one accepts the underlying assumptions of successive approximations, one must follow the method to its conclusion (Platnick et al., 1991), regardless of whether this results in topological changes or not, particularly when topological modification may depend on very little change in relative character weights. In one sense, topological changes that result from this reweighting technique might be taken as evidence that the method of successive approximations has *succeeded* by letting phylogenetic signal emerge from behind homoplastic noise, even though the reweightings applied are derived from "wrong" trees.

The treatment of two nonadditive transformation series (14 and 24) with successive approximations, we realize, may have unforeseen effects. We accept the risk. We also take the risk of discussing subjectively the results of the various analytical techniques described above. That is, what we choose to "believe" will be based on our a posteriori notions of possible errors caused by sample size and characterization problems.

SOURCES OF CHARACTERS STUDIED: We used standard morphological characters as described by Hartweg and Tihen (1946), Tihen (1954), Bogert and Porter (1967), Campbell (1982, 1984), Hidalgo (1983), Good and Schwenk (1985), Good (1988), Casas-Andreu and Smith ("1990" [1991]), and Flores-Villega and Sánchez (MS). We have attempted to arrange the transformations in the same order as discussed by Good (1988) and to use, where appropriate, many of the same character transformations that he employed.

AVAILABLE MATERIAL: We examined representatives of all species (see Appendix 1 for

ingroup material examined). For clarity of comparison between the results of our analyses and those of Good (1988), bear in mind that his specimens of "*Abronia aurita*" were four specimens of *A. gaiophasma*, his "*A. ochoterenai*" were two specimens of *A. smithi*, and his "*A. vasconcelosii*" consisted of one specimen of *A. aurita* (the holotype of *A. vasconcelosii*) and one specimen of *A. anzuetoi*. He never saw specimens of *A. fimbriata* (which was then considered to be a synonym of *A. aurita*) nor did he see specimens of *A. deppii*; his and most previous authors' *A. deppii* is actually a different species currently being described elsewhere (Flores-Villela and Sánchez, ms), herein referred to as *Abronia* species "Guerrero."

TRANSFORMATION SERIES ANALYZED

Numbers in brackets, following our numbers, refer to Good's (1988: 115–129) numbered transformations. Some character transformations that were used by Good are excluded from our analyses, because intraspecific variation approaches or equals interspecific variation, because we did not agree with his observations, or because we thought they represented some transformation that was already recognized by some other character transformation series. Some transformations that we considered *too* variable to use a priori are discussed a posteriori in Results. Additional transformations that were excluded from our analysis are discussed under related Character Transformations, under Results, and under Comparison with the Phylogenetic Hypothesis of Good (1988). Because we have grouped illustrations around our dichotomous key, figures referenced in the following section will follow Results.

1. [10] Supranasal scales (fig. 51): (0) not expanded or only moderately expanded; (1) strongly expanded, in contact at midline. In *Abronia reidi*, and *A. fimbriata*, the expanded supranasals extend transversely across the front of the snout to meet at the midline. Seven of eight *A. ornelasi* also exhibit this condition; UTA R-6075 has medially expanded supranasals that fail to contact medially. Good (1988: 12, 116) hypothesized an intermediate character (supranasals expand-

ed and triangular, extending partially across the snout) exhibited in *A. mitchelli* and variably in *A. matudai* and *A. salvadorensis*. However, *A. matudai* is quite variable among the four available specimens (one slightly expanded, two moderately expanded, and one greatly expanded, though not contacting at the midline), and one specimen (KU 195560) of *A. salvadorensis* shows the moderately expanded condition. Moreover, the first taxonomic outgroup of *Abronia*, *Mesaspis*, shows sufficient interspecific variation that we have restricted ourselves to using only the condition of medially contacting supranasals for purposes of analysis, the only condition that could be polarized adequately with respect to the outgroups. See discussion of posterior internasal scale size in Transformation Series Excluded from Analysis.

2. [15] Frontonasal scale (fig. 52): (0) present; (1) absent. *Abronia fimbriata*, *A. leurolepis*, some *A. oaxacae* (e.g., AMNH 92737, 98003), and some *A. lythrochila* (e.g., IHN 764) and *A. taeniata* (e.g., UMMZ 111128) lack a frontonasal. Previous reports of occasional frontonasal scale absence in *A. ochoterenai* are based on the holotype of *A. leurolepis* (IBUNAM 340), which had been allocated to *A. ochoterenai* by Hartweg and Tihen (1946), Tihen (1954), and Casas-Andreu and Smith ("1990" [1991]). The report by Hidalgo (1983) of frontonasal scale absence in *A. aurita* is based on specimens of *A. fimbriata*. Boulenger's (1885) report of the frontonasal ("azygous prefrontal") being absent in *A. aurita* is apparently due to confusion caused by Bocourt's (1878 [1870–1909]) description of specimens he erroneously referred to *Gerrhonotus (Abronia) auritus*, which are actually *A. fimbriata*. Although we consider it most likely that absence of the frontonasal is derived in *Abronia*, the condition is variable in out-taxa—predominantly absent in *Barisia* and variably present in *Mesaspis*. For this reason we treat this transformation as unpolarized (i.e., the hypothetical ancestor is coded as unknown).

3. [16] Frontonasal-frontal scale contact: (0) absent; (1) present. Contact is found in *A. ornelasi* (the only species to have broad contact in all specimens) and is variably present in *Abronia reidi* (one of two specimens—Werler and Shannon, 1961), *A. taeniata* (fide

Good, 1988: 13; we saw none in our sample, but we did not see all of Good's specimens), *A. species* "Guerrero," *A. deppii* (e.g., contact in ZMB 1150 and MZFC 2015), and in *A. mixteca* (e.g., contact in AMNH 91000 and UTA R-19650, 25769, 25771). Also, *A. aurita* lacks contact in 5 of a sample of 37 specimens (including the holotype). *Abronia fimbriata* and *A. leurolepis* lack frontonasals and are therefore coded as unknown. Although *A. oaxacae* and *A. lythrochila* lack a frontonasal in a minority of specimens, in those that have a frontonasal, there is no contact, so these species are coded as "0." Good reported frontonasal-frontal contact in one of his four "*A. aurita*" (= *A. gaiophasma*). We have the examined these specimens (MVZ 143461, 144537, 160608–09) and find no contact, although one specimen (MVZ 143461) has a median prefrontal scale that might appear to be part of the frontal, which would then be interpreted as contacting the frontonasal. This transformation is coded as unpolarized because the frontonasal scale is predominantly absent in *Barisia* and, if present, variably in contact with the frontal in species of *Mesaspis*.

4. [19] Canthal scales (fig. 69): (0) present, separate from posterior internasal scale; (1) absent, fused with posterior internasal scale. One of two specimens of *A. reidi* (the holotype) has a canthal on the left side; on the right it is fused with the posterior internasal. In *A. ornelasi* a canthal is absent on one side in UTA R-6219, and on both sides in UTA R-6074, but otherwise present. Canthals are absent in *A. mixteca* with the exception of UTA R-7825 and R-6989, which have them on one side and UTA R-25769 which has them on both sides. The right side of the holotype of *A. leurolepis* shows fusion of the canthal and the posterior internasal. The specimens of *A. matudai* have canthals, except for one side on the holotype. *Abronia graminea* and *A. taeniata* predominantly lack discrete canthals, but have been reported to have them in a minority of specimens (Good, 1988: 14; left side of UMMZ 111125). *Abronia lythrochila* is also variable, with a minority of specimens showing loss of discrete canthals on one or both sides. Species in which absence of canthals (= fusion with posterior internasals) has not been reported are *A.*

mittelli, *A. bogerti*, *A. chiszari*, *A. fuscolabialis*, *A. ochoterrenai* (the reports by Hartweg and Tihen [1946] and Tihen [1954] being based on the holotype of *A. leurolepis*), *A. smithi*, *A. aurita* (Hidalgo's, 1983, earlier report of fusion being based on specimens of *A. fimbriata*), *A. gaiophasma*, *A. anzuetoii*, *A. salvadorensis*, and *A. montecristoi*. Species for which free canthals have never been reported are *A. species* "Guerrero," *A. deppii*, *A. oaxacae*, and *A. fimbriata*.

5. [23, 33] Anterior superciliary scale: (0) similar in length to the following scales in the series; (1) elongate with respect to following scales, frequently bringing it into contact with the prefrontal. *Abronia chiszari* and *A. bogerti* exhibit noticeably lanceolate anterior superciliaries, also seen in one of the two specimens of *A. reidi* (UIMNH 73732) and some specimens of *A. ornelasi* (AMNH 137783, UTA R-12499). This elongation of the superciliary sometimes brings it into contact with the prefrontal (i.e., in the juvenile paratype of *A. reidi*, one side of the holotype of *A. chiszari*, and on both sides of the second known specimen of *A. chiszari* [UNAM-LT 3151], and in two of eight specimens of *A. ornelasi* [AMNH 137783, UTA R-12499]). Good (1988: 15, 19, 117) treated these as independent transformations, but they are clearly causally related.

6. [32] Superciliary–cantholorear scale contact (fig. 59): (0) present; (1) absent. Contact is absent in *A. species* "Guerrero" (variably), *A. smithi* (variably), *A. deppii*, *A. salvadorensis* (contact absent only in the holotype), *A. oaxacae* (variably; contact present in AMNH 98003), and rarely (fide Good, 1988: 18) in *A. graminea*. In all cases, this appears to be due to the fusion of the (blunt) anterior superciliary with the anteriormost lateral supraocular scale.

7. [38] Posterior subocular and the lower primary temporal: (0) in contact or very narrowly separated; (1) broadly separated. The apomorphic condition was reported by Good for all species of *Abronia*, except for *A. mittelli*, *A. reidi*, *A. ornelasi*, on one side of the holotype of *A. kalaina* (*A. fuscolabialis*), and variably in *A. graminea*. Additionally, it is variable in *A. taeniata*, *A. fimbriata*, and there is fairly broad contact in *A. leurolepis* and *A. ochoterrenai*. In the holotype of *A. kalaina* (=

A. fuscolabialis) contact is made on one side; in an adult *A. fuscolabialis* from near Toton-tepec (UTA R-9899) no contact is made on either side, but a juvenile from near the same locality (UTA R-14147) exhibits narrow contact on both sides. *Abronia salvadorensis* is difficult to code for this condition because the subocular and postocular series are poorly differentiated in most specimens, although when they are distinguishable the subocular series is widely separated from the lower primary temporal; even when the subocular series is difficult to discern, the lower primary temporal is well into the topographic position of a postocular scale. Homology in the condition found in *A. deppii*, *A. species* "Guerrero," *A. bogerti*, and *A. chiszari* is arguable inasmuch as other transformations posited suggest that the particular lower primary temporal referenced in this transformation hypothesis may be absent (fused or lost) in these species, rendering coding for this transformation dubious. We have taken the naive position that the lowest primary temporal in these species is "the" lower temporal element. One specimen of *A. gaiophasma* (KU 190851) exhibits fusion between the lower primary temporal and the first post-orbital supralabial. However, those specimens that lack this fusion clearly have no subocular-lower primary temporal contact; therefore we have coded this species as "1."

8. [43, 44] Tertiary temporal number: (0) four; (1) two-three. The plesiomorphic number is clearly four, but in *Abronia bogerti* (fig. 62), *A. chiszari* (fig. 64), and *A. reidi* (fig. 56; contra Good, 1988: 20) it is reduced to three, and in *A. oaxacae* it is reduced to two or three. See discussion under Transformations Excluded from the Analysis. Good hypothesized that in *A. chiszari* and *A. bogerti* the number of tertiary temporals is reduced to three with a concomitant expansion of temporal rows one and two (his Character Transformation 43), and in *A. oaxacae* reduced to two with a concomitant increase in the size of all of the temporal scales (his Transformation 44). Although this is plausible, it cannot, of course, be ascertained without reference to a preexisting phylogenetic hypothesis, so for purposes of our analysis we regard reduced numbers a priori as synapomorphic.

9. [46] Secondary temporal scale number:

(0) four; (1) three. With the exception of *A. mitchelli*, *A. ornelasi*, and *A. reidi*, Good reported that all other species of *Abronia* have some frequency of appearance of the derived feature (variable in *A. montecristoi* [one side of unique specimen] and *A. mixteca*). We agree that *A. mitchelli* and *A. reidi* have four secondary temporals. However, two of the eight known specimens of *A. ornelasi* (one side of AMNH 137783, both sides of UTA R-6074) have three secondary temporals. One of our specimens of *A. taeniata* (KU 54055) has four secondary temporals on one side and two of our *A. graminea* have four on one side (KU 26486-87). Out of a sample of 12 *A. mixteca*, one specimen has three secondary temporals (UTA R-5790), all others have four. Two of the four specimens of Good's "*A. aurita*" (= *A. gaiophasma*), MVZ 143461 and 160609, have four secondary temporals, perhaps by anomalous scale division, although these have been reported to have three (Good, 1988: 21). Other species that have four secondary temporals are *A. ochoterenai*, *A. leurolepis*, *A. matudai* (all four specimens, contra Good, 1988: 21), *A. lythrochila* (all of our sample, including UTA R-3354, which Good [1988: 21] reported as having three; nevertheless we must accept Good's report of variability because we have not seen all of his material). *Abronia smithi* is variable with three of seven specimens showing reduction to three on one side (UMMZ 197260) or both (UIMNH 52085-86, 34197) and three specimens showing four secondary temporals on both sides (CAS 163888, 169850, UTA R-30202). *Abronia aurita* is variable with three or four. Of six *A. anzuetoi*, four show four secondary temporals on one side (AMNH 109053-54, UMMZ 129013) or both (AMNH 102177), the remaining specimens show three. *Abronia salvadorensis* is variable, KU 184047 (both sides, contra Good, 1988: 21) and KU 195561 have three secondary temporals, and KU 195560 and UTA R-26108 have four secondary temporals. The unique specimen of *A. montecristoi* has three secondary temporals on the left side and four on the right side, the difference being due to an enlarged "third" secondary scale on the left side which penetrates inferiorly to contact the first secondary and excludes to exclude the "second" tem-

poral scale from contact with the primary temporal series. The modal condition in this species, however, cannot be decided from this one specimen. Species that have only three secondary temporals reported are *A. fimbriata*, *A. oaxacae*, *A. species* "Guerrero," *A. deppii*, *A. fuscolabialis*, *A. chiszari*, and *A. bogerti*.

10. [47, in part] Upper primary temporal(s) (fig. 52): (0) separate parietals from contact with the median supraoculars; (1) reduced, allowing contact between the parietals and median supraoculars. Although Casas-Andreu and Smith ("1990" [1991]: 322) reported the condition to be variable in *Abronia ochoterenai*, this was due to their inclusion in *A. ochoterenai* of IBUNAM 340, the holotype of *A. leurolepis*. Good (1988: 22) reported this as variable in *A. matudai*, but we find contact in all four specimens, and although he reported contact in his "*A. aurita*" (= *A. gaiophasma*), we see broad separation in these same specimens. Good (1988: 22) also reported contact in his "*A. vasconcelosii*" (one specimen of *A. aurita*, the holotype of *A. vasconcelosii*, MNHN 2017; one specimen of *A. anzuetoi*, the holotype, UMMZ 129013). However, the holotype of *A. anzuetoi* lacks contact.

In species with reduction in the size or number of upper primary temporals, the parietals may contact the median supraoculars, although several species are variable in this attribute, including *Abronia aurita*, *A. fimbriata* (no contact in the lectotype, MNHN 1189), *A. lythrochila* (no contact in LACM 130124), and *A. anzuetoi*, and the unique specimen of *A. leurolepis* has contact on one side. This transformation is correlated with Good's Character Transformations #48 and #49 inasmuch as the parietal contacts the median supraoculars only in those species that have reduced upper primary temporals (although these transformations were excluded from this analysis for other reasons).

11. [50, 52, in part] First postorbital supralabial: (0) not enlarged; (1) enlarged. In *Abronia species* "Guerrero," *A. deppii*, *A. gaiophasma* (variably; KU 190851 enlarged), *A. chiszari*, and *A. bogerti* the derived condition obtains. On topographic grounds it appears that this enlargement of the first postorbital supralabial to $2 \times$ the height of

the next anterior supralabial may be due to fusion with the lowest primary temporal (see discussion under Transformation 11). However, excepting *A. gaiophasma*, there is no evidence for rejecting other alternatives and some specimens of *A. deppii* and *A. species* "Guerrero" have supralabials following this scale that are also enlarged. Besides possibly affecting contact of the subocular and first primary temporal, this apparent scale fusion would affect the number of primary temporals in contact with the postoculars, reducing this number from two to one. Good (1988: 22) hypothesized that in *A. bogerti* and *A. chiszari* the reduction in the number of primary temporals was due to loss at the top of the series with concomitant enlargement of the lower primary temporals. We do not dispute the size of these temporals. However, in light of the "enlargement" of the first postorbital supralabial into an area coextensive with the topographic position of the lower primary temporal in other species, we think that Good's hypothesis is unwarranted, but we cannot reject his notion on this basis.

12. [51] Lower temporal elements: (0) not expanded; (1) expanded. *Abronia chiszari* and *A. bogerti* have greatly expanded lower primary temporals (much as *A. gaiophasma* has a more dorsal longitudinal series of very large temporals) and somewhat less expanded adjacent secondary temporals. This results in the number of primary temporals in contact with the postorbital scale series being reduced to one. This transformation has not been combined with the following because #12 is a function of size of the lower primary temporal, while #13 is a function of the size of the second primary temporal. See following discussion.

13. [52, in part] Number of primary temporals contacting postoculars ("primary temporals in contact with orbit," of other authors): (0) two (or one); (1) three. *Abronia reidi*, *A. ornelasi*, *A. montecristoi*, and *A. smithi* (variably; UMMZ 197260) have the derived condition of three primary temporals contacting the postoculars. The condition in the one specimen of *A. smithi* showing three primary temporals in contact with the postocular series we consider not homologous with the others because the contact is due to elongation of the upper postocular rather than the

more ventral placement of the suture between the second and third primary temporals seen in the apomorphic condition coded here. The unique holotype of *A. montecristoi* has three primary temporals in contact with postoculars contra Hidalgo's (1983: 8) statement that only two scales contact the postoculars. See Transformation Series #12 for discussion of species that have one temporal in contact with the postoculars.

14. [54] Number of occipitals (interoccipital + occipitals of Good, 1988, and Bogert and Porter, 1967) (fig. 58): (0) one; (1) two; (2) three; (3) five. The usual number in *Abronia* is the primitive number for gerrhonotines, one. The unique specimen of *A. mitchelli*, perhaps anomalously, has two; three are seen in *A. oaxacae* and *A. mixteca*; and five are seen in *A. montecristoi*. Also, although the holotype of *A. salvadorensis* has one occipital, the other three known specimens have three. Because "one" is clearly the plesiomorphic condition, we have coded *A. salvadorensis* as having three occipitals. Because we have no compelling reason to hypothesize a particular polarity for this set of conditions, beyond regarding the 0 condition as plesiomorphic, we consider this transformation nonadditive.

15. [57] Posterolateral head scales (fig. 60): (0) not strongly convex (not knoblike); (1) strongly convex (knoblike). Knobby posterolateral head scales, reflecting the development of underlying skull casquing, as seen in a more developed (but nonhomologous) fashion in *Laemancus* (Corytophanidae), is seen in the *A. deppii* group: *A. graminea*, *A. taeniata*, *A. fuscolabialis*, *A. species "Guerrero," A. deppii* (weakly), *A. mixteca*, and *A. oaxacae* (extremely developed). Good posited an intermediate condition exemplified by *A. fuscolabialis*, *A. graminea*, and *A. taeniata*. We regard this as incautious characterization, inasmuch as at least UTA R-9899 (*A. fuscolabialis*) and KU 105834 (*A. graminea*) have casquing as strong as found in *A. mixteca*, and no other species are nearly as strongly casqued as *A. oaxacae*. However, the condition in *A. taeniata* and *A. deppii* (not *A. species "Guerrero"*) is arguable with regard to intermediacy; these species exhibit relatively weakly developed dorsolateral knobiness (although the condition is clearly present). Nevertheless, an objective definition of

conditions does not seem possible, so we take the conservative position of hypothesizing only a single transformation.

16. [58] Supra-auricular scales (fig. 50): (0) not protuberant; (1) protuberant, not spine-like; (2) strongly protuberant, spine-like. Protuberant, but not spine-like, supra-auricular scales are seen only in mature *A. matudai*. The supra-auricular scales are more well developed, spine-like, in *A. ochoterenai*, *A. leurolepis*, *A. smithi*, *A. lythrochila*, *A. aurita*, *A. gaiophasma*, *A. anzueto*, *A. leurolepis*, and *A. fimbriata*. In all species of *Abronia* occurring west of the Isthmus of Tehuantepec, the supra-auricular scales are small, roundish, and nonprotuberant.

17. [61, in part] Supralabial in contact with the orbit (subocular-postocular scale series): (0) antepenultimate; (1) penultimate. This transformation was posited by Good to be derived four times: (1) by shortening of the mouth in *A. fuscolabialis* (and its junior synonym *A. kalaina*); (2) through expansion of the lower temporal elements in *A. chiszari* and *A. bogerti*; (3) in *A. species "Guerrero"* (as *A. deppii*) through loss (or fusion) of the lowest anterior temporal; and (4) in *A. oaxacae*, *A. smithi* (as *A. ochoterenai*), *A. matudai* (variable), *A. lythrochila*, *A. aurita* (as *A. vasconcelosii*), *A. gaiophasma* (as *A. aurita*), *A. salvadorensis*, and *A. montecristoi*, through loss of the posteriormost supralabial. One of our specimens of *A. salvadorensis* (UTA R-26108) has the penultimate condition on the left side. As discussed previously, *A. fuscolabialis* (including *A. kalaina*) has not shortened its mouth and we consider (contra Good, 1988) the supralabial in the orbit to be the antepenultimate. It is not clear, certainly not a priori, what the "loss" of the lowest primary temporal (likely a fusion of the lower primary temporal and adjacent supralabial) in *A. species "Guerrero"* (the *A. deppii* of most previous authors) and *A. deppii* has to do with this hypothesized transformation, nor is it clear what evidence supports the notion that the condition in *A. bogerti* and *A. chiszari* was arrived at by a different mechanism than in *A. deppii* and *A. species "Guerrero"* without reference to a preexisting phylogenetic hypothesis. Although it might be reasonable a posteriori to judge the condition in *A. bogerti* and *A. chisz-*

ari and *A. deppii* and *A. species* "Guerrero" as did Good, a priori it cannot be defended inasmuch as the "hypothesis" is clearly an a posteriori "explanation."

18. [64] Posteriormost infralabial: (0) not remarkably longer than the preceding infralabial; (1) lengthened to approximately twice the length of the preceding infralabial (apparently due to the fusion of the ultimate and penultimate infralabial). The apomorphic condition is seen in *A. aurita*, *A. leurolepis*, *A. anzuetoi*, *A. lythrochila*, and *A. deppii* (variably).

19. [65] Postmental scale (fig. 65): (0) divided; (1) single. This transformation must be considered unpolarized because of uncertain outgroup comparison (i.e., "1" in most *Mesaspis* and "0" in *Barisia*). Although it is relatively constant in some species, it is variable in *Abronia lythrochila*, *A. gaiophasma*, *A. ochoterenai*, *A. smithi*, *A. matudai*, *A. anzuetoi*, *A. aurita*, *A. species* "Guerrero," and *A. oaxacae* (e.g., AMNH 90997—Bogert and Porter, 1967; contra Good, 1988: 25). Species in which a divided postmental has never been reported are *A. fimbriata*, *A. salvadorensis*, *A. montecristoi*, and *A. leurolepis*. The level of intraspecific variability of this character surprised us inasmuch as this had been considered a pivotal character in the definition of species groups (Tihen, 1954).

20. [70] Number of transverse rows of dorsal scales: (0) more than 38; (1) less than 38. Good did not regard variation in the number of transverse rows of dorsal scales to be informative in *Abronia*. However, although characterization of a transformation series is not possible among most species of *Abronia*, *A. chiszari* and *A. bogerti* stand out as having particularly high dorsal counts. Unfortunately, although *Mesaspis* species show high dorsal counts, two members of the second taxonomic outgroup, *Barisia*, can have low counts: *Barisia rudicollis* (IBUNAM 2701 counted as about 33 by Good [1988: 27] and as about 27–29 by Tihen [1949b: 239]) and *Barisia imbricata* (34–42: Tihen, 1949b; Good, 1988: 27; Guillelte and Smith, 1982). This variation in outgroups renders this transformation unpolarizable a priori.

Our observations among *Abronia* are: *A. bogerti* (1 specimen), 39; *A. chiszari* (2), 39–47, *A. reidi* (2), 34–36; *A. ornelasi* (8), 30–33;

A. mitchelli (1), 34; *A. montecristoi* (1), 28; *A. matudai* (4), 33–37; *A. ochoterenai* (2), 31–33; *A. salvadorensis* (4), 31–32; *A. leurolepis* (1) 31; *A. gaiophasma* (7), 28–30, *A. fimbriata* (16), 27–30; *A. anzuetoi* (6), 27–28; *A. smithi* (11), 27–30; *A. lythrochila* (9), 28–30; *A. aurita* (46), 27–31; *A. fuscolabialis* (3), 28–32; *A. mixteca* (64), 28–31; *A. oaxacae* (8), 27–29; *A. graminea* (6), 23–29; *A. taeniata* (3), 28–34; *A. deppii* (5): 27–29; *A. species* "Guerrero" (9), 24–28. Again, some subjectivity on counting landmarks may be evident; where we report 29–32 rows in *A. oaxacae*, Good and Schwenk (1985) reported 27–28.

21. [74] Dorsal scale row orientation (fig. 57): (0) parallel to the ventrolateral fold; (1) oblique to the ventrolateral fold. The oblique orientation of the dorsal scale rows relative to the ventrolateral fold occurs in *A. species* "Guerrero," *A. deppii*, *A. oaxacae*, and *A. mixteca*. The previous report (Campbell, 1982) of oblique dorsal scale rows in *A. mitchelli* was due to the exuberance of youth.

22. [75, in part] Osteoderms under first two rows of nuchal scale rows: (0) present, moderately to well-developed; (1) very poorly developed. *Abronia deppii* and *A. species* "Guerrero" have extremely "flimsy" nuchal scales that are strikingly different from specimens of all other species that we have examined. Some smaller *A. mixteca* also approach this condition, but large adults are clearly "armored" in the nuchal region. Good (1988) used development of body osteoderms as a character in his analysis. Although we concur with the trends that he noted, we found individuation of characters to be overly subjective. See discussion of this in "Characters Excluded from Analysis."

23. [76] Longitudinal nuchal scale row number: (0) eight; (1) six; (2) four. *Abronia chiszari* and *A. bogerti* are the only species to have eight nuchal scale rows; most *Abronia* exhibit six. However, all *A. oaxacae*, a minority of *A. graminea*, and one *A. fuscolabialis* (UTA R-9899), perhaps anomalously, have four rows.

24. [77, in part] Lateral neck scales: (0) subimbricate or granular laterals, moderately to strongly distinct from both ventrals and dorsals, numbering 8–14 between dorsals and ventrals; (1) imbricate, reduced to 6–7 scales between dorsals and ventrals, very weak or

no distinction between laterals and ventrals and dorsals; (2) very enlarged (particularly along the oblique lateral fold and below this fold), knobby, about the size of the ventrals, and strongly distinct from dorsals.

Good (1988: 29, 121) considered this transformation as additive: (0) granular (*A. mitchelli*, *A. ornelasi*, *A. reidi*, "*A. ochoterenai*" [= *A. smithi*], *A. matudai*, *A. lythrochila*, *A. vasconcelosii* [= *A. anzueto* and *A. aurita*], "*A. aurita*" [= *A. gaiophantasma*], *A. salvadorensis*, and *A. montecristoi*); (1) subgranular (*A. chiszari*, *A. bogerti*, *A. fuscolabialis*, *A. taeniata*, and *A. graminea*); (2) enlarged ("*A. deppii*" [= *A. species* "Guerrero"], *A. mixteca*, and *A. oaxacae*). However, there is little in the morphology of these animals that would suggest that this could be considered a polarized transformation, and characterization difficulties require redefinition of more objectively scored conditions. The plesiomorphic condition of lateral neck scales is to have a relatively large number of small granular scales running in a band from the ear to over the shoulder, readily distinguishable from both dorsal and ventral scales. It may be synapomorphic for *Abronia* to have the number of granules (counted in a line between ventrals and dorsals) reduced to about 14. The number of lateral scales varies from about 6 to about 14 with the variation within this interval very difficult to individuate. Two conditions are readily characterized, however. *Abronia chiszari* and *A. bogerti* have 6–7 large, subimbricate laterals with almost no distinction from ventrals or dorsals. *Abronia taeniata* and some *A. graminea*¹⁵ reduce to 7–9 lateral neck scales, but distinction between these and the dorsals is strong and including this in the *A. bogerti*–*A. chiszari* class (lacking lateral-dorsal distinction) adds insurmountable characterization problems. Some *Abronia anzueto* reduce to about seven lateral granules, but again this is with strong lateral-dorsal distinction. *Abronia fuscolabialis* also shows a condition approaching that in the *A. chiszari*–*A. bogerti* class in minimizing the distinction of dorsals and laterals, but lateral counts are 8–10.

In *Abronia* species "Guerrero," *A. deppii*,

¹⁵ At least based on our sample, we agree with Tihen (1954) that lateral neck scales are generally larger in *A. taeniata* than in *A. graminea*, contra Good (1988: 29).

A. mixteca, and *A. oaxacae* the lateral scales are very enlarged and "pebbly," particularly along the oblique lateral fold (sensu Frost, 1992) and below this line. Beyond the term "enlargement" there is no morphological reason to suggest homology between the conditions in the *A. chiszari*–*A. bogerti* class and the *A. deppii*–*A. mixteca*–*A. oaxacae*–*A. species* "Guerrero" class, so we considered this a nonadditive set of characters.

25. [79] Ventrolateral fold: (0) well-developed; (1) strongly reduced. *Abronia oaxacae*, *A. mixteca*, *A. deppii*, and *A. species* "Guerrero" all show reduction in the development of the ventrolateral fold. This may be related to the reduction of osteoderm development in these species.

26. [83] Lateral ventral scale rows (fig. 66): (0) not expanded in comparison with adjacent ventrals; (1) noticeably wider than adjacent ventrals, particularly along posterior third of ventrolateral fold. Good reported this condition only in *A. matudai* and *A. ochoterenai* (= *A. smithi*). We have found this character to be considerably more widespread, found also in *A. ornelasi*, *A. smithi*, *A. leurolepis*, *A. ochoterenai*, *A. lythrochila* (variable; e.g., absent in UTA R-12137), *A. aurita*, *A. gaiophantasma*, *A. anzueto*, *A. fimbriata*, *A. montecristoi*, and *A. salvadorensis*. See discussion under the following transformation series.

27. [82] Longitudinal ventral scale row number: (0) 12, or (1) 14. Good (1988: 29) combined this transformation with the previous one, hypothesizing (0) 12 scale rows, no lateral expansion → (1) 14 scale rows, with lateral expansion → (2) secondary reduction to 12 scale rows, with lateral expansion. We detect no necessary relationship between the number of ventral rows and lateral ventral scale row expansion and certainly do not support Good's implication that lateral expansion is due to fusion of lateral scale rows, or has anything to do with secondary reduction in the number of scale rows. *Abronia gaiophantasma* sometimes has 15–16, rather than 14, ventral scale rows. *Abronia salvadorensis* is variably 14 (KU 184047, 195561) or 12 (UTA R-26108, KU 195560), as are *A. taeniata*, *A. graminea*, *A. deppii*, *A. species* "Guerrero," and *A. matudai*, and *A. mixteca* sometimes has 16 (e.g., MZFC 4420). All *A.*

oaxacae, *A. fuscolabialis*, *A. gaiophasma*, *A. lythrochila*, *A. aurita*, and *A. anzueto* have 14. Hartweg and Tihen's (1946) report of 14 ventrals in *A. ochoterenai* is based on a specimen (IBUNAM 312) which was subsequently identified as *A. lythrochila* (then newly distinguished) by Smith and Alvarez del Toro (1963).

28. [98] Body scale coloration: (0) scale edges colored as the middle of the scales or weakly edged with lighter color; (1) edged with yellow, making the squamation appear as a mosaic (fig. 12B). *Abronia reidi* and *A. ornelasi* exhibit the apomorphic condition of having the body appear "checkered" or mosaiclike because of the bright yellow edging on the body scales. Some *A. fimbriata* approach this condition laterally, but the mosaiclike aspect is never approached. Particularly after preservation, individuals of some species in the *A. aurita* group (e.g., *A. gaiophasma* [e.g., UTA R-19646], *A. lythrochila* [e.g., UTA R-3354], *A. ochoterenai* [IBUNAM 339], *A. smithi* [UTA R-30202]) show lighter scale edges, but, again, this does not approach the mosaic appearance of *A. ornelasi* and *A. reidi*. *Abronia montecristoi* appears to have shared this mosaic appearance in life and, with trepidation, we code it as having the apomorphic condition.

29. Circumorbital region coloration (figs. 10A, B; 11C, D): (0) same color as head; (1) strikingly yellow to yellow-orange. *Abronia aurita*, *A. anzueto*, *A. graminea*, and *A. smithi* have bright yellow circumorbital regions. In other species the circumorbital region is colored the same as the body and head. This characteristic is easily scorable for preserved animals because the yellow becomes white in preservative, a color that is almost always strikingly different from that of the adjacent head.

30. Infralabial scale coloration (fig. 10A): (0) ground color of lower jaw; (1) orange or red. In *Abronia lythrochila*, *A. aurita*, *A. anzueto*, and *A. fimbriata* the margins of the lower lips are orange to red, this coloration sometimes (e.g., adult males of *A. aurita*) extending onto the supralabials and well on to the head. *Abronia ochoterenai*, *A. montecristoi*, and *A. leurolepis* are coded as unknown because specimens are old preserved animals in which the condition, if present, has faded.

CHARACTER TRANSFORMATIONS EXCLUDED FROM ANALYSIS

Numbers in brackets refer to Good's (1988) numeration of transformations. Some of these features proved to be illuminating a posteriori (see Results and Discussion) but could not be used a priori because of characterization problems or because of extensive intra-specific variation. Some simply did not survive scrutiny of specimens.

[4] Nasal scale extending posteriorly to supralabial three. Good (1988) reported the apomorphic condition in *A. graminea* (variable), *A. taeniata* (variable), *A. species "Guerrero"* (his "*A. deppii*"), *A. mixteca* (variable), and *A. oaxacae* (variable). We have also found this to be variable in most other species for which there are adequate samples, including *A. aurita* and *A. gaiophasma*. Because this attribute appears to be variable in all species that have appreciable samples we have excluded this transformation from a priori use.

[7] Posterior internasal size. Good (1988: 11) stated that in *A. graminea*, *A. taeniata*, *A. species "Guerrero"* (= his "*A. deppii*"), *A. mixteca*, and *A. oaxacae* the posterior internasals "have approximately doubled in size relative to the antenno-canthal fusion seen in those species." We were unable to verify this; in other species that have fusion of the posterior internasals and canthals there is no perceivable difference between scale sizes from those in Good's large posterior internasal group. Particularly against the rather large amount of intra- and interspecific variability in the sizes of the pertinent scales we find this statement to be dubious. Additionally, most species of *Abronia* that do not regularly show fusion of the posterior internasals and canthals already have posterior internasals that are at least twice the surface area of the anterior internasals (e.g., *A. aurita*, *A. anzueto*, *A. lythrochila*, *A. smithi*, *A. bogerti*, *A. ochoterenai*, and *A. gaiophasma*). Nevertheless, this trend cannot be characterized in any way objective enough to warrant its use, particularly when it is confounded with fusion of the posterior internasals with adjacent canthals.

[36] Subocular number reduced to two or

three. This transformation was rejected for use because intraspecific and intraorganismal variability was considerably greater than previously reported (e.g., *A. ornelasi* [2–3], *A. smithi* [2–4], *A. matudai* [2–4], *A. gaiophasma* [2–5], *A. lythrochila* [2–4], *A. aurita* [2–3], *A. anzuetoi* [2–3], *A. fimbriata* [1–3]), intraspecific variation virtually equalling interspecific variability.

[42] Condition of fourth temporal row. Good (1988: 20, 118) considered this to be a three-character transformation: (0) fourth row present and unmodified (*A. mitchelli*, *A. reidi*, *A. ornelasi*); (1) fourth row reduced (*A. chiszari*, *A. bogerti*, *A. graminea*, *A. taeniata*, *A. fuscolabialis*, *A. species* “Guerrero” [then referred to *A. deppii*], *A. mixteca* [variably absent], *A. smithi* [then referred to *A. ochoterena*], *A. matudai*, *A. salvadorensis*, *A. montecristoi*); (2) fourth row lost (*A. oaxacae*, *A. mixteca* [variably], *A. lythrochila*, *A. gaiophasma* [Good’s “*A. aurita*”). Unfortunately, this characterization is obviated by observational errors, individual variation, and a multiplicity of morphologies that appear more similar in print than on the specimens. For instance, “reduction” of a fourth row may be due to apparent fore-aft shortening (as seen in *A. reidi* and *A. chiszari*) or in the lower scales in the third temporal series penetrating posteriorly to the preauriculars and thereby shortening the fourth row along a dorsoventral axis (as in several examples discussed below). Also, distinguishing between a very reduced fourth row of temporals and preauricular scale rows can result in some very uncomfortable subjectivity in coding.

We agree with Good that *A. mitchelli* has four unmodified temporal rows, although the fourth is clearly narrower than the third (figs. 67, 68). The condition in *A. ornelasi* is not the same. Most of the eight known examples of this species have a slightly to moderately dorsoventrally reduced fourth row and one specimen (UTA R-12499) has only three temporal rows on its right side. This species has conditions very similar to those in some *A. deppii* and *A. fuscolabialis*, and might fit best in Good’s “reduced” category. *Abronia reidi* is also not comparable to *A. mitchelli*; the figure presented by Good (1988: 21, his fig. 6b) bears no resemblance (schematic or otherwise) to either known specimen of *A.*

reidi (see figs. 1–3 in Werler and Shannon, 1961; our figs. 28, 56). In the specimens of *A. reidi* the anterior three rows of temporals are expanded and the fourth is reduced in size (fore-aft length) with respect to the third row, except on the left side of UIMNH 73732, rendering this species comparable to some in Good’s “reduced” category. Both *Abronia reidi* specimens have conditions similar to that seen on the left side of both known specimens of *A. chiszari* in which there is a narrow fourth temporal row. Otherwise, in *A. chiszari* there are three large temporal rows with the fourth either very reduced or absent, depending on side and individual. The single specimen of *A. bogerti* has three temporal rows with no evidence of a fourth (not the “reduced” fourth temporal row fide Good, 1988: 20).

Of the species considered to have a “reduced” fourth row by Good, we have already dealt with *A. bogerti*, which, if its strong overall similarity to *A. chiszari* is suggestive, may have lost the fourth row by fore-aft reduction in size concomitant with expansion of the anterior rows. Other species considered to have “reduced” fourth rows have apparently done so by extension of the lowest tertiary temporal to the preauriculars, thereby “shortening” the fourth temporal row dorsoventrally without any diminution in scale size. However, even this categorical distinction between short fourth rows and complete fourth rows makes for severe characterization problems. Some *A. taeniata* (e.g., ZMB 1151) have complete fourth rows equally as large as the third row, and others (e.g., KU 54055) have the fourth row only slightly shortened by posterior penetration of the lower tertiary temporal. Other species that show this same kind of characterization difficulty between four rows of temporal and “3.5” rows are: *A. graminea*, *A. deppii*, and *A. species* “Guerrero.” All three of our specimens of *A. fuscolabialis* show a dorsoventrally shortened fourth row. *Abronia mixteca* is variable, generally showing the “shortened” condition but sometimes clearly having four rows (e.g., UTA R-19652); sometimes a count of three rows (e.g., UTA R-19651, R-19653) is possible because of scale irregularities in the second and third rows. Good’s characterization of *A. oaxacae*

as completely lacking a fourth temporal row is arguable. All specimens of *A. oaxacae* that we examined have what is likely a single fourth temporal (uppermost) remaining at the dorsolateral "corner" of the head casque, as seen also in some *A. mixteca*. However, if presence or absence is taken at ear level *A. oaxacae* and *A. mixteca* (variably) would "lack" a fourth temporal row. We agree with Good that some *A. smithi* and most *A. matudai* show the 3.5 row ("reduced") condition, although one specimen of *A. matudai* (LACM 75514) lacks a fourth row. Of those species that are supposed to lack evidence of a fourth temporal row, *A. lythrochila*, *A. aurita*, and *A. anzuetoi* may show evidence of a fourth row in the presence of row of very large "preauriculars" in the topographic position of the fourth temporal row of other species. *Abronia gaiophasma* (= "*A. aurita*" of Good) has the anterior two rows of temporals very enlarged with the third row reduced and no evidence of a fourth row. Contrary to Good (1988: 20), *A. montecristoi* and *A. salvadorensis* have four complete rows of temporals, and are not comparable with the "reduced" group. In fact, one specimen of *A. salvadorensis* (KU 195560) has five rows on one side and, although anomalous on the other, also appears to have at least a partial fifth row.

Because of the incongruence of Good's characterization of this transformation with our observations we have discarded this character. There is no doubt that evolution has resulted in among-species variation; unfortunately, we could not individuate characters that could be coded objectively.

[48–50] Number of primary temporals reduced from four to two or three. Good (1988) suggested that the number of primary temporals (i.e., loss of first, third, or fourth primary temporals) might provide useful characters for analysis. However, because of intraspecific variation in size, shape, and position of scales we have been unable to convince ourselves that we can always distinguish third from fourth primary temporals, or the homologies of irregular temporals in the second and third rows. In our material, for example, we have found the following numbers of primary temporals: *A. gaiophasma* (7 specimens): 3 (42%), 4 (57%); *A.*

matudai (4): 2 (75%), 3 (12.5%), 4 (12.5%); *A. fimbriata* (9): 2 (56%), 3 (44%); *A. ornelasi* (7): 4 (100%); *A. anzuetoi* (5): 2 (10%), 3 (90%); *A. aurita* (40): 2 (13%), 3 (74%), 4 (13%); *A. smithi* (4): 4 (100%); *A. leurolepis* (1) 3 (100%); *A. lythrochila* (7): 3 (86%), 4 (14%); *A. bogerti* (1): 2; *A. reidi* (1): 3 (100%); *A. salvadorensis* (4): 4 (100%); *A. montecristoi* (1): 4 (100%); *A. graminea* (5): 3 (40%), 4 (60%); *A. deppii* (3) 3 (100%); *A. species "Guerrero"* (5): 2 (40%), 3 (60%); *A. oaxacae* (4): 3 (75%), 1 (25%); *A. chiszari* (2) 3 (100%); *A. mixteca* (10) 3 (30%), 4 (70%); *A. anzuetoi* (6): 2 (17%), 3 (83%); *A. mitchelli* (1) 4 (100%); *A. smithi* (8): 3 (13%), 4 (75%), 5 (13%); *A. fuscolabialis* (3): 4 (100%); *A. ornelasi* (8) 4 (100%).

Contrary to the implications in Good's (1988) discussions of phylogenetic transformations in squamation, the homologies of temporal scales, particularly in rows 2 and 3, are frequently not clear. Temporal scale contacts form a Rubic's Cube analog, which can make simple assignments based on topography ambiguous. In other words, with the kind of variation present in some species, it is difficult enough to know how to code for number, much less how to know whether a particular scale might have been lost. We find intraspecific variation (and indeed, intraorganismal variation) to be great enough that we find Good's distinction between a number of transformations dealing with the fate of particular temporal scales to be dubious, certainly without a preexisting cladogram on which to evaluate variation. Possibly, if a cladogram already existed and one wished to "explain" scale morphology differences, these homology assessments could be made, but not a priori.

[55] Number of postoccipital rows (one, two, or three). In Good's (1988) analysis, this character transformation was rooted on the condition of two postoccipital rows. However, counting these rows is frustratingly subjective and considerable variation obtains. Following Campbell (1982: 359), we have counted postoccipital rows starting with the first transverse nuchal row that lies completely behind the level of the auricular opening. Thus, the number of postoccipital rows corresponds to the number of scales between the occipital(s) and the first transverse nuchal row. We do not know how Good counted these

scales. However, he reported three rows only in *A. mixteca* and *A. oaxacae*; he also reported *A. gaiophantasma* (as *A. aurita*) as having two, where we report from one to three in these species, and he reported three in *A. salvadorensis* and *A. montecristoi*, where we report two. We suspect strongly that these differences are due to the inherent subjectivity required to evaluate this morphology. Otherwise, *Abronia mitchelli* exhibits one row of postoccipitals, and a number of species exhibit three: *A. species* "Guerrero," *A. deppii*, *A. mixteca*, *A. smithi* (2–3), *A. matudai* (1–3), *A. lythrochila* (2–3), *A. aurita* (2–3), *A. gaiophantasma* (one specimen has one), *A. anzueto* (2–3), *A. fimbriata* (1–3). One specimen of *A. ornelasi* (UTA R-10545), previously reported by Campbell (1984) and not examined by Good (1988) (who nevertheless rejected Campbell's earlier observation—Good, 1988: 23), has a single postoccipital row due to several apparently anomalously enlarged nuchal scales directly behind the occipital.

[56] Postoccipital scale surface rugosity. Good (1988) reported rugose postoccipital scales (reflecting underlying osteoderm rugosity) in *A. graminea*, *A. taeniata*, *A. species* "Guerrero" (as "*A. deppii*"), *A. mixteca*, and *A. oaxacae*. We would add to this list at least *A. lythrochila*, *A. aurita*, and *A. gaiophantasma* (Good's "*A. aurita*"). Regardless, characterization of this morphology is extremely subjective and variation is strongly subject to effects of size and age.

[59] Preauricular scale condition. Good (1988: 24, 119) characterized this transformation as imbricate preauriculars versus granular preauriculars. His coding of species, however, was apparently subjective, i.e., most specimens of "*A. ochoterenai*" [= *A. smithi*] that he coded as having granular preauriculars clearly have posteriorly imbricate preauriculars (fig. 53). Because of intraspecific variability we were unable to objectively define states among species of *Abronia*. The widespread condition in *Abronia* is to have about four preauriculars variably very weakly imbricate but slightly bulbous, generally "aiming" in an upward direction, and in a single dorsoventral row immediately following the fourth row of temporal scales. *Abronia species* "Guerrero" and *A. deppii* usually have

reduced this row to 2–3 scales. *Abronia ornelasi* and *A. salvadorensis* arguably show incomplete second rows, but this is contingent on distinguishing small scales inside the ear canal (= meatal scales) from preauriculars. *Abronia matudai* sometimes has two rows, as do *A. gaiophantasma* and *A. fimbriata*, generally. *Abronia smithi* frequently has one or two rows of posteriorly imbricate preauriculars. *Abronia lythrochila*, *A. anzueto*, and *A. aurita* have an anterior "extra" row of preauriculars that are in the topographic position of the fourth row of temporals and may be homologous with these scales. *Abronia ochoterenai* and *A. leurolepis* have the same supernumerary row of preauriculars, but the scales in the anterior row are much smaller than in the previous species. However, it may be that these scales are homologous with those in *A. aurita*, *A. lythrochila*, and *A. anzueto*. Some *Abronia gaiophantasma*, some *A. fimbriata*, and some *A. smithi* approach this condition, but they usually do not have three rows of preauriculars. Regardless, characterization is sufficiently difficult that we will not speculate further here. In these two species the fourth row of temporals is completely lost and the first three rows of temporals are strongly expanded; whether this is a condition derived from the *A. aurita* condition in which the "anterior row of preauriculars" (= fourth row of temporals) is lost we hesitate to guess.

Absolute counts of preauriculars along the anterior margin of the auditory meatus are suggestive of a trend but cannot be used a priori. As noted by Good (1988), in part, there does seem to be possibly informative variation in preauricular scale size, although we could not characterize it adequately for this study: *A. ornelasi* (4–5), *A. mitchelli* (3), *A. chiszari* (4–5), *A. mixteca* (4–6), *A. montecristoi* (4–6), *A. ochoterenai* (6), *A. leurolepis* (5–6), *A. smithi* (4–6), *A. matudai* (5–6), *A. lythrochila* (5–7), *A. aurita* (5–7), *A. gaiophantasma* (6–8), *A. anzueto* (5–6), and *A. fimbriata* (4–6).

[61] See discussion under Transformation Series 17.

[62] Posterior margin of mouth showing "marked" shortening. Good and Schwenk (1985) and Good (1988) characterized *Abronia kalaina* and *A. fuscobialis* as showing a

“marked” shortening of the posterior extension of the mouth. Except for this very slight (and likely variable) attribute seen only in the unique specimen of *A. kalaina* (= *A. fuscolabialis*) and not in other specimens of *A. fuscolabialis* (contra Good, 1988: 25) we see no differences between these lizards and other specimens of *Abronia*.

[66] Postmental size. Good (1988) considered small postmental size a synapomorphy of *A. oaxacae* and *A. mixteca*. In a sample of 30 specimens of *A. mixteca* we have found the postmentals in that species to be very intrapopulationally variable, often larger than in other species of *Abronia*, although *A. oaxacae* clearly has small postmentals. We, therefore, have rejected this feature as uninformative a priori.

[68] Chinshield number/size. Good (1988) used a transformation in which postmental chinshield series were characterized by number and relative size. Good characterized *A. mitchelli*, *A. salvadorensis*, *A. species* “Guerrero” (as *A. deppii*), *A. oaxacae*, and *A. mixteca* as having four large chinshields, rather than the plesiomorphic three. In our observations, only *A. mitchelli*, *A. bogerti*, and *A. leurolepis* (all three species represented by unique specimens) could be coded as having, invariably, four large chinshields. The only one of Good’s hypodigm of *A. oaxacae* (UIMNH 48672) that we have examined has the 4-3 condition; our other specimens of *A. oaxacae* have 3-3 large chinshields. We also find *A. gaiophasma* (= Good’s “*A. aurita*”), *A. taeniata*, *A. species* “Guerrero” (his “*A. deppii*”), and *A. mixteca*, to be variable. All of our sample of *A. graminea* have four large chinshields rather than the three that Good reported so we assume that this species also is variable. Additional specimens of *A. salvadorensis* all have three large chinshields; only the holotype has four. So, although this might provide evidence supporting the monophyly of a group composed of the *Abronia* species with casqued heads, we find that deciding what is the last “large” chinshield is very subjective and have excluded this transformation from consideration.

Generally, in Good’s (1988) analysis of all gerrhonotines, unlike some other apparent morphoclines, he hypothesized several supposedly mutually apomorphic features (5

large; 4 large + 1 small; 4 large) derived from the plesiomorphic condition, 3 large + 1 small. We find this to be idiosyncratic. We think that either he should have treated it as a nonadditive set, with the ancestral condition hypothesized, or he should have posited the morphocline 5 large $\leftarrow$ 4 large + 1 small $\rightarrow$ 4 large $\rightarrow$ 3 large + 1 small. Nevertheless, in *Abronia* we found these conditions to be intraspecifically so variable as to be unusable. *Abronia mixteca* and *A. species* “Guerrero” (Good’s “*A. deppii*”) are particularly variable. Although we concur with Good (1988: 27) that Campbell’s (1982) suggestion that *A. chiszari* has four chinshields is in error, we still disagree with Good (1988: 27) in his statement that (contrary to Campbell, 1982) *A. bogerti* has three large chinshields. Because there is only one specimen of *A. bogerti* available for this observation (the holotype) one would think that we could agree. Nevertheless, this specimen has 4-4 large chinshields (although on the left side, scales two and three are mostly fused and the count could be taken as 4/3) and an undescribed species in the *A. bogerti* group from Chiapas, Mexico, has 4/4 large chinshields.

[71] Longitudinal rows of dorsal scales; reduction from 14-16 to 10-13. *Abronia matudai* (3 of 4 specimens), *A. mitchelli*, and *A. chiszari* have 16 scale rows. However, scoring other species for longitudinal dorsal scale rows is highly subjective because it is difficult to discriminate lateral fold scales from dorsal scales in many species. For a time during the development of this analysis we felt that this transformation and the following [72] were both reflecting an increase in the size of the dorsal scales. Likely, this is true. However, both transformations were sufficiently difficult to characterize that we excluded both from consideration. See discussion under the following transformation and under [81].

[72] Longitudinal dorsal scale row number at hind limbs. Although Good (1988) distinguished between characters of six, eight, or ten rows, we have found characterization to be extremely difficult. *Abronia graminea*, *A. fuscolabialis*, *A. montecristoi*, *A. salvadorensis*, *A. leurolepis*, and *A. taeniata* show 8 rows in our material, but *A. ornelasi* has 8-9, and *A. smithi*, *A. ochoterenai*, *A. matudai*, *A. fimbriata* (previously reported by Camp-

bell [1982] as *A. aurita*), *A. mitchelli*, *A. chiszari*, and *A. gaiophasma* have 8–10. The unique holotype of *A. bogerti* has 10. Only *A. oaxacae* has predominantly 6 scale rows; *A. mixteca*, *A. species* “Guerrero,” *A. deppii*, and *A. mixteca* predominantly have 7–8. Even though an a posteriori phylogenetic trend of decreasing scale number may be likely, this cannot be justified a priori.

[73] Dorsal scale keeling, weak or absent to strong. Good’s (1988: 28, 127) “a priori” coding of this transformation series in his all-gerrhonotine analysis appears to have been constructed on the basis of a posteriori reasoning: keeling absent → keeling strong (to very strong) → keeling weak. Nevertheless, even if we could characterize distinguishable conditions, because of ambiguous outgroup comparison (weak in most *Mesaspis*, strong in *Barisia*) this transformation would have to be considered unpolarized. Although Good excluded *A. chiszari* from this set, this species clearly has smooth scales; *A. bogerti* is very similar but does show some evidence of obtuse keeling. Also, some individuals of *A. mixteca* and *A. oaxacae* show paravertebral keeling, albeit weak, and would therefore be excluded from the set as defined by Good. We have been unable to arrive at a satisfactory method for coding; individual variation obviates any chance of avoiding a “slippery slope” of inclusiveness. Therefore, although some a posteriori trends may be visible, we cannot use this characteristic a priori.

[75] Dorsal osteoderms reduced or absent. Good (1988) characterized *A. mixteca* and “*A. deppii*” (= *A. species* “Guerrero”) as lacking dorsal osteoderms, and *A. oaxacae*, *A. mitchelli*, *A. reidi*, and the unique specimen of *A. kalaina* (= *A. fuscolabialis*) as having reduced osteoderms. We have attempted to evaluate the condition of osteoderms by probing with insect pins and/or with radiographs. It is clear that evaluation is largely dependent on semaphoront choice; old males have the best ossification. If the specimen is a juvenile (like the specimens of *A. chiszari* and *A. bogerti* available to Good), a subadult (like the holotype of *A. kalaina*), or a female (like the unique specimen of *A. mitchelli*) the character cannot be evaluated adequately. Nevertheless, although we agree that reduced middorsal osteoderm development is likely

a synapomorphy of (minimally) the *A. deppii* subgroup, we are puzzled about character definition among enough of the species of *Abronia* that we hesitate to use this transformation in our analysis. Additionally, this transformation, if it could be evaluated objectively, seems to be causally related to other transformations hypothesized by Good, such as his Character Transformation #79 (degree of fold development) or his Character Transformation #81 (lateral fold scale condition). However, we were able to discern one very distinct apomorphy related to this (see our Transformation Series 25).

[78] Gradual, rather than abrupt transition from the neck scales to the ventrals. Good (1988) mentioned this feature as characteristic of the unique specimen of *A. kalaina* (= *A. fuscolabialis*) and *A. fuscolabialis*. Although this might be considered a posteriori an autapomorphy of *A. fuscolabialis*, a priori we cannot differentiate this species from several others (e.g., *A. matudai*, *A. chiszari*, and *A. bogerti*), and attempting to distinguish among species merely results in insurmountable characterization problems.

[81] Gradual transition from lateral fold granulars to dorsals. We did not think that the distinction between characters was sufficiently objective to use a priori. However, a posteriori a trend may be evident. Our difficulty in counting longitudinal dorsal scale rows (see Good’s [1988] Character Transformation #71) was only partially due to this transformation.

[85] Nongranular scales on trailing edges of limbs. Good (1988: 30) regarded *A. species* “Guerrero” (his *A. deppii*), *A. mixteca*, and *A. oaxacae* to be the only species that exhibit nongranular scales on the trailing surfaces of the limbs. We were unable to find an objective distinction among conditions and could not verify this observation.

[86] “Tendency to gradual transition” (Good, 1988: 30) of granulars to nongranulars on the forearm present or absent. Like the previous transformation we were unable to perceive any definable distinctions among *Abronia* on this basis.

[93] Broad head present. Good (1988) coded all species of *Abronia*, except *A. reidi*, *A. mitchelli* (even though the single specimen is a female and this feature can only be ade-

quately evaluated in males), and *A. ornelasi* (though UTA R-12499, not examined by Good, does exhibit the apomorphy), to have broad heads. We question how he evaluated this in species for which there are (or were until very recently) no adult males (generally where the feature is best exhibited) in collections, such as in *A. mitchelli*, *A. chiszari*, and *A. bogerti*.

[97] Number of crossbands 6–8 or more than 9. Good coded *A. salvadorensis*, *A. graminea*, *A. taeniata*, *A. species* “Guerrero” (his “*A. deppii*”), *A. oaxacae*, and *A. mixteca* as having the lower number of crossbands and all other *Abronia* as having more than 9. We found this more difficult to characterize than Good *a priori* because of interspecific variation (although an *a posteriori* trend is likely), and we are confused as to how he could code *A. smithi* (his “*A. ochoterenai*”) inasmuch as this species is longitudinally striped in juveniles and lacks bands in adults. See following comment.

[99] Loss of dorsal pattern. Good (1988) reported the absence of color pattern in *A. smithi* (his “*A. ochoterenai*”), *A. matudai*, and *A. graminea*. We find this transformation to be extremely difficult to deal with; some species have a distinct pattern in adults, but in others it becomes obfuscated with age (as in *A. oaxacae*). In *A. fimbriata* the juveniles are longitudinally striped, a distinct crossbanding pattern develops in subadults, but all pattern is lost in adults. So, what little ontogenetic evidence there is points to nonhomology among those species exhibiting loss of adult pattern and we exclude this character from our analysis for this reason.

[100] Ventral marking. Good (1988) coded a number of features as independently derived from a condition of no ventral markings; only two of these concern *Abronia*. *Abronia chiszari* and *A. bogerti* were coded as having the apomorphic condition of “characteristic ventral speckling” and *A. kalaina* (= *A. fuscolabialis*) and *A. fuscolabialis* share crossbanding on the underside of the tail. Only the ventral coloration of *A. chiszari* and *A. bogerti* is possibly informative, the tail crossbanding of *A. fuscolabialis* and *A. kalaina* reduced to being an autapomorphy by reason of our synonymy of *A. kalaina* with *A. fuscolabialis*. We have hesitated to use the

ventral color pattern of *A. chiszari* and *A. bogerti* (“characteristic speckling” [Good, 1988: 33]) as a synapomorphy because of our lack of confidence in scoring other species in *Abronia* (e.g., *A. matudai*, *A. salvadorensis*, and *A. fimbriata*) for this characteristic.

[Not discussed by Good, 1988.] Pterygoid teeth. Gauthier (1982) suggested that lack of pterygoid teeth is a synapomorphy of *Abronia*. However, subsequently, Hidalgo (1983) reported large pterygoid teeth in the newly described *A. salvadorensis*. Unfortunately, Good (1987) considered reduction of pterygoid teeth as a synapomorphy of a group composed of *Barisia* (although some individuals of *B. imbricata*, like AMNH 71307, have well-developed pterygoid teeth) + *Mesaspis* (although some have pterygoid teeth; see below) + *Abronia*, and complete loss of pterygoid teeth as a synapomorphy of *Mesaspis* + *Abronia*. Apparently Good was unaware of Hidalgo’s (1983) earlier report of pterygoid teeth in *A. salvadorensis*. Additionally, his assertion of synapomorphy is puzzling in the face of his statement (1987: 292) that pterygoid teeth are “usually” absent (i.e., sometimes present) in *Mesaspis*. Assuming that the phylogeny of *Mesaspis* is as was hypothesized by Good (1988), for absence to be a synapomorphy of *Mesaspis* + *Abronia* requires the arbitrary choice of delayed transformation character optimization (DELTRAN). That is, this optimization requires reacquisition of pterygoid teeth in at least *M. gadovii*,¹⁶ inasmuch as *M. gadovii* was posited by Good to be the sister taxon of other *Mesaspis*, rather than independent loss in *Abronia* and “some” *Mesaspis*. In light of this putative synapomorphy being contingent on a choice among equally parsimonious character optimizations within one set of results, and adding the observation that some *Abronia*, as well, have pterygoid teeth, the loss of pterygoid teeth cannot be considered evidence of a special relationship of *Abronia* + *Mesaspis*.

We have attempted to survey the presence or absence of pterygoid teeth in *Abronia* using

¹⁶ *Mesaspis gadovii*: AMNH 90945–48, 98008 show some development of pterygoid teeth; 90944 does not. Pterygoid teeth do not appear in our skeletons of *M. moreletii* (AMNH 90980) or *M. viridiflava* (AMNH 103230).

radiographs and examining skeletons. Few *Abronia* skeletons are available and experiments with radiographing *Barisia imbricata* skeletons show that evaluating this characteristic via radiographs is extremely difficult because of the small size and poor definition of these teeth, and the difficulty of distinguishing pterygoid teeth against a background of the rugose cephalic osteoderms typical of the gerrhonotine clade. *Abronia deppii* (radiographs and direct observation of the holotype), *A. species* "Guerrero" (radiograph; reported by most previous authors as *A. deppii*), *A. fuscolabialis* (AMNH 85634, radiograph), *A. mixteca* (AMNH 91001, skeleton), *A. oaxacae* (AMNH 93208, skeleton), *A. aurita* (radiographs), *A. ochoterenai* (radiographs of both known specimens), *A. taeniata* (reported by Gauthier, 1982, and Good, 1987), *A. montecristoi* (Hidalgo, 1983; personal obs.), *A. lythrochila* (radiographs), *A. anzueto* (radiographs), *A. fimbriata* (radiographs and direct observation on AMNH 137786), and *A. ornelasi* (AMNH 137783, radiograph) lack pterygoid teeth. Only *Abronia leurolepis* (radiograph—pterygoid teeth tentatively identified), *A. salvadorensis* (Hidalgo, 1983; personal obs.), and *A. reidi* (UIMNH 73732, personal obs.) are known to have pterygoid teeth. We have also examined radiographs of *A. bogerti* (the unique holotype) and *A. chiszari* (UNAM-LT 3151) and cannot see pterygoid teeth in these specimens. However, their small size may make it impossible to see pterygoid teeth on radiographs. At this time we have not examined radiographs of *A. smithi*, *A. matudai*, *A. gaiofantasma*, or *A. mitchelli*. We have not attempted to use this character in our analysis of *Abronia* because of the difficulty of identifying pterygoid teeth in radiographs.

RESULTS

ANALYSIS 1. REFERENCE ANALYSIS OF "FIXED" CHARACTERS ONLY: When those transformations which showed intraspecific variation (Character Transformations 1–7, 9–11, 17–19, 23 (1 → 2 only), 26, and 27) (see Appendix 2) were excluded from analysis, 140 equally parsimonious trees were recovered (length = 24; ci = 0.792; ri = 0.902). Successive approximations reduced the number

under consideration to 38, but the strict consensus topology (fig. 29) remained the same. Evaluating a matrix in which Character Transformation 16 and 23 were reduced to binary transformations by a priori union of the apomorphic states ("simplified" coding) also resulted in the discovery of 140 equally parsimonious trees (length = 23; ci = 0.783; ri = 0.886), which differed only in the placement of *Abronia matudai*. In the "simplified" analysis *A. matudai* was placed in a consensus polytomy with the remainder of the *A. aurita* group, unlike in the analysis allowing a priori polarized multicharacter transformations, in which it was considered the sister taxon of the *A. aurita* group. This difference is due only to the different coding of Character 16 (supra-auricular scale condition). The support for the consensus stems (fig. 29) is relatively straightforward. Stem 1 (from fig. 29) is supported by: 8.1 (reduction from 4 to 3 or fewer tertiary temporals (convergent in *A. reidi* and *A. oaxacae*); 12.1 (expanded lower temporals); and 24.1 (imbricate neck scales). Stem 2 is supported unambiguously only by (23.1) the reduction from eight to six or fewer longitudinal nuchal scale rows. Stem 3, the *A. aurita* group, is supported only by (16.1) the presence of protuberant, but not spine-like, supra-auricular scales. Stem 4 is supported solely by (16.2) the presence of spine-like supra-auricular scales. Stem 5, the *A. deppii* group, is supported only by the casqued appearance of the head (15.1). Stem 6 is supported by three primary temporals in contact with the postocular scales as well as (28.1) the checkered appearance of the body scales. Stem 7 is supported unambiguously by three features: (21.1) oblique lateral scale rows, (24.2) large lateral neck scales, and (25.1) shallow ventrolateral fold. Stem 8 is supported only by (14.1) three occipital scales (convergent in *A. salvadorensis*), and Stem 9 is supported only by (22.1) nuchal osteoderms strongly reduced. Lack of resolution within polytomies is due predominantly to absence of evidence, although two features (30) color of circumorbital region and (29) lip color, were incongruent in the *A. aurita* group.

ANALYSIS 2. BASELINE ANALYSIS OF ALL DATA: When the data matrix (Appendix 2), with all polymorphisms included, was ana-

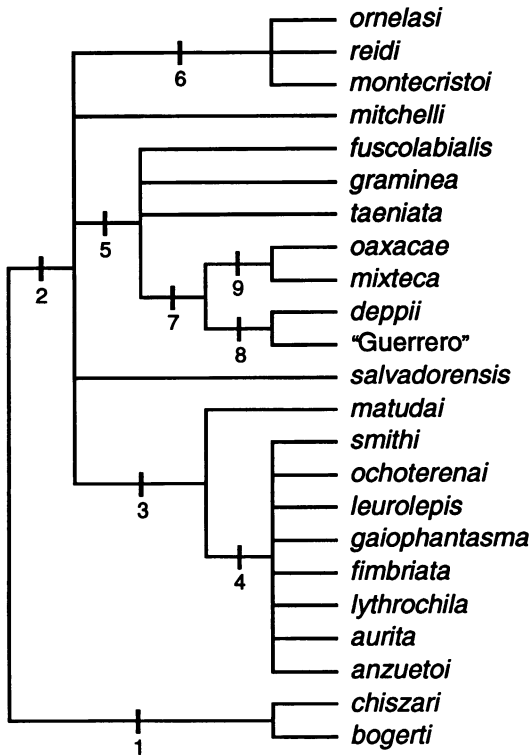


Fig. 29. Strict consensus of 140 equally parsimonious trees (24 steps, $ci = 0.792$, $ri = 0.902$) recovered from "fixed" characters-only analysis.

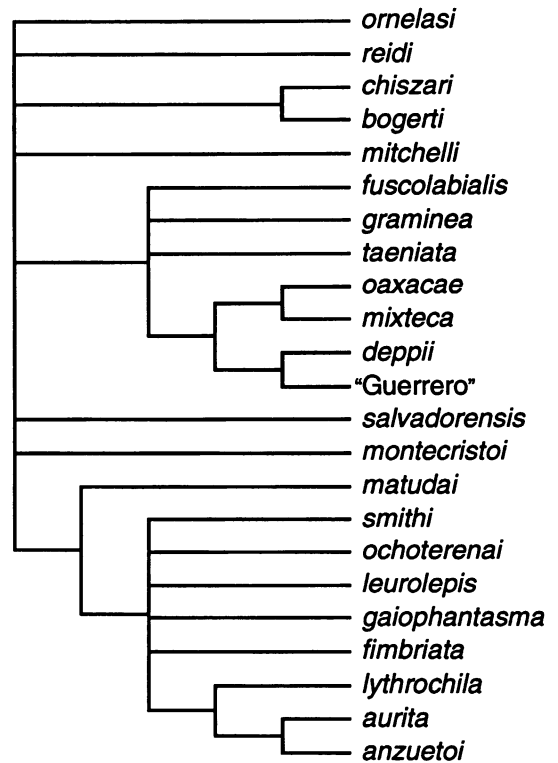


Fig. 30. Strict consensus of 1937 equally parsimonious trees (56 steps, $ci = 0.607$, $ri = 0.784$) from "baseline" analysis.

lyzed (referred to subsequently as the "baseline analysis"), we discovered 1937 trees of 56 steps ($ci = 0.607$; $ri = 0.784$). The strict consensus of these is shown in figure 30. When this "baseline" data matrix is optimized onto the 140 trees derived from the "fixed" data-only analysis (Analysis 1), it is clear that none of the "fixed" data-only trees minimize the length of an optimized tree for all of the data (length on "fixed" data-only trees = 64–67; $ci = 0.507$ – 0.531 ; $ri = 0.676$ – 0.706 —the "fixed" trees are 8–11 steps longer for all of the data than are those trees discovered using all data in the "baseline" analysis). The reason for this is when whole transformation series are rejected only because some taxa are variable, even when many taxa may be "fixed" for cells in that column of the matrix, there are fewer hypotheses of homology (marks of history) available to constrain global hypotheses of evolution. Nevertheless, the number of possible trees has grown enor-

mously by the addition of all of the "polymorphic" characters, implying that this class of characters is significantly more homoplastic than "fixed" characters, as predicted by Kluge and Farris (1969).

However, successive approximations, starting with the 1937 baseline trees,¹⁷ resulted in abandoning all except 78 of these trees. The strict consensus tree of these (also one of the equally parsimonious topologies) is shown in figure 31. The salient differences between the successively approximated trees and the original set of trees produced under the baseline analysis is that: (1) the *Abronia reidi* group + *A. montecristoi* is consistently

¹⁷ We recognize that using successive approximations on a matrix containing polymorphisms (i.e., {01}) that are optimized to one or the other character to minimize tree length may have unforeseen effects. We include this successive approximation only for comparison with results for the remaining analyses.

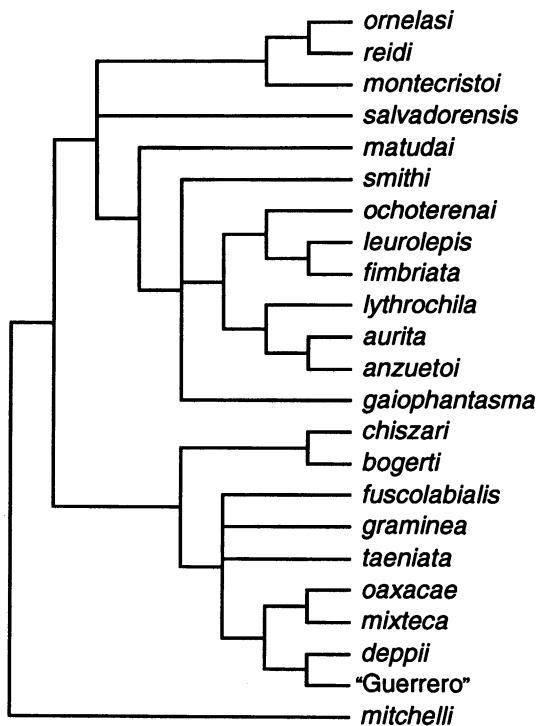


Fig. 31. Strict consensus of 78 equally parsimonious trees (56 steps, $ci = 0.607$, $ri = 0.784$) attained through successive approximations from 1937 "baseline" analysis trees.

supported after successive approximation; (2) considerably more resolution is revealed in the *A. aurita* group; (3) the *A. aurita* group is consistently placed in a monophyletic group in combination with the *A. reidi* group, *A. montecristoi*, and *A. salvadorensis*; (4) the *A. bogerti* group is consistently placed as the sister taxon of the *A. deppii* group; and (5) *A. mitchelli* is consistently placed as the sister taxon of all other *Abronia*. Resolution of the *A. fuscolabialis*–*A. graminea*–*A. taeniata* polytomy is not possible. Six alternatives among the *A. salvadorensis*–*A. aurita* group section are not rejected by the data, differing in: (1) whether *A. salvadorensis* is the sister taxon of the *A. aurita* group or in polytomy with the *A. aurita* group and the *A. montecristoi*–*A. reidi* group, or the sister taxon of the *A. aurita* group + (*A. montecristoi* + *A. reidi* group); (2) whether *A. gaiophasma* is the sister taxon of the clade containing *A. ochoterenai*–*A. anzueto*.

Compared with the "fixed" analysis (Anal-

ysis 1) the results of including "variable" characters has resulted in resolving relationships in group *A. ornelasi* + *A. reidi* + *A. montecristoi*; it has placed the *A. deppii* and *A. bogerti* groups as the composite sister taxon of the group composed of the *A. reidi* group, *A. aurita* group, *A. salvadorensis*, and *A. montecristoi*. Most trenchantly, the addition of "variable" characters has placed *A. mitchelli* as the sister taxon of all other *Abronia* and placed the *A. bogerti* group as the sister taxon of the *A. deppii* group.

A priori weighting of the transformations composed of "invariant" characters (8, 12–16, 20–22, 23 [only 0 → 1], 24–25, 28–30) two times the weight of "variable" characters resulted in the acceptance of 804 trees (minimum unweighted length = 56; $ci = 0.607$; $ri = 0.784$ —maximum unweighted length = 57; $ci = 0.596$; $ri = 0.775$). The strict consensus tree of these (fig. 32) is similar to that of the successively approximated trees (fig. 31), except that the *Abronia bogerti* group and *A. mitchelli* are in a consensus polytomy at the base of the cladogram rather than consistently placed, respectively, as the sister taxon of the *A. deppii* group, and as the sister taxon of all other *Abronia*. Also, less resolution obtains in the *A. aurita* group. A priori weighting of the "invariant" character transformations by three or four times resulted in the discovery of 544 trees of one step longer than the minimum found under equal weighting (i.e., length = 57; $ci = 0.596$; $ri = 0.775$), whose consensus differs from that shown in figure 32 only in having the *A. bogerti* group placed consistently as the sister taxon of all other *Abronia*. That is, with 2:1 a priori weighting the topology is ((*A. bogerti* group) (*A. mitchelli*) (*A. deppii* group) (other *Abronia*)) (fig. 32), but with 3:1 weighting the topology changes to ((*A. bogerti* group) ((*A. deppii* group) (*A. mitchelli*) (other *Abronia*))). This change is effected by the strong weighting on 23.1, eight transforming to six nuchal scale rows. In other words, it takes at least a three-fold differential weighting of "fixed" over "variable" characters a priori to make the entire data produce results similar to those found using "fixed" data only (Analysis 1).

Notably, a number of "variable" characteristics are coherent to varying degrees on the "fixed" trees (Analysis 1): 1.1 (enlarged supranasal scales), 2.1 (frontonasal absent),

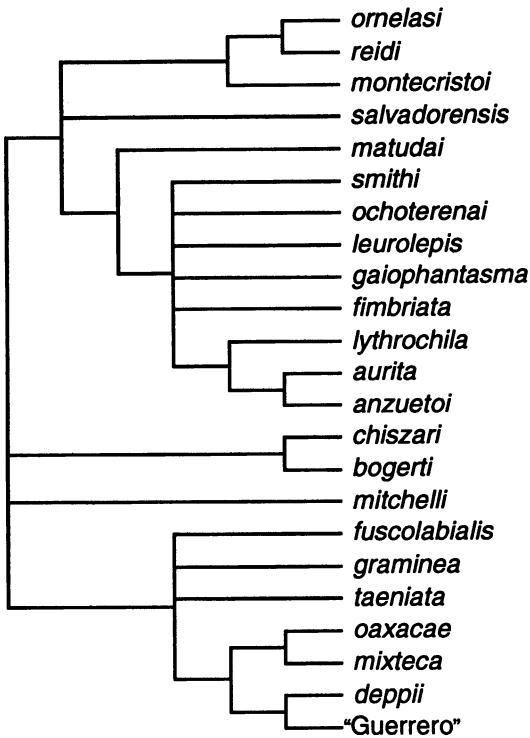


Fig. 32. Strict consensus of 804 trees reached by 2:1 "fixed" to "variable" character weighting in the "baseline" analysis (minimum unweighted length = 56; ci = 0.607; ri = 0.784—maximum unweighted length = 57; ci = 0.596; ri = 0.775).

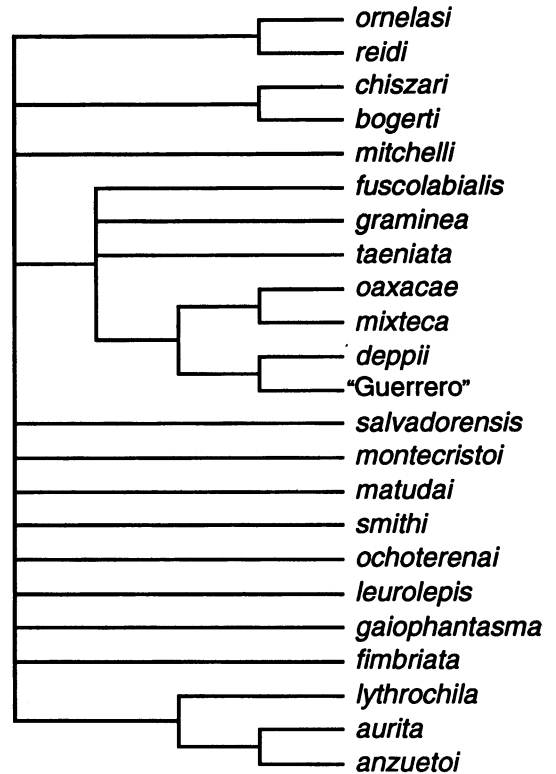


Fig. 33. Strict consensus of 11,000 equally parsimonious trees (length = 54, ci = 0.593; ri = 0.768) with character transformations 16 and 23 having apomorphic conditions (i.e., "1's and 2's") combined.

3.1 (frontonasal-nasal scale contact), 4.1 (canthal-posterior internasal fusion), 5.1 (anterior superciliary scale size), 6.1 (superciliary-canthalorear contact), 7.1 (broadly separated postocular and lower primary temporal), 9.1 (three secondary temporals), 10.1 (parietal-median supraocular contact), 17.1 (penultimate supralabial in contact with orbit), 19.0–1 (postmental scale condition), 23.0–1 (number of longitudinal nuchal scale rows), and 27.1 (14 ventral scale rows). When the "variable" cells are optimized onto the trees produced by the "baseline" matrix (Analysis 2) these transformations become even more coherent, thereby meeting our requirement that the preferred trees must summarize all of the implications of the data in the most parsimonious fashion possible.

Collapsing the additive multicharacter transformations to binary (i.e., "simplified" coding—lumping 1's and 2's as 1's in Char-

acter Transformations 16 and 23) made for great topological instability. Because of the memory limitations of the Macintosh IIfx computer used for these analyses, we stopped the analysis when it had found 11,000 equally parsimonious trees (length = 54, ci = 0.593; ri = 0.768). The strict consensus tree representing these is shown figure 33. The results from this "simplified" data matrix show less consistent resolution than those discovered by the multistate "baseline" matrix, evidenced particularly by the failure of the *A. aurita* group to resolve consistently as monophyletic with respect to *A. salvadorensis* and *A. montecristoi*. The reason for this is that Character 16 (supra-auricular scale condition) when reduced to containing only one apomorphic character is insufficient to resolve the group in the face of "pressure" from other character transformations.

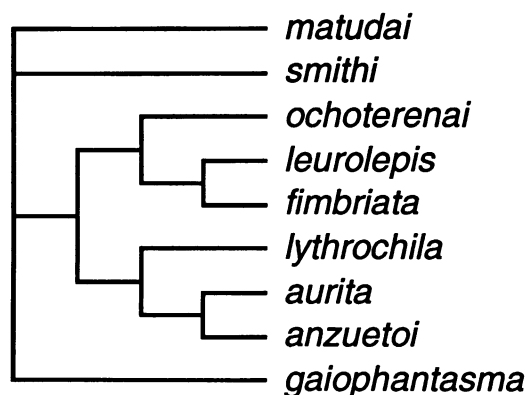


Fig. 34. Component of a strict consensus of 310 equally parsimonious trees (length = 54, ci = 0.593; ri = 0.768) selected by successive approximation from the previous 11,000.

Successive approximation reduced these 11,000 trees to 310 (fig. 34). The consensus of these trees is the same as for those trees discovered by successive approximations from the 1937 trees generated for the baseline data matrix (fig. 31), except in the placement of *A. matudai*. Allowing a priori multicharacter transformation resulted in the placement of *A. matudai* as the sister taxon of the remaining *A. aurita* group in figure 31 and in a polytomy at the base of the *A. aurita* group in figure 34. Again, these results are similar to those of the "fixed" analysis (Analysis 1; fig. 29) when Character Transformations 16 and 23 are "simplified."

Weighting the "invariant" character transformations two times the weight of the "variable" character transformations in this "simplified" matrix resulted in the discovery of 1976 trees (minimum unweighted length = 54; ci = 0.593; ri = 0.768—maximum unweighted length = 55; ci = 0.582; ri = 0.758) (strict consensus of these shown in fig. 35). The substantive difference from the consensus of the successively approximated trees (fig. 34) is that *A. mitchelli* is not consistently considered the sister taxon of all other *Abronia*, this position sometimes being taken by the *A. bogerti* group. Also, the position of *A. fimbriata* has changed, and somewhat less resolution obtains within the *A. aurita* group. Increasing the weighting of "invariant" character transformations three and four times

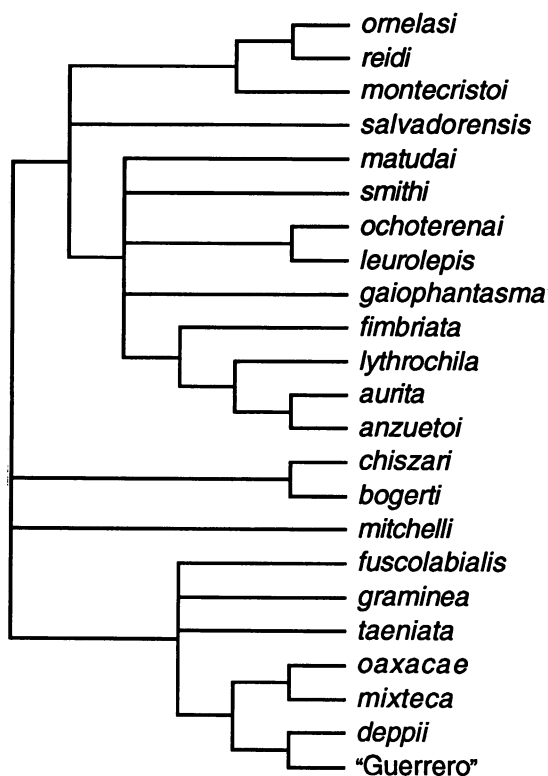


Fig. 35. Strict consensus of 1976 trees arrived at with 2:1 "fixed" to "variable" weighting and character transformations 16 and 23 with apomorphic conditions combined (minimum unweighted length = 54; ci = 0.593; ri = 0.768—maximum unweighted length = 55; ci = 0.582; ri = 0.758).

that of "variable" characters reduced the number of trees from 1976 to 1482 (those of unweighted length = 55; ci = 0.582; ri = 0.758). The strict consensus of this differs from 2:1 weighting (fig. 35) only in the consistent placement of the *A. bogerti* group as the sister taxon of all other *Abronia* rather than in a basal polytomy with *A. mitchelli*, the *A. deppii* group, and a group composed of the *A. aurita* group, *A. reidi* group, *A. salvadorensis*, and *A. montecristoi*.

ANALYSIS 3. "ANY INSTANCE" ANALYSIS: In the "any instance" analysis (see Appendix 3 for data matrix), the unpolarized but variable transformations (2, 3, and 19) were optimized a posteriori to maximize tree definition, as discussed under Methods. Considering Character Transformations 16 (supra-

auricular scale condition) and 23 (number of nuchal scale rows) as additive multicharacter transformations resulted in the discovery of 90 equally parsimonious trees (length = 80; ci = 0.438; ri = 0.694). Figure 36 shows the strict consensus for these 90 trees. The *Abronia bogerti* and *A. reidi* groups are highly corroborated. The *A. deppii* and *A. aurita* group are also consistently resolved. For most of the discovered equally parsimonious cladograms *Abronia mitchelli* forms the sister taxon of all other *Abronia*, but in some trees the *A. reidi* group forms the sister taxon of all other species.

The relationships among *A. fuscolabialis*, *A. graminea*, *A. taeniata*, and the rest of the *A. deppii* group are unclear under the assumptions of this analysis, with three topologies of these taxa obtaining under topological arrangements of near neighbors. In this analysis, *A. mixteca* appears as the sister taxon of a clade composed of *A. oaxacae*, *A. deppii*, and *A. species "Guerrero,"* rather than as the sister taxon of *A. oaxacae*, as previously posited by Bogert and Porter (1967) and Good (1988) (as well as in our Analyses 1 and 2). The evidence supporting *A. mixteca*–*A. oaxacae* monophyly is three occipital scales (Character 14.2). The conflicting evidence supporting the association of *A. oaxacae* with *A. deppii* and *A. species "Guerrero"* is character 6.1 (lack of superciliary-cantholoreal contact; variable in all three species, as well as in *A. graminea*, *A. smithi*, and *A. salvadorensis*) and 17.1 (penultimate supralabial in contact with the subocular-postocular scale series; variable in *A. oaxacae* and *A. deppii*; convergent widely elsewhere in the *Abronia* cladogram). A posteriori, one can argue that *A. oaxacae* shares with *A. deppii* and *A. species "Guerrero"* a more well-developed head casque than the rest of the species in the *A. deppii* group.

Abronia salvadorensis is usually placed as the sister taxon of the *A. aurita* group in this set of topologies, but sometimes as the sister taxon of *A. montecristoi* + *A. aurita* group, or in a polytomy with these two taxa, or sometimes as the sister taxon of *A. montecristoi* (in which case they form the sister taxon of the *A. aurita* group), and occasionally in the arrangement ((*A. salvadorensis* (*A. aurita* group (*A. montecristoi* + *A. ornelasi*

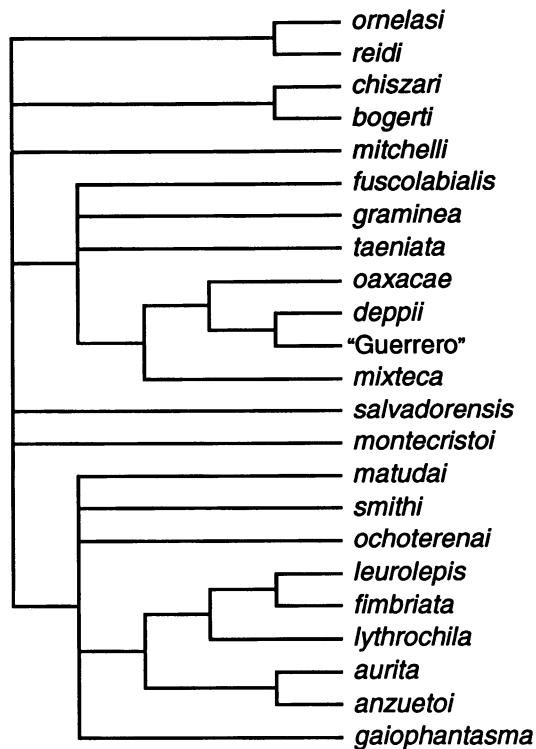


Fig. 36. Strict consensus of 90 equally parsimonious trees (length = 80; ci = 0.438; ri = 0.694) discovered in the "any instance" analysis.

group))). *Abronia montecristoi* is sometimes placed as the sister taxon of *A. salvadorensis* + *A. aurita* group and as the sister taxon of the *A. reidi* group.

The *Abronia aurita* group is corroborated in all topologies solely by 16.1 or 16.2 (supra-auricular scales enlarged to some degree). The 16.1 → 16.2 ordering is neither rejected nor supported by congruency with other characters. Seven alternatives of topology were discovered for the five nonresolved *A. aurita* group taxa (i.e., *A. smithi*, *A. ochoterenai*, *A. matudai*, *A. gaiophasma*, and the group containing *A. aurita* and *A. leurolepis*, among others).

Successive approximation resulted in the restriction of results to two trees of the original 90 (fig. 37). The only difference between these two trees is in the placement of *Abronia gaiophasma* as the sister taxon of *A. smithi* + *A. ochoterenai*, or in a polytomy with *A. smithi* + *A. ochoterenai* and the stem subtending the species including *A. aurita* and

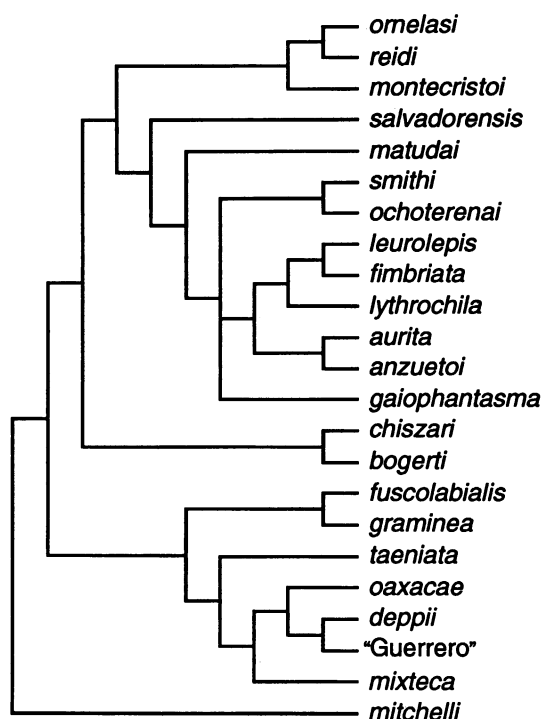


Fig. 37. Strict consensus of 2 trees selected from the previous 90 (length = 80; ci = 0.438; ri = 0.694) by successive approximations. See figure 43.

A. leurolepis. Compared with the original 90 trees, the successively approximated trees show a broad-structure resemblance to the "baseline" successively approximated results (fig. 31), the differences being that in the "any instance" results: (1) *A. salvadorensis* is consistently placed as the sister taxon of the *A. aurita* group; (2) a considerably different topology obtains within the *A. aurita* group; (3) *A. fuscolabialis*, *A. graminea*, and *A. taeniata* are consistently resolved; (4) the *A. bogerti* group is associated not with the *A. deppii* group, but with the group composed of the *A. aurita* group, *A. reidi* group, *A. montecristoi*, and *A. salvadorensis*, this due to weighting of the character 17.1 (penultimate supralabial entering orbit).

Weighting "fixed" character transformations twice as much as "variable" ones resulted in finding 10 trees (minimum unweighted length = 80; ci = 0.432; ri = 0.687—maximum unweighted length = 81; ci = 0.432; ri = 0.687) (two of these trees were

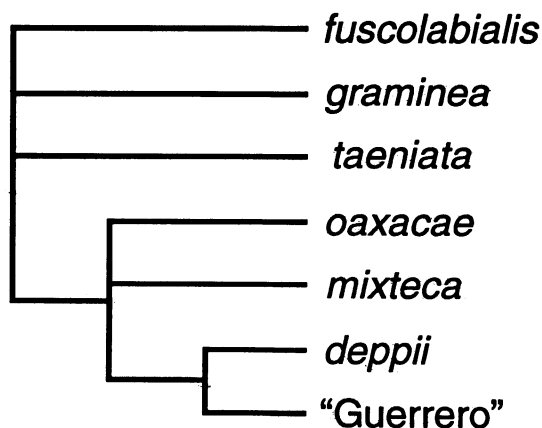


Fig. 38. Component of a strict consensus of 10 trees found by 2:1 "fixed" to "variable" character weighting within the "any instance" data matrix (minimum unweighted length = 80; ci = 0.432; ri = 0.687—maximum unweighted length = 81; ci = 0.432; ri = 0.687).

those discovered by successive approximation), the only consensus difference from that seen in figure 37 being that *A. fuscolabialis*, *A. graminea*, and *A. taeniata* were not consistently resolved (the relevant part of the strict tree of these shown in fig. 38). Changing the ratio of weighting from 2:1 to 3:1 resulted in 48 trees being discovered (minimum unweighted length = 81; ci = 0.432; ri = 0.687—maximum unweighted length = 83; ci = 0.422; ri = 0.673), the consensus of which shows reduced consensus resolution among major groups of *Abronia* over those seen in previous "any instance" analyses (fig. 39). Increasing the weighting ratio to 4:1 reduces the number of trees from 48 to 42 (those with an unweighted length = 83), and consistently places the *A. bogerti* group as the sister taxon of the rest of *Abronia*, but has no other effect on topology. This change in the position of the *A. bogerti* group as differential weighting of "fixed" character transformations is increased as an effect consistently seen previously.

Again, if the "any instance" data set is optimized onto the trees discovered by the "fixed" characters-only analysis (the 140 trees found by Analysis 1), one gets a minimum length of 96 (ci = 0.365; ri = 0.585) and a maximum length of 105 (ci = 0.333; ri = 0.524), which is a minimum of 16 steps lon-

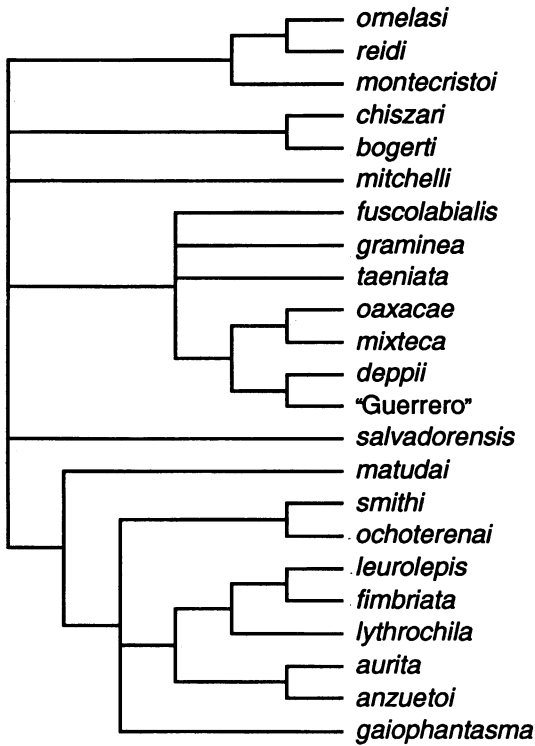


Fig. 39. Strict consensus of 48 trees found by 3:1 "fixed" to "variable" character weighting within the "any instance" data matrix (minimum unweighted length = 81; ci = 0.432; ri = 0.687—maximum unweighted length = 83; ci = 0.422; ri = 0.673).

ger than that produced by the "any instance" results for the "any instance" matrix. In other words, the "fixed" data allow trees to be discovered that are 20% poorer at describing the character distributions in the "any instance" matrix, than the trees discovered by using all of the data in the "any instance" matrix.

Coding Character Transformations 16 and 23 as binary (i.e., "simplified" coding—1's and 2's combined as 1's in the data matrix) resulted in the discovery of 56 trees (length = 75; ci = 0.440; ri = 0.696) summarized in a strict consensus shown in figure 40. The trenchant difference between these results and those found under the assumption of multi-character additivity was that the *Abronia aurita* group failed to resolve consistently, once again because the *ordered* distinction between 16.1 and 16.2 was necessary to accomplish resolution. Successive approximation

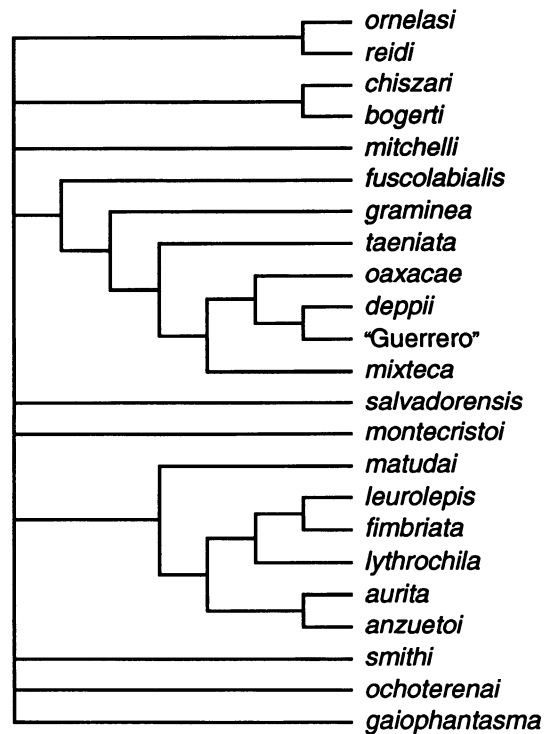


Fig. 40. Strict consensus of 56 equally parsimonious trees found when apomorphic characters in transformations 16 and 23 of the "any instance" data matrix were combined (length = 75; ci = 0.440; ri = 0.696).

of these 56 trees resulted in only five trees of the 56 trees being retained (consensus of these is shown in fig. 41).

A weight of two on "fixed" character transformations resulted in discovering 15 trees (minimum unweighted length = 75; ci = 0.440; ri = 0.696—maximum unweighted length = 76; ci = 0.434; ri = 0.688). The only difference between this consensus and that of the trees discovered by successive approximations (fig. 41) is that with 2:1 weighting, *A. graminea* and *A. taeniata* form a consensus polytomy with the *A. deppii* subgroup, rather than as successive out-taxa. When the "fixed" character transformations were weighted three times over the "variable" character transformations 54 trees were discovered (minimum unweighted length = 76; ci = 0.434; ri = 0.688—maximum unweighted length = 78; ci = 0.423; ri = 0.674) (strict consensus in fig. 42). With this a priori

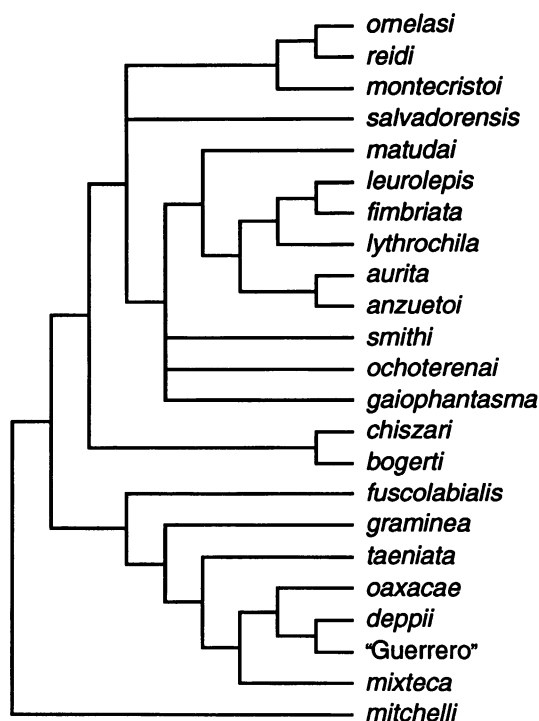


Fig. 41. Strict consensus of 5 equally parsimonious trees selected among the previous 56 by successive approximations (length = 75; ci = 0.440; ri = 0.696).

weighting, resolution among the species groups dissolves and *A. mixteca* becomes the sister taxon of *A. oaxacae*. Placing the differential weighting at 4:1 resulted in retaining 44 of the 54 trees discovered under 3:1 weighting (i.e., those with unweighted length = 78). The only difference between 4:1 weighting and 3:1 weighting is that the *Abronia bogerti* group is consistently (and familiarly) placed as the sister taxon of the rest of *Abronia*.

ANALYSIS 4. UNSCALED ANALYSIS: Character numbers in this section do not refer to those in the discussion of characters or in the basic data matrix, but to a recoded matrix, shown in Appendix 4, which was derived from the general matrix. Because there has been a fair amount of character recoding for reasons detailed under Methods and Materials, this is the simplest recourse. The characters that were "polymorphic coded" (i.e., expanded from 0 → 0/1 → 1 to 0 → 1 → 2) were 1–7, 9–11, 17–19, 23 (only 1 → 2), and 26–27.

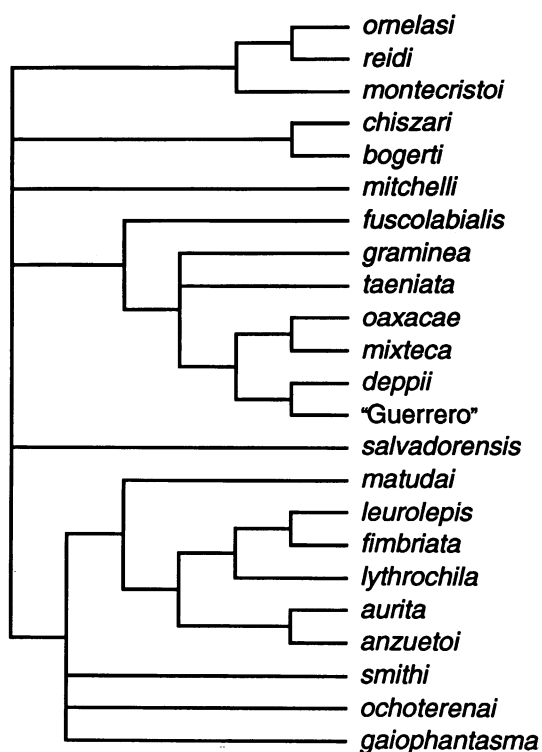


Fig. 42. Strict consensus of 54 trees discovered for the simplified "any instance" data matrix using a 3:1 a priori weighting of "fixed" over "variable" characters (minimum unweighted length = 76; ci = 0.434; ri = 0.688—maximum unweighted length = 78; ci = 0.423; ri = 0.674).

Those left unrecoded were 8, 12–16, 20–22, 23 (only 0 → 1), 24–25, and 28–30. Parsimony analysis of this matrix yielded 138 trees of 120 steps (ci = 0.417; ri = 0.657) (fig. 43). Successive approximation selected one tree from among these (fig. 44), which is also one of the two topologies discovered by "any instance" coding and successive approximation summarized in figure 37. Because this is our preferred tree, apomorphies by stems and lists of changes within transformation series are presented in Appendices 5 and 6.

A priori weighting of this data set by 2:1 is equivalent to the method of scaling, which is discussed subsequently under the "scaled analysis" results.

If the "unscaled" matrix is optimized upon the 140 "fixed" data only topologies (from Analysis 1), the best that the "fixed" data trees can do with the "unscaled" matrix is to

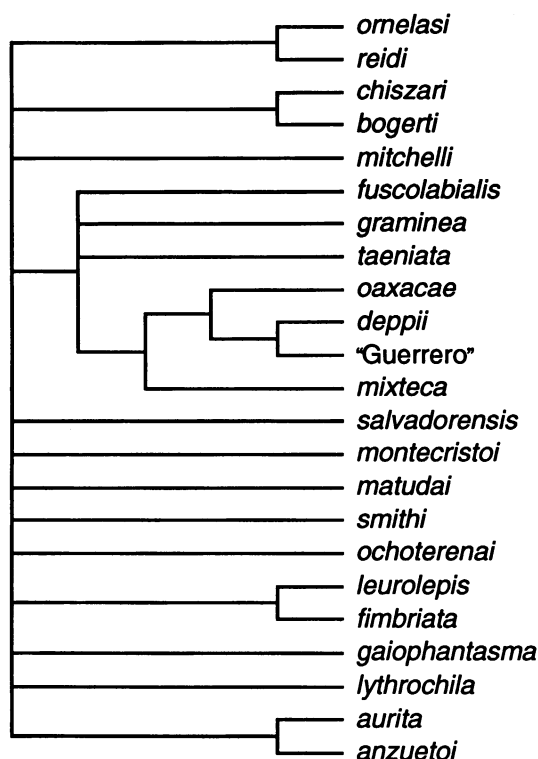


Fig. 43. Strict consensus of 138 equally parsimonious trees discovered using the "unscaled" data matrix (120 steps; $ci = 0.417$; $ri = 0.657$). See figure 37.

produce a solution of 147 steps ($ci = 0.340$; $ri = 0.525$) [maximum is 158 steps ($ci = 0.316$; $ri = 0.471$)], which is 27 steps (18%) poorer than the trees produced by all of the "unscaled" data.

Because the effect of a priori statements of multicharacter polarity in characters 16 and 23 continued to concern us, we, as in the other analyses, reduced these two transformations to binary ("simplified" coding) in a subanalysis. We discovered 104 trees (length = 114; $ci = 0.412$; $ri = 0.656$) (fig. 45 shows the strict consensus). Successive approximation reduced the number of trees under consideration to six, but did increase the length from 114 to 115 ($ci = 0.409$; $ri = 0.651$) (strict consensus shown in fig. 46).

ANALYSIS 5. SCALED ANALYSIS: As explained in Methods, this analysis is really an extension of the previous one, where transformations from "fixation" to "fixation" are

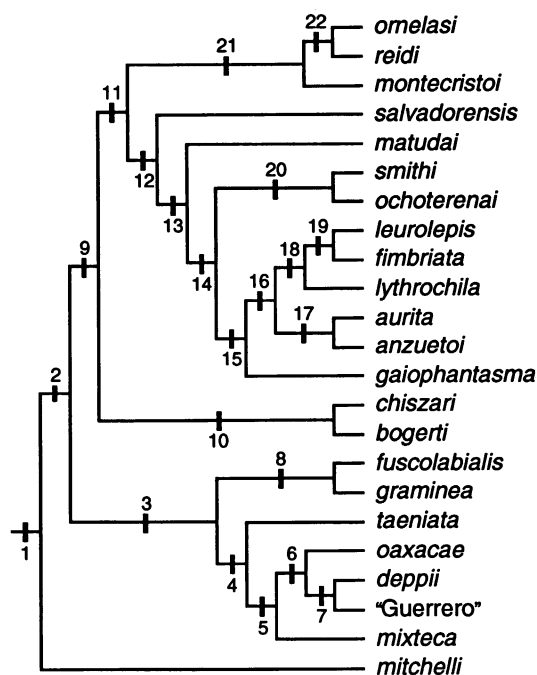


Fig. 44. Single tree selected among the previous 138 (fig. 43) by successive approximations (120 steps; $ci = 0.417$; $ri = 0.657$).

weighted twice 2:1 over the transformations from "fixation" to "variability." That is, in a transformation hypothesized to transform from 0 to 1, the interval was set at two (rather than the normal one), and in a transformation hypothesized to transform from 0 to 0/1, the interval from 0 to 0/1 was set at one. Under the central assumption of the scaled analysis, all character transformations must go through some period of polymorphism (or variability) before fixation. The effect of this a priori weighting is to make "fixations" of equal weight. Running the scaled matrix we discovered two trees (undifferentially weighted length = 120; $ci = 0.417$; $ri = 0.657$), which differ solely in whether *A. fuscolabialis* is considered the sister taxon of the rest of the *A. deppii* group or the sister taxon of *A. graminea*. One of these is the same as our preferred tree found in the "unscaled" analysis shown in figure 44 (*A. fuscolabialis* as the sister taxon of *A. graminea*).

A priori weighting of "fixed" characters over "variable" ones by a ratio of 3:1 resulted in discovering five trees, including some lon-

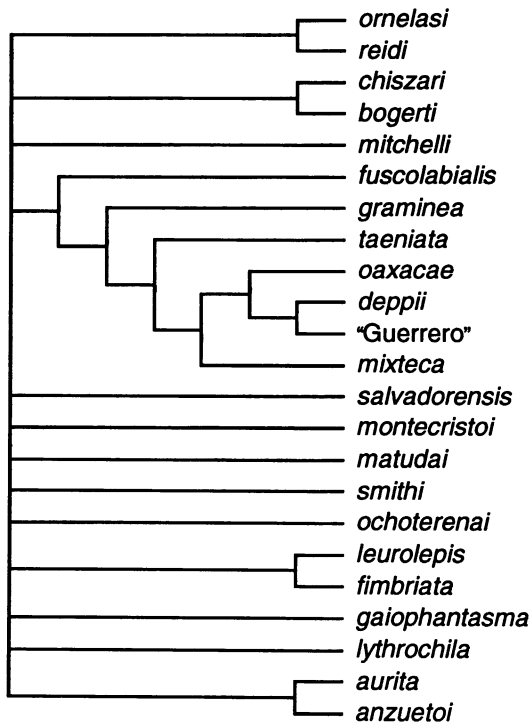


Fig. 45. Strict consensus of 104 equally parsimonious trees (length = 114; ci = 0.412; ri = 0.656) discovered when character transformations 16 and 23 were collapsed to binary.

ger than those discovered without a priori weighting (other than scaling) or successive approximations (minimum unweighted length = 120; ci = 0.417; ri = 0.657—maximum unweighted length = 122; ci = 0.410; ri = 0.657). The only topological difference between this consensus and that of the two trees discovered without a priori weighting (other than scaling) (see fig. 44 for one of these) is that *A. fuscolabialis*, *A. graminea*, and *A. taeniata* are in a consensus polytomy with the *A. deppii* subgroup, and *A. mixteca* fails to be placed consistently as the sister taxon of the *A. deppii* subgroup. When the relative weight of fixed characters was elevated to four, 18 equally parsimonious trees were discovered, some of which distorted the undifferentially weighted length of the tree by three steps (minimum unweighted length = 122; ci = 0.410; ri = 0.657—maximum unweighted length = 125; ci = 0.400; ri = 0.632). In these (see strict consensus in fig. 47) *A. salvadorensis* fails to resolve consistently with

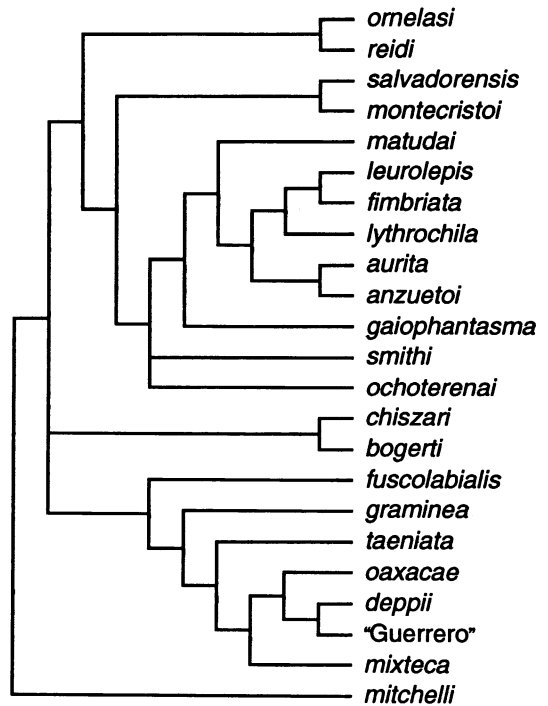


Fig. 46. Strict consensus of 6 trees discovered by successive approximation (length = 115; ci = 0.409; ri = 0.651) starting with the previous 104 trees (simplified "unscaled" data matrix).

the *A. aurita* group and *A. mitchelli* and the *A. bogerti* group alternate as the sister taxon of the other members of *Abronia*, rendering them in a consensus polytomy at the base of *Abronia*. When the weight of "fixed" characters is placed at four times that of the "variable" characters, only 15 trees of the 18 previous remained (those with an unweighted length of 125 steps) in which the *A. bogerti* group was placed as the sister taxon of the rest of *Abronia*.

As in the previous analysis we attempted to evaluate the effects of a priori decision of multicharacter polarity by collapsing Transformations 16 and 23 to binary. Running this simplified matrix, we discovered 28 trees (unweighted length = 115; ci = 0.409; ri = 0.651). The strict consensus of these 28 trees is shown in figure 48. Successive approximation reduced the number of trees under consideration to six, but the strict consensus remained as in figure 48.

As in the previous analysis, a priori weight-

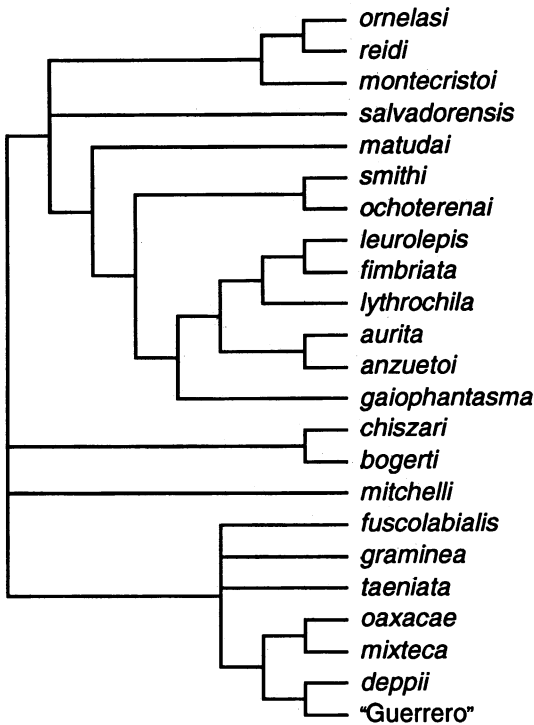


Fig. 47. Strict consensus of 18 trees discovered under the assumption of 4:1 weighting of "fixed" over "variable" characters.

ing of "fixed" over "variable" characteristics in the "simplified" matrix had effects. When the a priori weighting scheme of 3:1 was selected (rather than the 2:1 of scaling), 84 trees were discovered (minimum unweighted length = 115; ci = 0.409; ri = 0.651—maximum length = 117; ci = 0.402; ri = 0.641), which are minimally two steps removed from the overall parsimony without a priori weighting. The only difference from results with 2:1 weighting is that (from fig. 48) the stem subtending *A. oaxacae* + *A. deppii* + *A. species* "Guerrero" collapses, and the sister stem of *A. graminea* collapses. Increasing the ratio of weighting from 3:1 to 4:1 results in the discovery of 288 trees (minimum unweighted length = 117; ci = 0.402; ri = 0.641—maximum unweighted length = 120; ci = 0.392; ri = 0.626). As predicted from other analyses, the only difference from the 3:1 weighting is in the failure of *A. mitchelli* to consistently be placed as the sister taxon of remaining *Abronia*, rendering it in a basal polytomy. Also, as predicted from previous

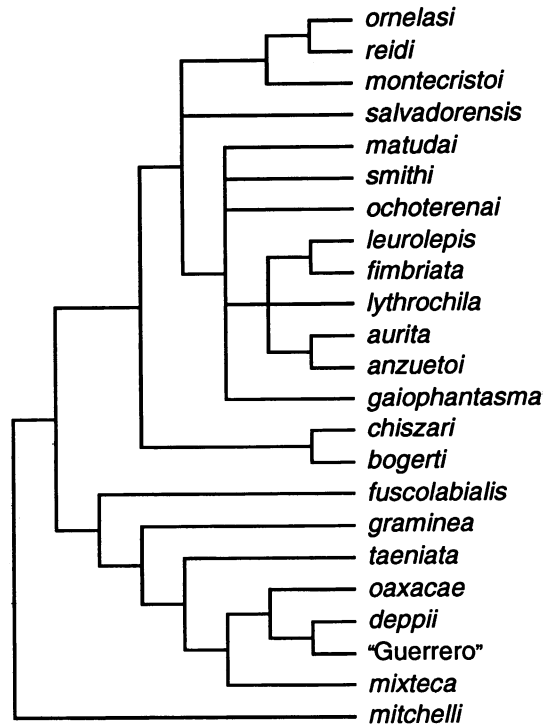


Fig. 48. Strict consensus of 28 equally parsimonious trees under the assumption of "scaling" (i.e., 2:1 weighting of "fixed" over "variable" characters) and collapsing of character transformations 16 and 23 to binary (unweighted length = 115; ci = 0.409; ri = 0.651).

analyses, differential weighting of "fixed" characters over "variable" ones by 5:1 to 8:1 allows the *A. bogerti* group to be placed as the sister taxon of other *Abronia*, with *A. mitchelli* in polytomy with the *A. deppii* group and a group composed of the *A. reidi* group, *A. montecristoi*, *A. salvadorensis*, and the *A. aurita* group (this resulting from the retention of 232 of the previous 288 trees [of unweighted length = 120]).

SUMMARY OF RESULTS AND RECOMMENDATIONS REGARDING ANALYTICAL TECHNIQUES

Clearly, all of the approaches that we have used have drawbacks, but the central issue, that intraspecifically variable characters can carry historical signal, is supported, even though sampling error has likely obfuscated some of this signal. The fact that much of the

evidence from "variable" characters was congruent, or logically consistent, with the tree built solely with a matrix excluding all character transformations that had any polymorphic cells in the matrix (Analysis 1) is evidence that "variable" characters can be included as phylogenetic evidence. More importantly, they *must* be included because the "fixed" data-only results are considerably less efficient at describing the distribution of all data (including intraspecifically variable features) than those trees produced by including "variable" characters, regardless of coding method. This means that there are organismal characters not efficiently "explained" by topologies discovered by analysis of "fixed" characters alone.

With respect to techniques taken to include intraspecifically variable characteristics in analysis, we can make some recommendations. We reject the "baseline" approach to data analysis because it allows variable cells in a data matrix to act only marginally or not at all as "tree-building" evidence (and always within a model that restricts their evolution to terminal stems). We also reject the "any instance" approach because of the problem of informative character reversal being rendered invisible to parsimony measures. We prefer the "unscaled" approach because it maximizes the topological connection among hypothesized homologs and minimizes the number of process assumptions required to make hypotheses of pattern. Nevertheless, the process assumption of the "scaled" approach (that of variability existing from "fixation" to "fixation") is a minimal insult to our theoretical purity. Although the inherent a priori weighting of "fixed" over "variable" character transformations in the "scaled" approach should have the property of buffering the effects of poor individuation of characters, we consider this unsatisfactory because it lowers the parsimony cost of including as evidence character evolution which is detectable only as variability in terminal taxa. Also, the effects of mixing the inherent a priori weighting of the "scaled" approach with the a posteriori weighting of successive approximation is unknown, but likely is not good. Nevertheless, if (1) "variable" characters really are carrying phylogenetic signal, (2) characterization problems are minimized, and (3)

sample sizes of organisms are sufficient, the "scaled" and "unscaled" approaches to data analysis should yield very similar, if not identical, results. If they do not, the implication is that the data set is suffering from sampling and/or characterization problems. That they very nearly agree in our analyses is evidence that we have captured at least a fair measure of the phylogenetic signal. However, that this does not mean that sampling and characterization problems are absent.

Although the heuristic comparisons that we have presented can hardly be taken as forming a rigorous test of a proposition, it does appear that intraspecifically variable characters are more prone to homoplasy than are "fixed" characters (as predicted by Kluge and Farris, 1969). We think that the method of successive approximations is a theoretically defensible means of reducing the noise-to-signal ratio (contra Frost et al., 1991, and Cannatella and de Queiroz, 1989; see Guyer and Savage, 1992), thereby allowing the information content of "variable" characters to be apprehended. In part, our position stems from the observation that the method of successive approximations increased the congruence among results derived from matrices whose preliminary results were quite different. More fundamentally, although the issue of how to select among weighting functions remains to be solved, we believe that all of the implications of data need to be explored.

As noted earlier, we take seriously Stevens' (1991) concern for the effect of the reification of continuous characters into discontinuous ones through the imposition of discontinuous definitions, although we do not see the problem as theoretically tractable. Most of his discussed examples rest more on sloppy individuation of characters and scoring by incautious systematists, than on the inherent problems of imposing discontinuous characterization on continuous variation. Nevertheless, several of the "variable" characters (as well as some of the "fixed" ones) that we have scored for cephalic squamation are just the kinds of characters that concerned Stevens, particularly those having to do with various scale contacts reflecting scale positions. However, as published character definitions we could not reject these features out of hand without attempting to evaluate their

possible contribution to tree resolution. Nevertheless, having used these features in this set of analyses, we do not think that we have uncovered serious problems with respect to characterization. The effect of low a priori differential weighting of what we called "fixed" transformation series was not overwhelming, although heavy differential a priori weighting did cause *A. mitchelli* to move "into" the body of the cladogram and the *A. bogerti* group to move "out" of it. This seems to have been due to one character transformation, number of transverse dorsals, and cannot be considered strong evidence that characterization problems plagued this analysis.

The empirical data to reject the use of multicharacter transformations are not produced by this analysis. With respect to the "intermediacy" of *A. matudai* in having protuberant, but not spinelike, supra-auricular scales (Character 16.1), the ontogenetic hypothesis of transformation from no enlarged supra-auricular scales to moderately enlarged supra-auricular scales in old adults (*A. matudai*) to very enlarged supra-auricular scales starting with subadults (the other members of the *A. aurita* group) is not rejected in our analyses of choice (either "unscaled" or "scaled"). Neither is it strongly supported. When this three-character transformation is reduced to a single binary transformation by union of a priori apomorphies, the topology of the *A. aurita* group changes considerably, as do the topological relationships of near neighbors (e.g., *A. montecristoi* and *A. salvadorensis*).

At this time, we prefer to retain our hypothesis of intermediacy of *A. matudai* in the supra-auricular scale character as well as the cladograms that result from this assumption for reasons detailed above. The other multicharacter transformation that we employed, the number of nuchal scale rows (Character Transformation 23) we retain because its additivity was corroborated by other features, although the rooting of the transformation was not.

So, in summary, we consider that intra-specifically variable characters have provided evidence of evolutionary propinquity; we think that successive approximation has helped illuminate the historical signal; and we stand by the two additive multicharacter

transformations that we hypothesized. What this means practically is that, with the reservations discussed below, we accept the results illustrated in figure 44 ("unscaled" analysis followed by successive approximations), which are closely approximated by the results of the "scaled" analysis (fig. 48).

DISCUSSION OF EVIDENCE AND POSSIBLE ERRORS

Regardless of our discussion of most-parsimonious cladograms, the amount of evidence supporting particular choices of intergroup relationships is not great. The only effect of this concern would be to accept solutions of less resolution, not accept alternative solutions that are less parsimonious for our set of data. Our greatest worry for parsimonious solutions of our data regards the position of *Abronia mitchelli*. Because *A. mitchelli* is represented by a single specimen and the features that prevent it from joining the geographically proximate *A. deppii* group (7.1, no frequency of contact between the subocular and lower primary temporal, and 9.1, never four secondary temporals) are variable in the basal members of the *A. deppii* group, we suggest that there is a possibility that the hypothesized "basal" phylogenetic position of this particular specimen is due to sampling error and that, in agreement with our "fixed" character-only analysis (Analysis 1) it may possibly be more closely related to the *A. deppii* group than our results suggest.

Beyond this, if additional evidence placed the *A. bogerti* group (as do some of our character analyses) as the sister taxon of the rest of *Abronia*, we would not be surprised. The features that tie the *A. bogerti* group to other species of *Abronia* faunistically east of the Isthmus of Tehuantepec are: (7.2) subocular never in contact with the lower primary temporal; (17.1) some frequency of penultimate supralabial in contact with the subocular scale series. Features that would place them as the sister taxon of the rest of *Abronia* are the high number of (20.0) dorsal and (23.0) nuchal scale rows. The *Abronia bogerti* group is composed of species that resemble members of *Elgaria*, while some other members of *Abronia* (e.g., *A. salvadorensis* and *A. mitchelli*) resemble members of *Mesaspis* in general

habitus. Alternatively, the resemblance of the *A. bogerti* group and *Elgaria* may be due to heterochrony inasmuch as species in the *A. bogerti* group are small and also resemble young *Abronia* in body shape.

The association of *A. montecristoi* with the *A. reidi* group does not rest on overwhelming evidence: (13.1) three primary temporals contacting the postocular series; and (28.1) scale coloration. The coloration character may be coded in error for *A. montecristoi* because the unique specimen is strongly faded. The temporal scale character, however, is evidence. In the "unscaled" analysis in which the three-character supra-auricular scale character transformation was reduced to binary, followed by successive approximation (fig. 46), *A. montecristoi* was placed most parsimoniously as the sister taxon of *A. salvadorensis*. This is due to a single feature, a single postmental scale (19.2), which is variable in the putative nearest relatives and could be an artifact of sampling (i.e., *A. montecristoi* is based on a unique specimen), or, the additional or reinterpretation of evidence may support this association. Monophyly of the *A. reidi* group (*A. reidi* and *A. ornelasi*) is well corroborated by a number of features: (1.1) some frequency of supranasal scale expansion (fixed in *A. reidi*; convergent in *A. fimbriata*); (3.1) some frequency of frontonasal-nasal scale in contact (fixed in *A. ornelasi*; convergent at some frequency in *A. aurita* and several members of the *A. deppii* group); (4.1) some frequency of canthal scales fused with posterior internasal scales (convergent elsewhere); (5.1) some frequency of prefrontal scales contact with the superciliaries (convergent in the *A. bogerti* group); (7.1) reversal to contact between the lower primary temporal scale and subocular (convergent at some frequency in "basal" members of the *A. deppii* group and *A. fimbriata* and *A. leurolepis*); and (17.0) antepenultimate supralabial in contact with the subocular-postocular scale series.

The association of the *Abronia reidi* and *A. aurita* groups with *A. montecristoi* and *A. salvadorensis* is supported by a single feature, expanded lateral ventral scales (26.1). Although this feature is apparently reversed in some representatives of *A. lythrochila*, it is otherwise easily seen in all specimens and is easily characterized.

We are not confident about the relationship of *Abronia salvadorensis* with the *A. aurita* group because this rests on a single variable feature, some frequency of increase from 12 to 14 ventral scale rows (27.1), a feature of considerable plasticity across *Abronia*. Nevertheless, this is the most parsimonious placement of *A. salvadorensis*.

Likewise, we are not confident about the posited phylogenetic structure within the *A. aurita* group. *Abronia matudai* is placed as the sister taxon of other members of the *A. aurita* group only because we have accepted the multicharacter polarity of small supra-auricular spines (16.1; seen only in *A. matudai*) being plesiomorphic with respect to large supra-auricular spines (16.2; seen in other members of the *A. aurita* group). Nevertheless, *A. matudai* is phenotypically similar to *A. salvadorensis*, something that would require explanation if these two species were not patristically adjacent. The association of *A. smithi* and *A. ochoterenai* on our preferred cladogram is surprising; however, they are united on this cladogram only by a reversal from some frequency of 14 ventral scale rows back to 12 rows (27.0). The sister taxon of this group (*A. gaiophantasma* to *A. anzuetoii*) is supported by a change to (27.2) fixation of 14 ventral scale rows from variably 14 or 12. So much being dependent on a character transformation of known plasticity (#27) does not inspire great confidence. However, with the possible exception of *A. leurolepis* (known from a single specimen), this group (*A. gaiophantasma*, *A. fimbriata*, *A. lythrochila*, *A. aurita*, and *A. anzuetoii*) is composed of large lizards, which are generally more robust than most other *Abronia* in this clade of lizards from east of the Isthmus of Tehuantepec plus the Sierra de Los Tuxtlas. Within the *A. aurita* group, we are confident that *A. fimbriata*, *A. lythrochila*, *A. anzuetoii*, *A. aurita*, and (with less confidence) *A. leurolepis* form a group. This is supported by (10.1) some frequency of reduced upper primary temporals (fixed in *A. fimbriata*; convergent in *A. reidi*, *A. matudai*, and the *A. bogerti* group); (18.2) strongly elongated posterior infralabial (reversed in *A. leurolepis*; also variable in *A. deppii*); and (30.1) red infralabials (not observable in *A. leurolepis*).

We think that there is a strong possibility that *A. leurolepis* is misplaced. The animal

in question is not conspecific with *A. ochoterenai* as was thought by previous authors, although it does resemble the smaller-bodied species in the *A. aurita* group (*A. ochoterenai*, *A. smithi*, *A. matudai*), not the more robust red-lipped species with which it is currently placed. Primarily, it is allied with *A. fimbriata* and *A. lythrochila* because of (2.1) some frequency of loss of the frontonasal scale and (4.1) some frequency of fused canthal-posterior internasal scales shared by these species. *Abronia fimbriata* and *A. leurolepis* are considered sister species on the basis of (2.2) loss of the frontonasal scale (note that *A. leurolepis* is based on a unique specimen and this character is variably present in *A. taeniata* and *A. oaxacae*, and some specimens of *A. gaiophasma* have small frontonasals); (7.1) some frequency of secondary loss of contact between the subocular and lower primary temporal; (19.2) single postmental scale (variable in most other members of the *A. aurita* group); and (27.0) secondary reduction from 14 to 12 ventral scale rows (convergent elsewhere). The association of *A. aurita* and *A. anzuetoi* is supported by a single feature, bright yellow circumorbital region (29.1; convergent in *A. graminea* and *A. smithi*). For those convinced that speciation by peripheral isolation is predominant, the widespread species, *A. aurita*, does have at least one apomorphy with respect to *A. anzuetoi*, this being (3.1) some frequency of frontonasal-nasal contact. Further, one could also argue a posteriori that the *A. aurita* color pattern of dendritic crossbands is also apomorphic inasmuch as this is not seen in near relatives. Therefore, the relationship of *A. aurita* and *A. anzuetoi* appears to be the results of a diagnostic partitioning rather than the "budding" speciation of college textbooks. *Abronia lythrochila* shares with *A. anzuetoi* and *A. aurita* the presence of multiple rows of preauricular scales. Even though we could not use this feature a priori because of characterization difficulties, in this topology it could be argued that this is evidence for a special relationship of *A. lythrochila* with *A. aurita* and *A. anzuetoi*, contra our preferred topology.

The monophyly of the *Abronia deppii* group is noncontroversial. The knobby posterior head shields (15.1) of members of the *A. deppii* group are unique and easily characterized.

The other feature supporting the monophyly of this group is highly plastic, some frequency of 14 ventral scale rows (27.1). We are confident about only two other stems in this group: that supporting the *A. deppii* subgroup and that subtending the *A. deppii*-*A. species* "Guerrero" species pair. The former of these is supported by (7.2) never any contact between the subocular scale and the lower primary temporal; (21.1) dorsal scale rows oblique with respect to the ventrolateral fold; (24.2) large, nonimbricate, pebbly scales along the oblique lateral neck fold; and (25.1) reduction of the ventrolateral fold. The *A. deppii*-*A. species* "Guerrero" species pair is supported by the (11.2) enlarged first postorbital supralabial, and (22.1) very "flimsy" dorsal squamation due to extreme reduction of dorsal osteoderms.

Abronia oaxacae is most parsimoniously placed as the sister taxon of the *A. deppii*-*A. species* "Guerrero" clade by: (4.2) "fixation" of canthal-posterior internasal scale fusion (variable in *A. graminea*, *A. taeniata*, and *A. mixteca*); (6.1) no superciliary-cantholoreale scale contact (apparently convergent in *A. graminea*); (9.2) three secondary temporals (variability uniting all *Abronia* except *A. mitchelli* with some reversal and some convergent fixation); and (17.1) some frequency of the penultimate supralabial contacting the orbit (convergent in the stem leading to the *A. aurita* and *A. reidi* groups). The earlier view of relationship of *A. oaxacae* was as the sister taxon of *A. mixteca* (Bogert and Porter, 1967; Good, 1988). This is supported by the number of occipital scales (14.2) and, possibly (27.2) fixation of the number of ventral scale rows at 14 or greater, and, if characterization could be adequately accomplished, the reduction of the fourth temporal scale row (Good's [1988] Character Transformation 42; see section on characters excluded from analysis above) might support this contention. There is no doubt that *A. oaxacae* and *A. mixteca* are similar phenotypically and geographically complementary. However, to consider these to be sister taxa requires the addition of two steps in our analyses. Conversely, *A. mixteca* has no unambiguous apomorphies with respect to *A. oaxacae* or the *A. deppii* species pair, and might actually retain the ancestral diagnosis of the *A. deppii* subgroup.

The relationships among the *A. deppii* subgroup, *A. taeniata*, *A. fuscolabialis*, and *A. graminea* are poorly resolved. On the basis of phenotypic similarity and geographic proximity we would have guessed that *A. fuscolabialis*, *A. graminea*, and *A. taeniata* were vicars of a single ancestor that was originally distributed from the mountains of Oaxaca to southern Tamaulipas, Mexico. However, our character analysis does not support this; there is not a single feature that could be construed unambiguously to be a synapomorphy of these three species. Good's (1988) arrangement (i.e., *A. fuscolabialis* ((*A. taeniata* + *A. graminea*) (*A. deppii* subgroup))) is only weakly supported by (4.1) some frequency of canthal-posterior internasal scale fusion being shared by all members of the *A. deppii* group, except *A. fuscolabialis*, although the feature of posterior extension of the nasal scale (Good's [1988] Character Transformation #4) may deserve more scrutiny, and no evidence supports *A. graminea* and *A. taeniata* as sister taxa (even though they have been considered conspecific). *Abronia fuscolabialis* might be considered the sister taxon of *A. graminea* on the basis of (23.1) some frequency of reduction from six to four nuchal scale rows, although this may represent specimen anomalies, as previously mentioned. The only feature tying *A. taeniata* with the *A. deppii* subgroup is (3.1) some frequency of no frontonasal-nasal contact. Although *A. fuscolabialis*, *A. graminea*, and *A. taeniata* are clearly diagnosable species, their pervasive plesiomorphy relative to the *A. deppii* subgroup renders any conclusions drawn about their interrelationships to be questionable.

In summary, we think that the hypotheses of relationship among the major species groups are only weakly corroborated and may change with reinterpretation of or new data. We also think that, with the exception of some general trends and the *A. aurita*-*A. anzuetoi* species pair, we are not sanguine about having accurately recovered the evolutionary history within the *A. aurita* group. We find the association of *A. salvadorensis* with the *A. aurita* group to have less than overwhelming support. Nevertheless, of the species east of the Isthmus of Tehuantepec it is most similar in general habitus to *A. matudai*, which

is patristically adjacent in our accepted cladograms. The structure of the *A. aurita* group is largely dependent on our assumption of the relative plesiomorphy of *A. matudai* in the development of supra-auricular spines. The association of the *A. reidi* group with the *A. aurita* group, *A. salvadorensis*, and *A. montecristoi*, as well as with the *A. bogerti* group, we find biogeographically intriguing, although we have seen other pat arrangements fall victim to additional evidence.

The *A. reidi* group is well supported, although we consider the association of *A. montecristoi* with the "core" species in this group to be tentative. The *A. bogerti* group is highly corroborated. We consider the placement of *A. mitchelli* dubious because of the possibility of sampling error. Within the corroborated *A. deppii* group we cannot confidently choose among possible hypothesized relationships among *A. taeniata*, *A. graminea*, *A. fuscolabialis*, and the *A. deppii* subgroup, although the *A. deppii* subgroup is well corroborated. The arrangement (*A. mixteca* (*A. oaxacae* (*A. deppii* + *A. species* "Guerero"))) is the most parsimonious for our data but worthy of further investigation.

COMPARISON WITH THE PHYLOGENETIC HYPOTHESIS OF GOOD (1988)

We found the phylogenetic signal in the squamation data of *Abronia* to be considerably weaker than that suggested previously by Good. We think that the reason his results were so much better supported is because of incautious formulation as well as a posteriori enhancement of transformation series to "fit" preconceived notions of relationship. Of course, this is something that is difficult to avoid because of the continual reevaluation of characters that goes on during a study. Nevertheless, it frequently leads to unexpected problems.

Because we modified or rejected a number of the characters that had been used by Good (1988) to formulate his cladogram of *Abronia*, our results are not immediately comparable. However, our "any instance" approach with successive approximations (fig. 37) is more congruent with the results of our pre-

ferred analysis ("unscaled" analysis with successive approximations—fig. 44) than with his results, implying that our differences with Good have more to do with the data than with the methods taken to analyze them. However, in spite of the differences in data and analytical methods, there are areas of commonality among our results and those of Good (fig. 49). We concur in the reality of the *A. reidi* and the *A. aurita* groups. Although Good considered the *A. bogerti* group to be part of his more inclusive *A. deppii* group, he did find both of the monophyletic groups that we refer to as the *A. bogerti* and *A. deppii* groups. Within the *A. deppii* group, he and we considered *A. fuscolabialis*, *A. graminea*, and *A. taeniata* to be outside of the *A. deppii* subgroup.

Places where we disagree are more numerous. Good's consideration of *A. montecristoi* as the sister taxon of the *A. aurita* group + *A. salvadorensis* was based on the presence of three suboculars (his Character Transformation 36), which we rejected as evidence because this feature is considerably more variable intraspecifically than previously reported. Other features that he considered to be evidence for the placement of *A. montecristoi* were the condition of the posterior supralabial (his Character Transformation 61), which we recharacterized, and the presence of a single postmental scale (his Character Transformation 65, our 19), which is overwhelmed by incongruent evidence in our analysis.

Good's consideration *Abronia matudai* and *A. smithi* (his "*A. ochoterenai*") as sister taxa was based on the presence of expanded lateral ventral scale rows (his Character Transformation 83; our 26, which we found to have a much wider distribution) and loss of dorsal pattern in adults (his Character Transformation 99). We did not use loss of dorsal pattern in adults in our analysis because of evidence of nonhomology in a number of taxa. Nevertheless, a posteriori inclusion of this as a putative homolog does not result in the placement of *A. matudai* and *A. smithi* as sister taxa.

Good's association of the *Abronia bogerti* group with the *A. deppii* group was based on the condition of neck scales (his Character

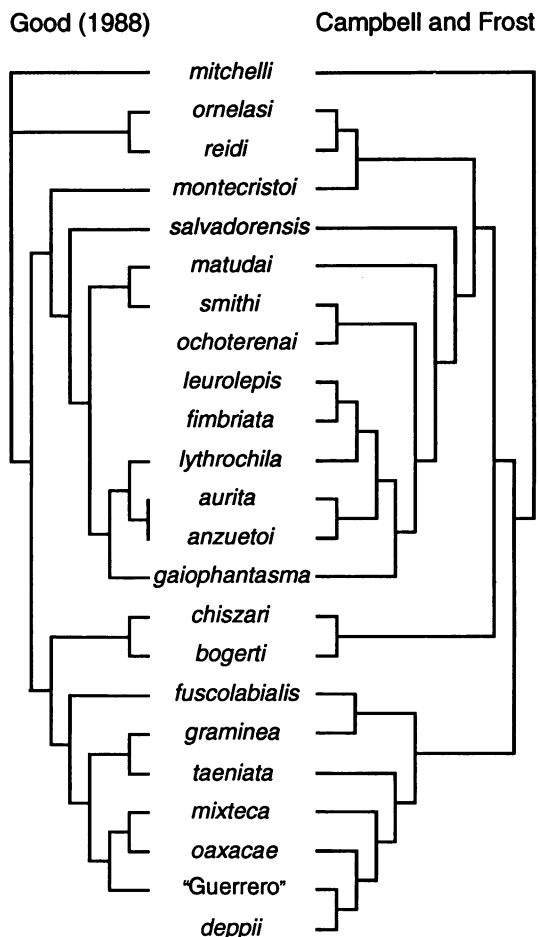


Fig. 49. Comparison of the phylogenetic results of Good (1988) and our preferred cladogram. *Abronia ochoterenai*, *A. leurolepis*, *A. fimbriata*, and *A. deppii* were not seen by Good. Good's specimens of "*A. ochoterenai*" were actually of the new species, *A. smithi*; representatives of *A. aurita* and *A. anzuetoii* constituted his specimens of *A. vasconcelosii* (= *A. aurita*); and *A. gaiophantasma* he considered (as did most recent authors) to be *A. aurita*.

Transformation 77; our 24), something that we do not think could be homologized between the *A. bogerti* and *A. deppii* groups, and on the condition of scales on the limbs (Good's Character Transformations 85 and 86), something that we could not see. The association of *A. graminea* and *A. taeniata* was based solely on the reduction of preauricular size (his Character Transformation 59),

a feature that we rejected as not characterizable, but which warrants further examination. We have previously discussed the alternative arrangements in the *A. deppii* subgroup.

RECOMMENDED TAXONOMY

The monophyly of *Abronia* is supported and we retain this taxon. Each of the subsidiary species group that we recognize is monophyletic and we formally name them. We associate *A. montecristoi* with the *A. reidi* group in the hope that further investigations will support our conclusion. *Abronia mitchelli* and *A. salvadorensis* we relegate to monotypic subgenera as a consequence of our applying subgeneric names to the former *A. aurita* and *A. deppii* groups. The following taxonomy, although not naming all stems, is logically consistent with the recovered phylogeny:

Abronia Gray, 1838

Abaculabronia, new subgenus

Abronia montecristoi Hidalgo, 1983

A. ornelasi Campbell, 1984

A. reidi Werler and Shannon, 1961

Abronia Gray, 1838, new rank as subgenus

Abronia deppii (Wiegmann, 1828)

A. fuscolabialis (Tihen, 1944)

A. graminea (Cope, 1864)

A. mixteca Bogert and Porter, 1967

A. oaxacae (Günther, 1885)

A. taeniata (Wiegmann, 1828)

A. species "Guerrero"

Aenigmabronia, new subgenus

Abronia mitchelli Campbell, 1982

Auriculabronia, new subgenus

Abronia anzueto, new species

A. aurita (Cope, "1868" [1869])

A. fimbriata (Cope, "1884" [1885])

A. gaiophantasma, new species

A. leurolepis, new species

A. lythrochila Smith and Alvarez del Toro, 1963

A. matudai (Hartweg and Tihen, 1946)

A. ochoterenai (Martín del Campo, 1939)

A. smithi, new species

Lissabronia, new subgenus

Abronia salvadorensis Hidalgo, 1983

Scopaeabronia, new subgenus

Abronia bogerti Tihen, 1954

A. chiszari Smith and Smith, 1981

ACCOUNTS AND DIAGNOSES

"Diagnoses" in the following section are designed to meet the requirements of the International Code of Zoological Nomenclature (1985) and for utility in identification, and, except for the generic account, are not merely lists of apomorphies, nor are they exhaustive lists of characters that serve to differentiate these taxa from each other. For lists of apomorphies see Appendices 5 and 6.

GENUS *ABRONIA* GRAY, 1838

TYPE SPECIES: *Gerrhonotus deppii* Wiegmann, 1828.

DIAGNOSIS: *Abronia* can be distinguished from all other gerrhonotines (*Coloptychon*, *Gerrhonotus*, *Barisia*, *Elgaria*, and *Mesaspis*) in the combination of having: (1) the fifth row of temporal scales absent (except, probably anomalously, on one side of one specimen of *A. salvadorensis*) (present in all other genera); (2) large, well-clawed limbs (smaller

limbs in all other genera); and (3) a reduced lateral fold (much better developed in all other genera), particularly between the anterior limb and ear.

CONTENT: Subgenus *Abronia* Gray, 1838; *Abaculabronia*, new subgenus; *Aenigmabronia*, new subgenus; *Auriculabronia*, new subgenus; *Lissabronia*, new subgenus; *Scopaeabronia*, new subgenus.

DISTRIBUTION: Northeastern Mexico (southwestern Tamaulipas) southward in the Sierra Madre Oriental to Oaxaca, Morelos, and the southern portion of the state of Mexico, the Sierra Madre del Sur and central Oaxacan highlands, the Sierra de Los Tuxtlas, the Sierra Madre de Chiapas (including western portion in southeastern Oaxaca), and the Meseta Central of Chiapas, to the highlands of Guatemala, southern Honduras, and northern El Salvador (fig. 1).

ETYMOLOGY: Greek: *habros* (pretty, graceful) + Latin: *-ia* (pertaining to), in reference

to the generally graceful and attractive appearance of these lizards.

Abaculabronia, New Subgenus

TYPE SPECIES: *Abronia reidi* Werler and Shannon, 1961.

DIAGNOSIS: *Abaculabronia* can be distinguished from all other subgenera in having frequent prefrontal-anterior superciliary contact (found otherwise only in *Scopaeabronia*), in lacking expanded lower temporal elements (enlarged only in *Scopaeabronia*), in having three primary temporals contacting postocular scale series (only two in other groups), in lacking protuberant head shields on posterolateral "corners" of the head (found only in the subgenus *Abronia*), in lacking protuberant supra-auricular scales (present in *Auriculabronia*), in having fewer than 38 transverse rows of dorsal scales (a greater number found only in *Scopaeabronia*), in having fewer than eight longitudinal rows of nuchal scales (eight appearing only in *Scopaeabronia*), and in having the lateralmost rows of ventral scales expanded (not seen in *Abronia*, *Scopaeabronia*, and *Aenigmabronia*).

CONTENT: *Abronia montecristoi* Hidalgo, 1983; *A. ornelasi* Campbell, 1984; *A. reidi* Werler and Shannon, 1961.

DISTRIBUTION: Southern Mexico in the Sierra de Los Tuxtlas and extreme southeastern Oaxaca; northwestern El Salvador (fig. 26).

ETYMOLOGY: Latin: *abacula* (mosaic) + *Abronia*; referencing the checkered color pattern of the dorsal squamation.

COMMENTS: *Abaculabronia* is the *Abronia reidi* group of earlier authors, plus *A. montecristoi*.

Abronia, New Rank As Subgenus

TYPE SPECIES: *Gerrhonotus deppii* Wiegmann, 1828.

DIAGNOSIS: *Abronia* is distinguished from the other subgenera in lacking prefrontal-anterior superciliary contact (found only in *Scopaeabronia* and *Abaculabronia*), in lacking expanded lower temporal scales (found only in *Scopaeabronia*), in having two primary temporals contacting the postocular scale series (three in *Abaculabronia*), in having protuberant head shields on posterolateral "corners" of head (not in other subgenera), in

lacking protuberant supra-auricular scales in adults (present in *Auriculabronia*), in having fewer than 38 transverse rows of dorsal scales (more than 38 in *Scopaeabronia*), in having six or fewer longitudinal rows of nuchal scales (eight in *Scopaeabronia*), in having the lateralmost rows of ventral scales not expanded (expanded in *Lissabronia*, *Auriculabronia*, and *Abaculabronia*).

CONTENT: *Abronia deppii* (Wiegmann, 1828); *A. fuscolabialis* (Tihen, 1944); *A. graminea* (Cope, 1864); *A. mixteca* Bogert and Porter, 1967; *A. oaxacae* (Günther, 1885); *A. taeniata* (Wiegmann, 1828); *A. species* "Guerrero."

DISTRIBUTION: Mexico north and west of the Isthmus of Tehuantepec, including the Sierra Madre Oriental (Tamaulipas to Oaxaca), eastern portion of the Transverse Volcanic Cordillera, the Sierra Madre del Sur, and the highlands of central Oaxaca.

ETYMOLOGY: As for the genus.

COMMENT: This is the *Abronia deppii* group as used by us in this manuscript.

Aenigmabronia, New Subgenus

TYPE SPECIES: *Abronia mitchelli* Campbell, 1982.

DIAGNOSIS: *Aenigmabronia* is distinguished in lacking prefrontal-anterior superciliary scale contact (present in *Scopaeabronia* and *Abaculabronia*), in lacking expanded lower temporal scales (present in *Scopaeabronia*), in having two primary temporals contacting postocular scale series (unlike the three in *Abaculabronia*), in lacking protuberant head shields on posterolateral "corners" of the head (present in the subgenus *Abronia*), in lacking strongly protuberant supra-auricular scales (present in *Auriculabronia*), in having fewer than 38 transverse rows of dorsal scales (38 or more in *Scopaeabronia*), in having less than eight longitudinal rows of nuchal scales (eight in *Scopaeabronia*), and in not having the lateralmost rows of ventral scales expanded (expanded in *Lissabronia*, *Auriculabronia*, and *Abaculabronia*).

CONTENT: *Abronia mitchelli* Campbell, 1982.

DISTRIBUTION: Southern Mexico, known only from the Sierra Juárez in northern Oaxaca (fig. 26).

ETYMOLOGY: Greek: *aenigma* (enigma) + *Abronia*, referring to the enigmatic phylogenetic position of this particular species.

Auriculabronia, New Subgenus

TYPE SPECIES: *Gerrhonotus auritus* Cope, "1868" [1869].

DIAGNOSIS: *Auriculabronia* is distinguished from other subgenera in *Abronia* in lacking a prefrontal-anterior superciliary scale contact (present only in *Scopaeabronia*), lacking expanded lower temporal scales (expanded as in *Scopaeabronia*), in having two primary temporals contacting postocular scale series (three in *Abaculabronia*), in lacking protuberant head shields on posterolateral "corners" of the head (head casquing present in the subgenus *Abronia*), in having strongly protuberant supra-auricular scales in adults unlike all other groups, in having fewer than 38 transverse rows of dorsal scales (38 or more in *Scopaeabronia*), in having less than eight longitudinal rows of nuchal scales (eight in *Scopaeabronia*), and in having the lateralmost rows of ventral scales expanded (not expanded in *Scopaeabronia*, *Abronia*, and *Aenigmabronia*).

CONTENT: *Abronia anzueto*, new species; *A. aurita* (Cope, "1868" [1869]); *A. fimbriata* (Cope, "1884" [1885]); *A. gaiophasma* new species; *A. leurolepis*, new species; *A. lythrochila* Smith and Alvarez del Toro, 1963; *A. matudai* (Hartweg and Tihen, 1946); *A. ochoteranai* (Martín del Campo, 1939); *A. smithi*, new species.

DISTRIBUTION: Southern Mexico (Chiapas) and Guatemala.

ETYMOLOGY: Greek: *auricula* (having ears) + *Abronia*, referring to the protuberant supra-auricular scales that characterize this group.

COMMENTS: This is the *Abronia aurita* group, excluding *A. montecristoi* and *A. salvadorensis*, as used by previous authors.

Lissabronia, New Subgenus

TYPE SPECIES: *Abronia salvadorensis* Hidalgo, 1983.

DIAGNOSIS: *Lissabronia* is distinguished from all other subgenera in lacking prefrontal-anterior superciliary scale contact (con-

tact in *Scopaeabronia* and *Abaculabronia*), in lacking expanded lower primary temporal scales (expanded in *Scopaeabronia*), in having two primary temporals contacting the postocular scale series (three in *Abaculabronia*), in lacking protuberant head shields on the posterolateral "corners" of the head (head casquing in the subgenus *Abronia*), in lacking protuberant supra-auricular scales in adults (present in *Auriculabronia*), in having fewer than the 38 or more transverse rows of dorsal scales (38 or more in *Scopaeabronia*), in having fewer than the eight longitudinal rows of nuchal scales (eight in *Scopaeabronia*), and in having the lateralmost rows of ventral scales expanded (not expanded in *Aenigmabronia*, *Scopaeabronia*, and *Abronia*).

CONTENT: *Abronia salvadorensis* Hidalgo, 1983.

DISTRIBUTION: Uplifts of the Sierra de Opalaca in Honduras and the Sierra de Montecillos in Honduras and adjacent El Salvador (fig. 26).

ETYMOLOGY: Greek: *lissos* (polished) + *Abronia*, referring to the polished appearance of the dorsal squamation in this species.

Scopaeabronia, New Subgenus

TYPE SPECIES: *Abronia bogerti* Tihen, 1954.

DIAGNOSIS: *Scopaeabronia* is distinguished from all other members of the genus *Abronia* in having prefrontal-anterior superciliary scale contact (seen otherwise only variably in *Abaculabronia*), in having the lower primary temporals expanded (unlike all other *Abronia*), in having two primary temporals contacting postocular scale series (three in *Abaculabronia*), in lacking protuberant head shields on the posterolateral "corners" of the head (present in the subgenus *Abronia*), in lacking protuberant supra-auricular scales in adults (present only in *Auriculabronia*), in having 38 or more transverse rows of dorsal scales (fewer in all other members of the genus), in having eight longitudinal rows of nuchal scales unlike all other *Abronia*, which have fewer, and in not having the lateralmost rows of ventral scales expanded (expanded in *Lissabronia*, *Abaculabronia*, and *Auriculabronia*).

CONTENT: *Abronia bogerti* Tihen, 1954; *A. chiszari* Smith and Smith, 1981.

DISTRIBUTION: Southern Mexico, including the Sierra de Los Tuxtlas (Veracruz), extreme southeastern Oaxaca, and western Chiapas (fig. 26).

ETYMOLOGY: Greek: *skopaios* (dwarf) + *Abronia*, referring to the small size of these species compared with other *Abronia*.

COMMENTS: This is the former *Abronia bogerti* group.

SUGGESTIONS FOR FUTURE WORK

Our understanding of the evolution within *Abronia* will be influenced in the future by the discovery of new taxa (e.g., Brodie and Savage, 1993; Campbell, 1994; Frost, unpublished data) as well as by advances in the philosophy and methods of data analysis.

Nevertheless, we think that we have pushed nearly to the limit the attempt to recover phylogenetic signal from external morphological data without having to resort to unwarranted assumptions about the evolutionary process. Further advances necessarily must come from the addition of other lines of evidence (e.g., osteology evaluated through CT imagery, DNA sequences, allozymes). Unfortunately, the rate at which *Abronia* species are having their habitats destroyed makes it unlikely that data acquisition that requires live animals will be broadly successful. However, we and other workers have been patiently acquiring frozen tissues, and techniques for extracting DNA from fluid-preserved specimens are becoming increasingly successful. We hope that these other data will result in progress in our understanding being made before there are no more *Abronia* to be studied.

KEY TO THE SPECIES OF *ABRONIA*

Even though the species of *Abronia*, when compared side-by-side, are easily distinguished, writing a dichotomous key to these species has proved difficult because of the intraspecific variability of several external characters. Identification of specimens is best accomplished by consulting photographs, original diagnoses, and descriptions, with due regard to geography. Nevertheless, for quick reference we provide the key below. We have indicated by footnotes potential problem areas in identification. Juveniles are not common in collections, but these lack the distinctive spinelike supra-auricular scales present in the adults of some species. Two species, not addressed in our phylogenetic analysis because of their late discovery, are being described elsewhere (*Abronia* species “Chiapas,” a member of *Scopaeabronia* being described by Campbell, 1994, from Chiapas, Mexico; and *Abronia* species “Guatemala,” a member of *Auriculabronia*, similar to *A. anzuetoi* and *A. aurita*, from eastern Guatemala, being named by Brodie and Savage, 1993). These species are included in this key for completeness.

- 1. Adults with spinelike supra-auricular scales¹⁸ (fig. 50A) 2
- Adults without spinelike supra-auricular scales (fig. 50B, C) 10
- 2. Supranasals expanded, meeting at dorsal midline (fig. 51A); frontonasal scale absent (fig. 52A) *A. fimbriata* (figs. 6, 7, 10D–F)
- Supranasals not expanded, not meeting at dorsal midline (fig. 51C); frontonasal scale present or not¹⁹ (fig. 52A, B) 3
- 3. Ventral longitudinal scale rows 12 4
- Ventral longitudinal scale rows 14 or more (or, if 12, with the lowest tertiary temporal enlarged and contacting the second primary temporal scale) 6
- 4. Frontonasal scale absent (fig. 52A); dorsal body scales virtually without keels; posterior-most infralabial markedly elongate
..... *A. leurolepis* (figs. 16, 17)
- Frontonasal scale present (fig. 52B); dorsal body scales keeled; ultimate infralabial not markedly elongate compared with penultimate infralabial 5

¹⁸ Adult specimens of *Abronia matudai* have bluntly protuberant, but not spinelike, supra-auriculars (fig. 50B).

¹⁹ Only one specimen in a sample of nine *A. lythrochila* (IHN 764) lacks a frontonasal.

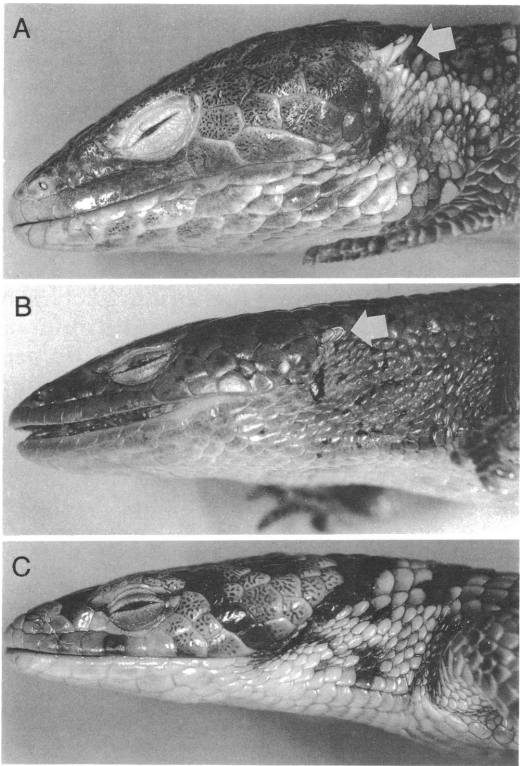


Fig. 50. Supra-auricular scales: **A**, Spinelike (e.g., *A. aurita*, male, UTA R-26567). Note also circumorbital region set off in hue from surrounding ambient head color. **B**, Protuberant (e.g., *A. matudai*, male, MVZ 161022). **C**, Not protuberant (e.g., *A. taeniata*, female, KU 54055).

- 5. Posterior subocular contacting lower anterior temporal; preauriculars granular and in multiple rows (fig. 53A); three primary temporals; circumorbital region not bright yellow *A. ochoterenai* (figs. 13, 14)
Posterior subocular not contacting lower anterior temporal; preauriculars usually subimbricate to imbricate (fig. 53B); usually four or five primary temporals; circumorbital region bright yellow *A. smithi* (figs. 11E, 15)
- 6. Circumorbital region not distinctly set off in coloration from ambient head color ... 7
Circumorbital region distinctly set off (paler or bright yellow) from ambient head color (fig. 50A) 8
- 7. Dorsal longitudinal scale rows 12³; dorsum brownish; preauriculars not in distinctive multiple rows of tubercular scales (fig. 53B); second primary temporal (behind the corner of the eye) and the following secondary

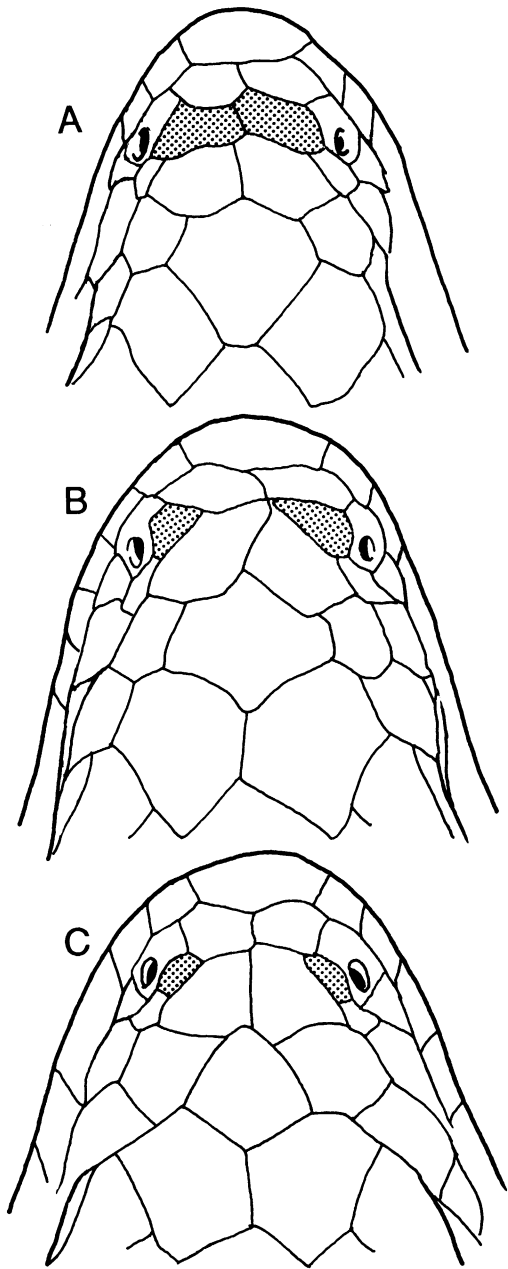


Fig. 51. Supranasal scales: **A**, Expanded, meeting at dorsal midline (e.g., *A. ornelasi*, male, AMNH 137783). **B**, Partially expanded (e.g., *A. mitchelli*, female, UTA R-10000). **C**, Not expanded (e.g., *A. anzuetoi*, female, AMNH 109053).

temporal much larger (about 3×) than the following tertiary temporal (fig. 54A)
..... *A. gaiophantasma* (fig. 11A–B)
Dorsal longitudinal scale rows 14–15; dorsal

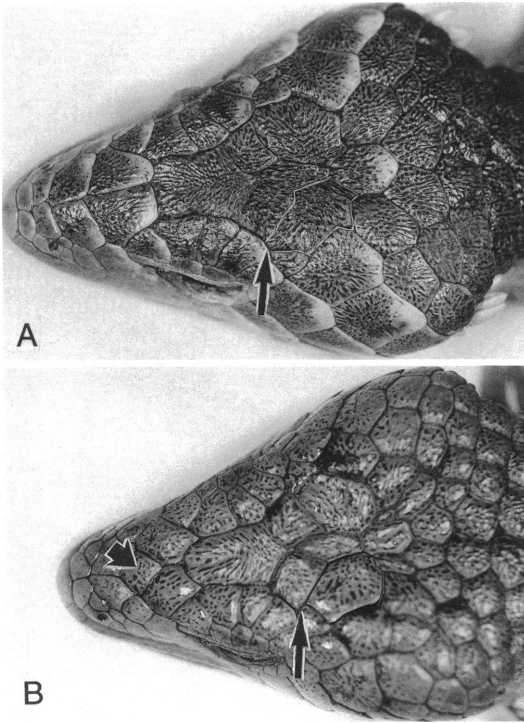


Fig. 52. Frontonasal and parietal scales: **A**, Frontonasal scale absent and parietal scales in contact with the median supraocular rows (e.g., *Abronia fimbriata*, male, UTA R-30325). **B**, Frontonasal scale present and parietal scales excluded from contact with the median supraocular scale row by primary temporal scale contact with frontoparietals (e.g., *A. salvadorensis*, female, KU 195560).

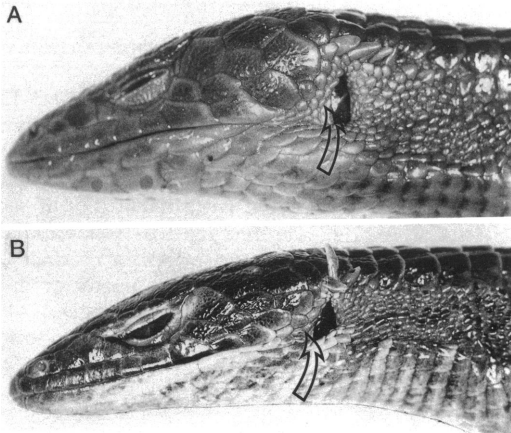


Fig. 53. Preauricular scales: **A**, Granular and in multiple rows (e.g., *A. ochoterenai*, male, IBUN-AM 339). **B**, Subimbricate to imbricate (e.g., *A. smithi*, male, UTA R-30202).

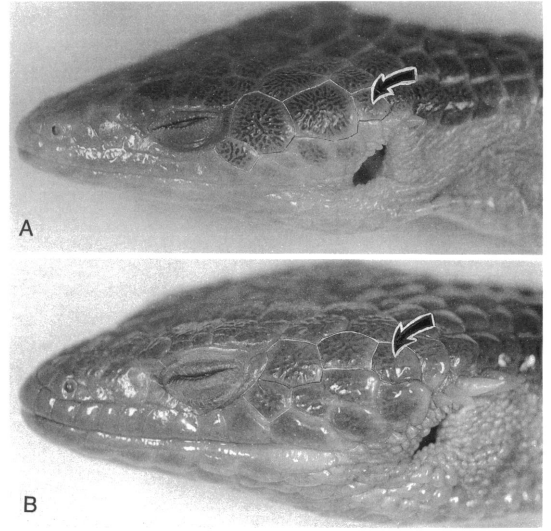


Fig. 54. Temporal scales: **A**, Second primary temporal (behind corner of eye) and following secondary temporal much larger (about 3 times) than following tertiary temporal (e.g., *A. gaiophantasma*, male, KU 192096). **B**, Second primary temporal and the following secondary temporal not strikingly larger than following tertiary temporal (e.g., *A. lythrochila*, male, UTA R-3354).

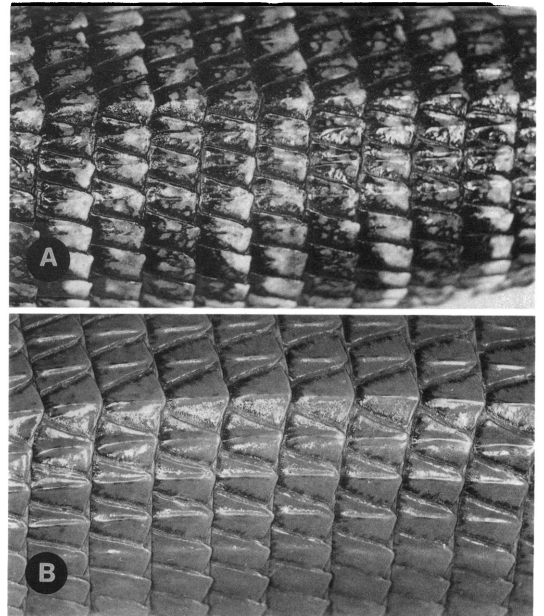


Fig. 55. Dorsal body scale coloration: **A**, Heavily pigmented with black, anterior portion of scales almost entirely dark (e.g., *A. aurita*, male, UTA R-19675). **B**, Sparsely pigmented with black, anterior portion of scales not black (e.g., *A. anzuetoii*, male, UMMZ 129013).

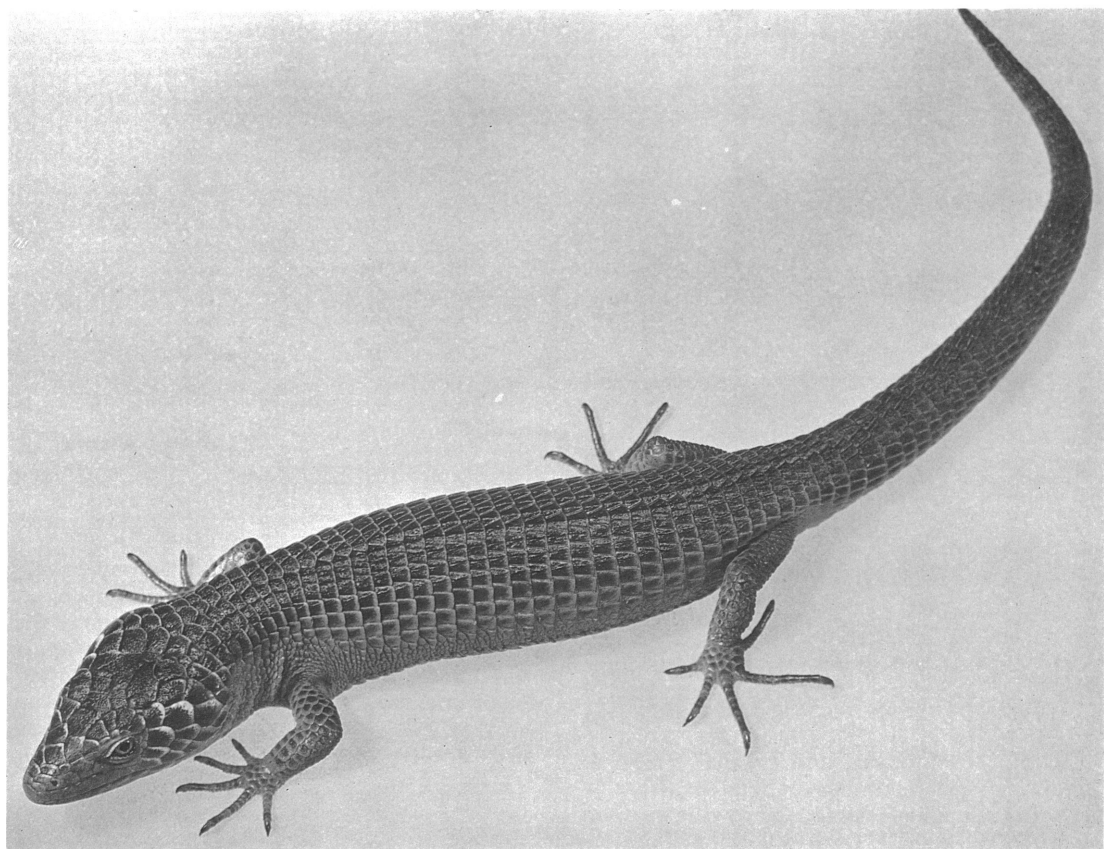


Fig. 56. *Abronia reidi*, male holotype (UIMNH 67062), 91.2 mm SVL, 180.2 mm TL; from crater rim of Volcán San Martín, 1642 m, Veracruz, Mexico. [Photograph courtesy of J. Werler. Previously published by Werler and Shannon (1961).]

- color variable; preauriculars in distinctive multiple rows of granular to tubercular scales (fig. 53A); second primary temporal and the following secondary temporal not strikingly larger than following tertiary temporal (fig. 54B) *A. lythrochila* (fig. 11F, 58A)
8. Dorsal body scales heavily pigmented with black, with anterior portion of scales almost entirely dark (fig. 55A); body ground coloration pea-green, yellow-green, or pale turquoise *A. aurita* (figs. 3, 4, 10A–C, 50A)
Dorsal body scales not heavily pigmented with black (fig. 55B); body ground coloration tan to pale coffee, or dark emerald green . . . 9
9. Circumorbital region bright yellow; body ground coloration dark emerald green or dark blue-green; dorsal body scales sparsely pigmented with black, anterior portion of scales not black (fig. 55C)
..... *A. anzueto* (figs. 9, 11C–D)
Circumorbital region white or very pale tan; body ground coloration pale coffee or yellowish brown; dorsal body scales very sparsely pigmented with black, if at all . .
..... *Abronia* species “Guatemala”
10. Supranasals greatly expanded, in contact at dorsal midline²⁰ (fig. 51A); posterior and dorsal edges of scales distinctly pale . . 11
Supranasals usually not expanded; if so, only

²⁰ One specimen of eight *A. ornelasi* (UTA R-6075) has expanded supranasals that do not meet at the dorsal midline.

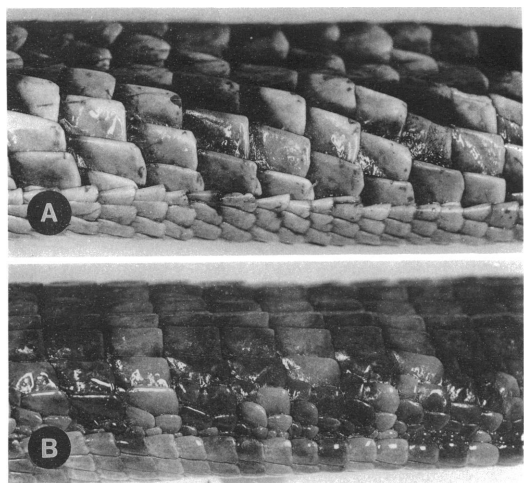


Fig. 57. Arrangement of scales on sides of body with respect to dorsolateral fold: **A**, Oblique longitudinal rows (e.g., *Abronia* species “Guerrero,” male, UTA R-4451). **B**, Parallel longitudinal rows (e.g., *A. fuscolabialis*, male UTA R-9899).

- moderately and not in contact at dorsal midline (fig. 51B–C); dorsal color pattern variable 12
11. Four anterior temporals; parietal not contacting median supraocular series; frontonasal contacting frontal
..... *A. ornelasi* (figs. 12B, 51A)
- Three anterior temporals; parietal narrowly contacting median supraocular series; frontonasal may or may not contact frontal²¹
..... *A. reidi* (figs. 28, 56)
12. Longitudinal scale rows on side of body arranged in oblique rows with respect to dorsolateral fold (fig. 57A); dorsal body scales very slightly keeled, usually almost flat ...
..... 13
- Longitudinal scale rows on sides of body arranged parallel to dorsolateral fold (fig. 57B); dorsal body scales with definite keel .. 16
13. Two primary temporals contacting postocular series; three occipitals (fig. 58B) 14
- A single (lower) primary temporal contacting

²¹ *Abronia reidi* is known from two specimens. In one (the adult holotype) the frontonasal is broadly separated from the frontal by the prefrontals; in the other (juvenile paratype) contact is made between the frontonasal and frontal. In the eight known specimens of *A. ornelasi* the frontonasal contacts the frontal.

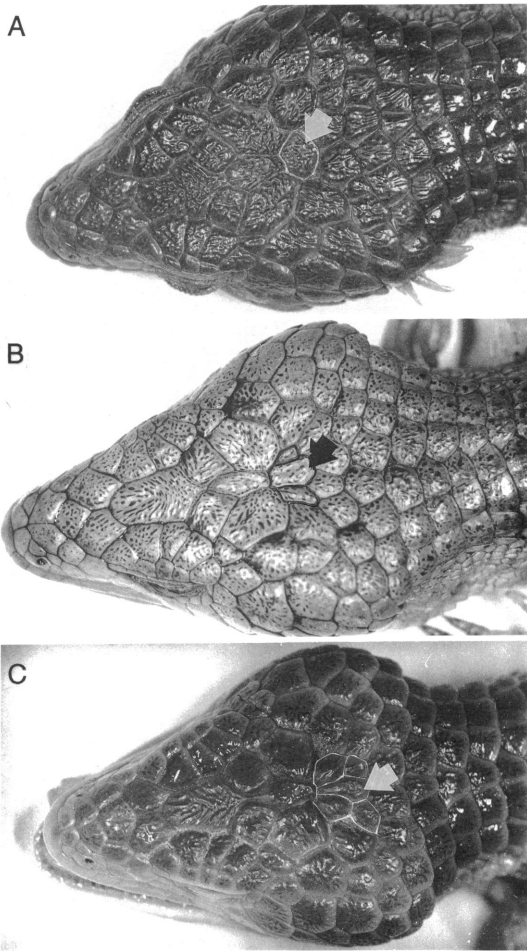


Fig. 58. Occipital scales: **A**, One (e.g., *A. lythrochila*, male, UTA R-3354). **B**, Three (e.g., *A. salvadorensis*, male, KU 195560). **C**, Five (e.g., *A. montecristoi*, male, KU 184046).

- postocular series²²; a single occipital (fig. 58A) 15
14. Minimum of six nuchals in transverse row across nape; anterior superciliary contact-

²² The anterior corner of the second anterior temporal may just barely contact the uppermost scale in the postocular series; conversely, in *A. mixteca* and *A. oaxacae* two anterior temporals are in broad contact with the postocular series and the second anterior temporal may be the only temporal scale making contact with the upper postocular scale.

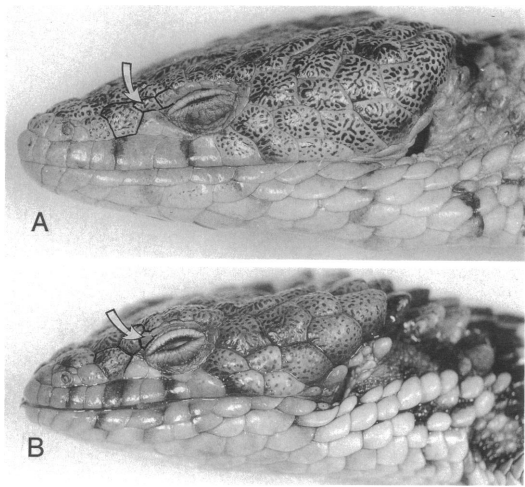


Fig. 59. Anterior superciliary scales: A, Contacting cantholoreal (e.g., *A. mixteca*, male, UTA R-19647). B, Not contacting cantholoreal (e.g., *A. oaxacae*, female, AMNH 90997).

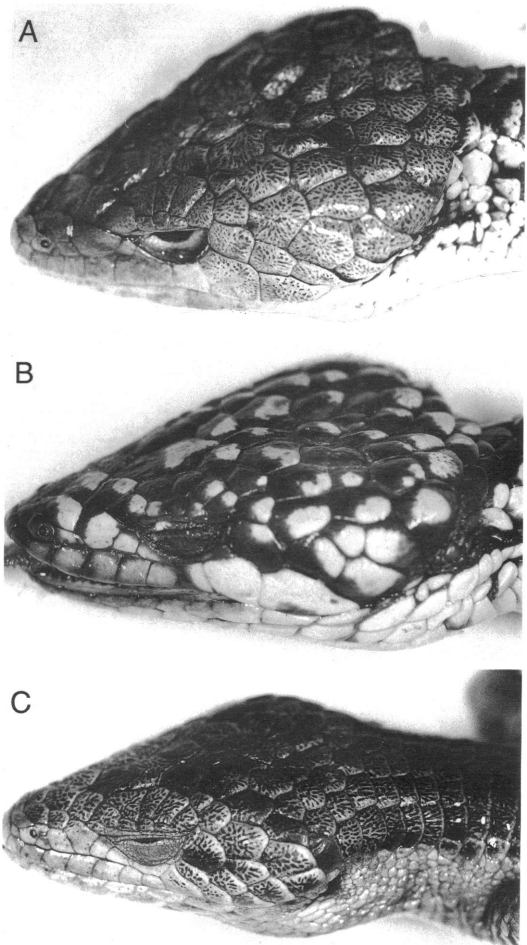


Fig. 60. Posterolateral head casquing: A, Strongly developed, posterior head scales knobby (e.g., *Abronia* species "Guerrero," male, UTA R-4451). B, Moderately developed, posterior head scales somewhat knobby (e.g., *A. deppii*, male, ZMB 1150). C, Not developed (e.g., *A. ornelasi*, male, UTA R-12499).

- ing cantholoreal (fig. 59A)
..... *A. mixteca* (fig. 12D)
- Minimum of four nuchals in transverse row across nape; anterior superciliary usually not contacting cantholoreal²³ (fig. 59B)
..... *A. oaxacae* (fig. 12F)
- 15. Knoblike posterolateral head scales strongly developed (fig. 60A); black vermiculations on posterior head scales distinct
... *Abronia* species "Guerrero"²⁴ (fig. 12E)
- Knoblike posterolateral head scales not as strongly developed (fig. 60B); black vermiculations on posterior dorsal head scales absent or faint *A. deppii*²⁴ (fig. 61)
- 16. Posterolateral head scales not particularly convex, definitely not giving the head the appearance of being helmeted (fig. 60C) 17
- Posterolateral head scales strongly convex, domed, or knobby, giving the head the appearance of being helmeted (figs. 60A, B) 23

²³ In 11 of 12 specimens of *A. oaxacae* examined by Bogert and Porter (1967).

²⁴ A more thorough consideration of *A. deppii* and a similar undescribed species (*Abronia* species "Guerrero" in this key) is currently being undertaken (Flores-Villela and Sánchez, MS).

- 17. Parietal-median supraocular contact (fig. 52A) 18
- No parietal-median supraocular contact (fig. 52B) 21
- 18. Supra-auricular scales protuberant, not spine-like (fig. 50B); no contact between the prefrontal and superciliary; four secondary and four tertiary temporals; six nuchal rows *A. matudai* (figs. 18, 19)
- Supra-auricular scales not protuberant (fig. 50C); contact between the prefrontal and

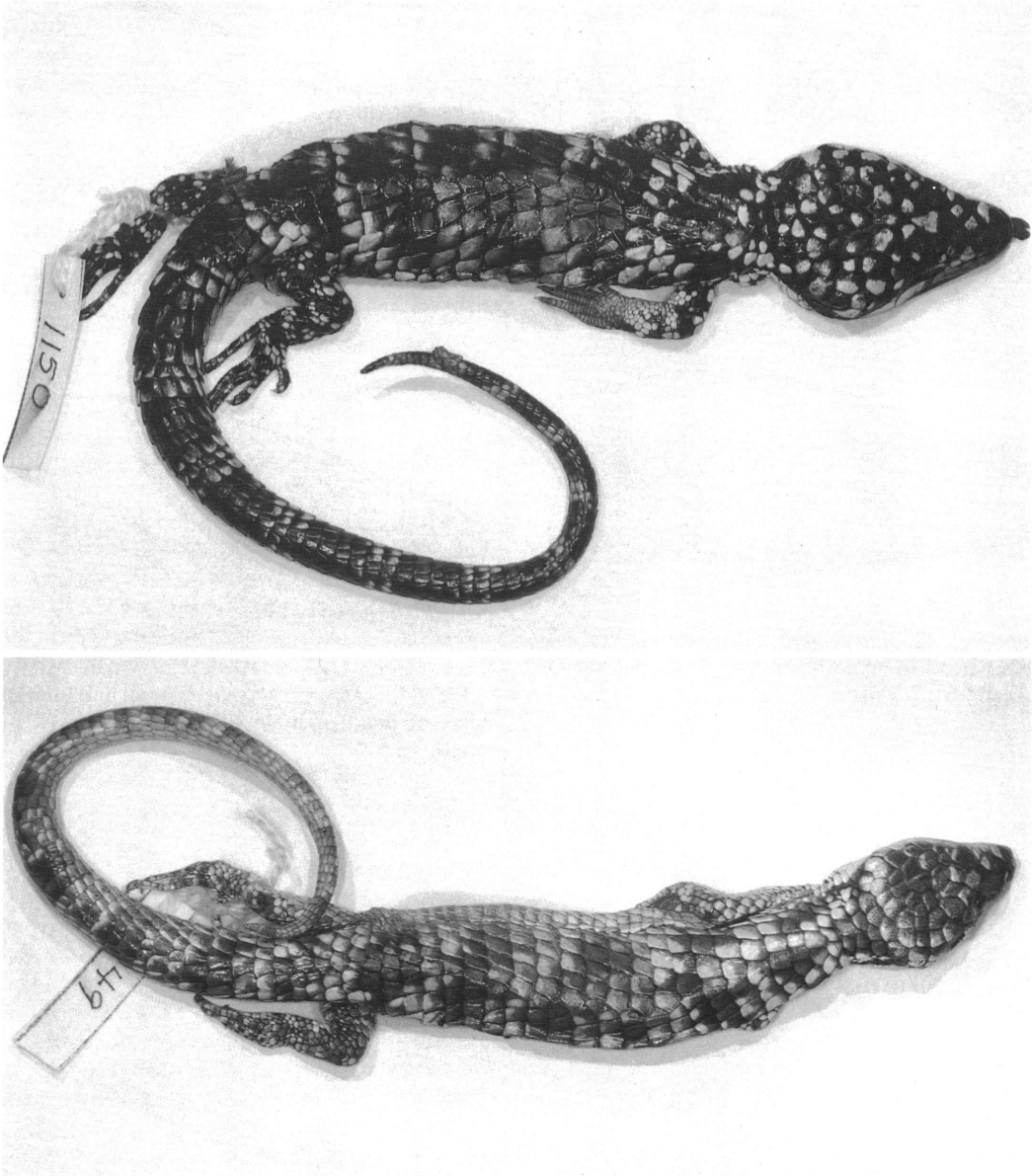


Fig. 61. *Abronia deppii*, (above) male lectotype (ZMB 1150), 99 mm TL, 223 mm TL; (below) male paralectotype (ZMB 1149), 95 mm SVL, 209 mm TL. Both specimens from “Mexico.”

- anterior superciliary; three secondary and three tertiary temporals; eight nuchal rows 19

19. Ten ventral longitudinal scale rows; 2 lateral supraoculars; broad frontonasal-frontal scale contact
.....*Abronia* species “Chiapas” (fig. 12C)
- Twelve ventral longitudinal rows; 3–4 lateral supraoculars; no frontonasal–frontal contact 20

20. Two anterior temporals
..... *A. bogerti*²⁵ (fig. 62)

²⁵ Known only from the holotype.

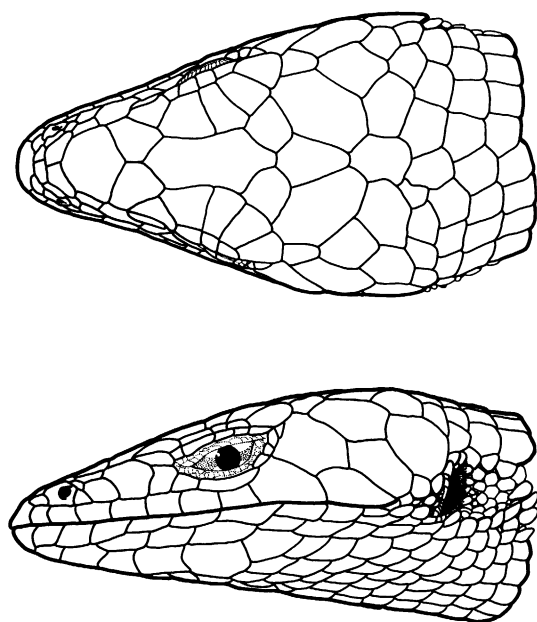


Fig. 62. *Abronia bogerti*, dorsal and lateral aspects of head of male holotype (AMNH 68887), head length 12.5 mm.

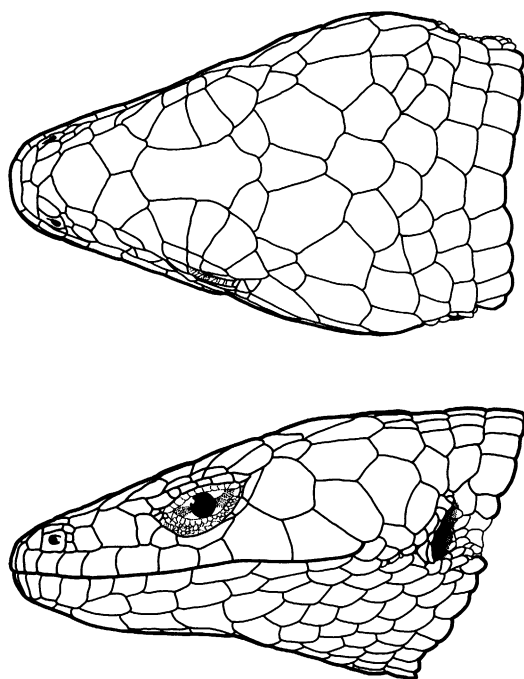


Fig. 64. *Abronia chiszari*, dorsal and lateral aspects of head of male (UNAM-LT 3151), head length 13.9 mm.

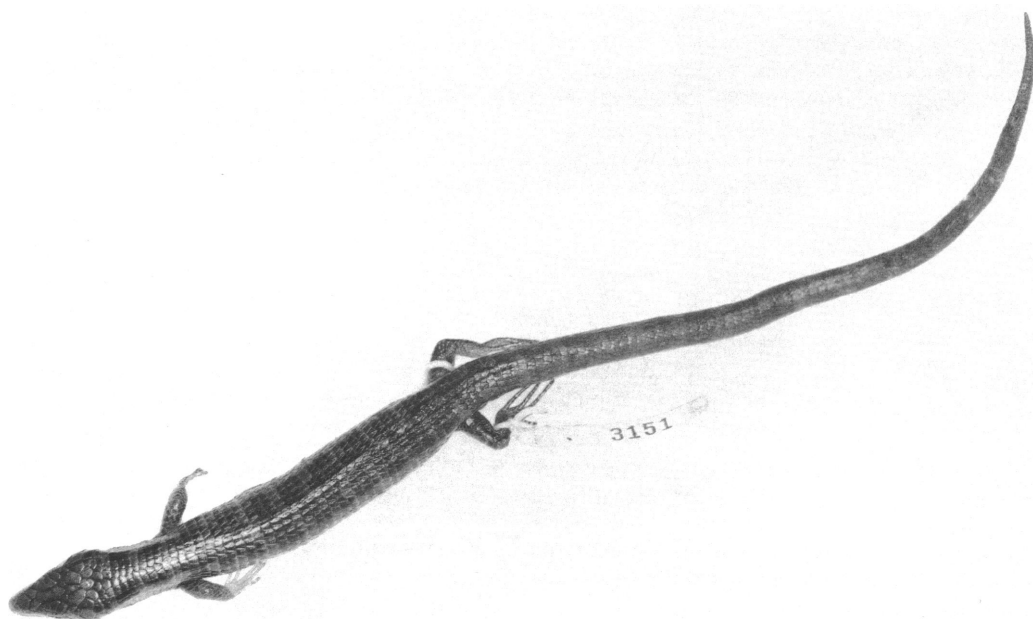


Fig. 63. *Abronia chiszari*, male (UNAM-LT 3151), 75 mm SVL, 190 mm TL; from Santa Marta, near Bastonal, Veracruz, Mexico.

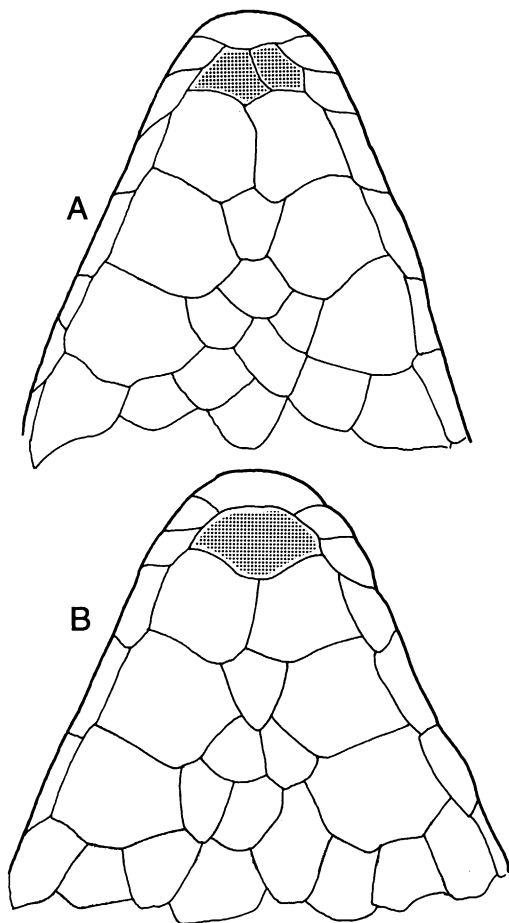


Fig. 65. Postmental scale: A, Divided (e.g., *A. ochoterenai*, male, IBUNAM 339). B, Single (e.g., *A. lythrochila*, male, UTA R-3354). Both of these species are variable for this character.

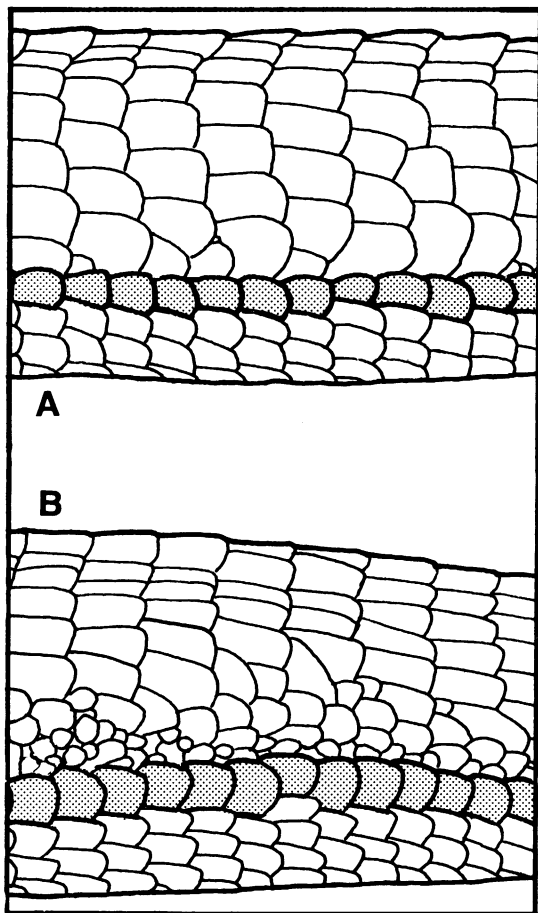


Fig. 66. Lateral row of ventral scales (shaded): A, Not noticeably enlarged relative to adjacent ventrals (e.g., *A. mixteca*, female, AMNH 102649). B, Noticeably enlarged (e.g., *A. aurita*, male, AMNH 137787).

- Three anterior temporals
 *A. chiszari*²⁶ (figs. 63, 64)
 21. Postmental divided (fig. 65A); lateral row of
 ventral scales not noticeably enlarged relative
 to adjacent ventrals (fig. 66A)
 *A. mitchelli* (figs. 67, 68)
 Postmental single (fig. 65B); lateral row of
 ventral scales noticeably enlarged relative
 to adjacent ventrals (fig. 66B) 22
 22. Three primary temporals in contact with
 postoculars; five occipitals in only known
 specimen (fig. 58C)
 *A. montecristoi* (figs. 24, 25)

²⁶ Known only from the holotype and one additional specimen.

- Two primary temporals in contact with post-
 oculars; one or three occipitals (fig. 58A,
 B) *A. salvadorensis* (figs. 22, 23)
 23. Discrete canthals present (fig. 69A); tail with
 complete or narrowly incomplete cross-
 bands ventrally
 *A. fuscolabialis* (figs. 12A, 20, 21)
 Discrete canthals usually absent (fig. 69B); tail
 without crossbands ventrally 24
 24. Dorsum usually uniformly green; sometimes
 showing 6–8 faint crossbands on body; nu-
 chals often 4 *A. graminea* (fig. 70)
 Dorsum with 6–8 dark crossbands, these
 sometimes fused longitudinally along the
 midline; nuchals 6 .. *A. taeniata* (fig. 71)

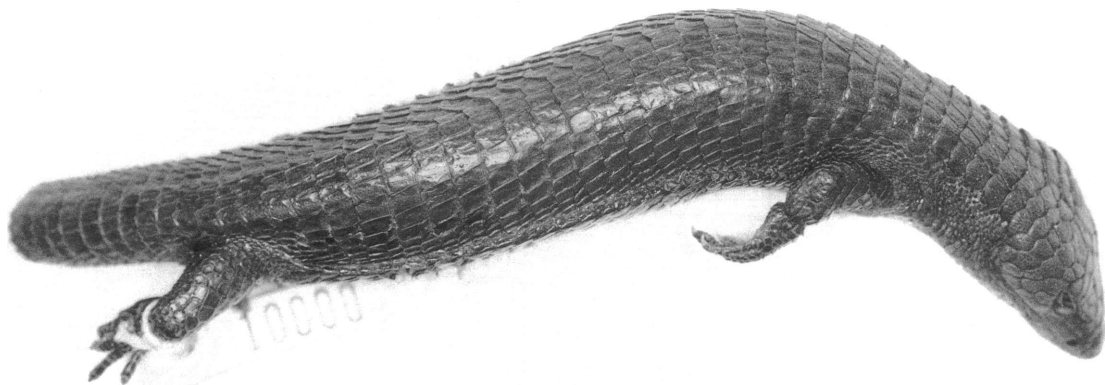


Fig. 67. *Abronia mitchelli*, female holotype (UTA R-10000), 105 mm SVL; from Cerro Pelón, 2750 m, N slope Sierra Juárez, Oaxaca, Mexico.

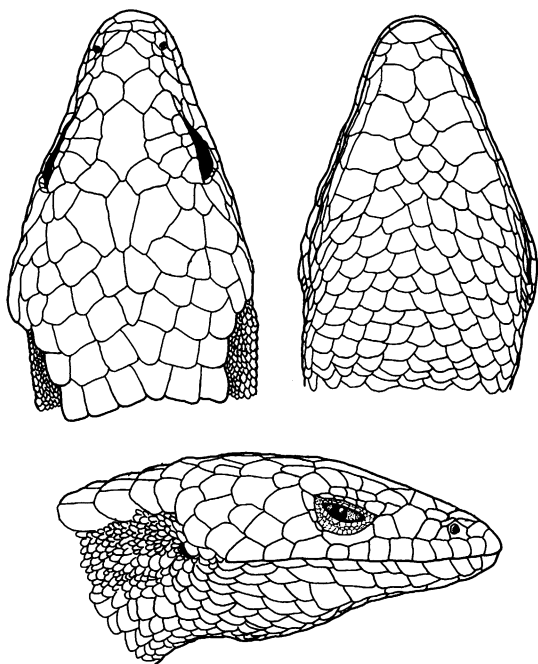


Fig. 68. Dorsal, ventral, and lateral aspects of the head of *Abronia mitchelli* (holotype, UTA R-10000).

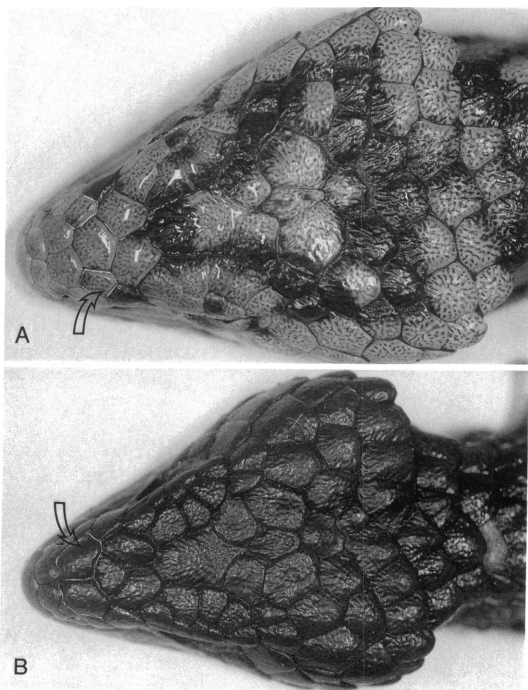


Fig. 69. Canthal scales: A, Discrete from posterior internasals (e.g., *A. fuscolabialis*, male, UTA R-9899). B, Fused with posterior internasals (e.g., *A. graminea*, male, KU 26486).



Fig. 70. *Abronia graminea*. Mexico: Veracruz; Cumbres de Acultzingo, Puerto del Aire, 2286 m.

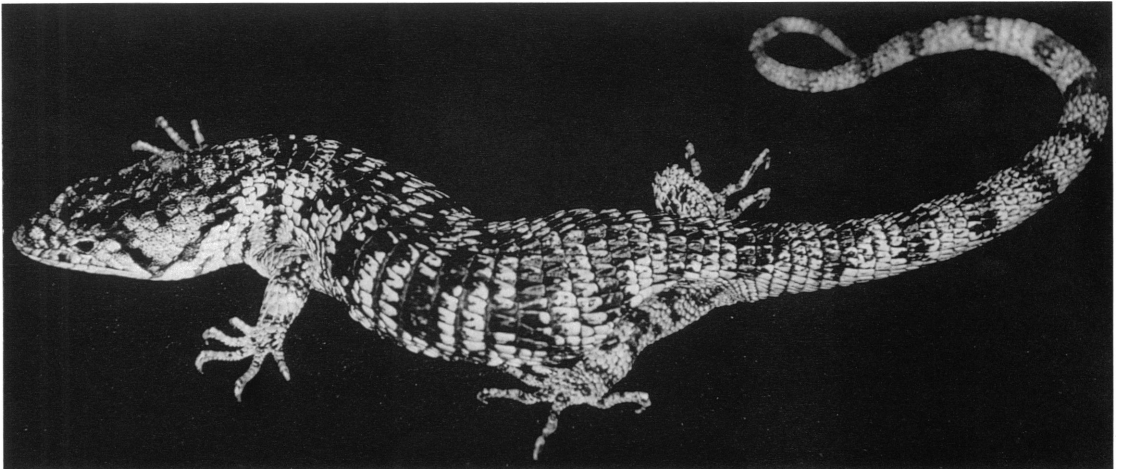


Fig. 71. *Abronia taeniata*. Mexico: Hidalgo; Lago Tejocotal. [Photo by William E. Duellman.]

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APPENDIX 1 Specimens Examined

For purposes of diagnosis and phylogenetic analysis, we have examined a combined total of 242 specimens, representing all described species of *Abronia*. We have examined the holotypes of 17 of these.

Abronia anzueto. — (6 specimens; see Holotype and Paratypes in species account).

A. aurita. — (57 specimens; see Material Examined in species account).

A. bogerti. — (1 specimen) MEXICO: *Oaxaca*: N of Niltpec, between Cerro Atravesado and Sierra Madre, probably between 2500 and 4500 ft (AMNH 68887, holotype).

A. chiszari. — (2 specimens) MEXICO: *Veracruz*: 2.5 mi E Cuetzalapan (UTA R-3195, holotype); Santa Marta Volcanic Range, near Bastonal, 800 m (UNAM-LT 3151).

A. deppii. — (5 specimens) MEXICO: no other data (ZMB 1149, holotype; ZMB 1150, paratype); *México*: Valle de Bravo, Avándaro (MZFC 2016); Valle de Bravo, 1.0 km SW Valle de Bravo (UTA R-31634); *Morelos*: derrame del Chichinautzin (MZFC 2015).

A. fimbriata. — (17 specimens; see Material Examined in species account).

A. fuscolabialis. — (4 specimens; see Material Examined in species account).

A. gaiophasma. — (7 specimens; see Holotype and Paratypes in species account).

A. graminea. — (6 specimens) MEXICO: *Veracruz*: 3 km W Acultzingo (KU 26484–87, 26827); Pico de Orizaba, Xometla, 2545 (KU 105834).

A. leurolepis. — (1 specimen; see Holotype in species account).

A. lythrochila. — (9 specimens) MEXICO: *Chiapas*: 8 km NW San Cristóbal de Las Casas, 2385 m (UTA R-3354); 10.3 mi (by Mex. Hwy. 190) SE San Cristóbal de Las Casas (LACM 130124); 15 mi S San Cristóbal de Las Casas (CAS 141906); “vicinity of San Cristóbal de Las Casas” (personal commun., A. Ramírez; IHN 763–65, 881); 12.1 km ESE Teopisca, Tulanca, 2073 m (UTA R-12137); Comitán, Santa Rosa (IBUNAM 312).

A. matudai. — (4 specimens; see Material Examined in species account).

A. mitchelli. — (1 specimen) MEXICO: *Oaxaca*: N slope Sierra Juárez, Cerro Pelón, 2750 m (UTA R-10000, holotype).

A. mixteca. — (72 specimens) MEXICO: *Guerro*: Malinaltepec, 2 km S Paraje Montero, 2250 m (MZFC 4420); *Oaxaca*: Tejocotes [sometimes given as “El Tejocote”], 2286–2400 m (AMNH 91000 [holotype], 91001, 98002, 100680–81, 100683–85, 102640–55, 108594–99; KU 106303 [paratype]; UTA R-4711–14, 5702–04, 5786–90, 6126, 6159–64, 6228, 6246, 6248, 6825, 6827, 6989, 7737, 7824–25, 10277, 10542–43, 12138–45, 13597–605, 19647–53, 25769–72, 30324); ca. 7 km W Tejocotes, 7800' (AMNH 90998); 0.5 mi. W San Vicente Lachixió (AMNH 98859); 14 km S and 8 km E Nochixtlán (FWMSH 7355).

A. montecristoi. — (1 specimen; see Material Examined in species account).

A. oaxacae. — (13 specimens) MEXICO: *Oaxaca*: Luvina, Rancho Ocote (AMNH 65809); 3.5 mi N Cumbre del Estudiante (AMNH 92737); 1.7 mi E Ixtlán de Juárez, 2200 m (AMNH 102656–57); 2.0 mi E Ixtlán de Juárez, 7200 ft (AMNH 90997, 93208); Loma Grande, 8200 ft, above and S El Punto (AMNH 98003); Santo Domingo Chontecomatlán (UIMNH 48672); near El Punto (toward Ixtlán), off the Oaxaca–Tuxtpec highway (UIMNH 51270, 50156–57); Cerro San Felipe (AMNH 100686–97).

A. ochoterenai. — (2 specimens) MEXICO: *Chiapas*: Comitán, Santa Rosa (IBUNAM 339, lectotype; IBUNAM 338, paralectotype).

A. ornelasi. — (8 specimens) MEXICO: *Oaxaca*: Cerro Baúl, 1500–1600 m (UTA R-6641, holotype; UTA R-6074–75, 6219–20, 10545, AMNH 137783 [formerly UTA R-7710], paratypes); Colonia Rodolfo Figueroa, 19 km NW Rizo de Oro, 1524 m (UTA R-12499).

A. reidi. — (1 specimen) MEXICO: *Veracruz*: crater rim of Volcán San Martín, 5370 ft (UIMNH 73732, paratype).

A. salvadorensis. — (4 specimens; Material Examined in species account).

A. smithi. — (11 specimens; see Holotype and Paratypes in species account.)

A. taeniata. — (17 specimens) MEXICO: no other data (ZMB 1151 [considered a paratype of *A. deppii*, in error, by Taylor, 1969: iv]); *Hidalgo*: 3 km W Xochicoatlán (KU 54055); Río Chinameca, 8 km N Tianguistengo, 1020 m (KU 101144); Lago Tejocotal, 7 mi E Acaxochitlán, 7300 ft (UMMZ 118218); 10.5 mi SW Huachinango (UMMZ 123043). *Tamaulipas*: ca. 6 mi. WNW Gómez Farías, ca. 5000 ft (AMNH 101975); 5 mi NW Gómez Farías near Rancho del Cielo (UMMZ 111116–17, 111119–20, 111122–23, 111125–26, 111128, 111130); along trail between Gómez Farías to La Joya de Salas, below Agua Zarca, 5300 ft elev. (UMMZ 111118).

Abronia species “Guerrero.” — (10 specimens) MEXICO: *Guerrero*: Omilteme, 2134 m (UTA R-4451, 5553, 5645–46, 5653–54); 1.6 km N Puerto del Gallo, 2621 m (UTA R-4151); 0.8–1.6 km NE Puerto del Gallo, 2560–2804 m (UTA R-12135–36); vicinity of Chilpancingo (AMNH 72543).

A. species (*A. bogerti* group). — MEXICO: *Chiapas*: Municipio de Jiquipilas, Rancho El Recuerdo, Cerro La Vela, Sierra Madre de Chiapas, alt. 1350 m (IHN 1177—transparency only); Municipio Ocozocuatla, Parque Laguna Belgica (specimen lost—transparency of *A. Ramírez Velazques*, IHN).

APPENDIX 2

General Data Matrix Showing Intraspecific Variability. ? = unknown; 8 = 0/1; 9 = 1/2.

	0000000001111111112222222223 123456789012345678901234567890
<i>Abronia ornelasi</i>	801880008000100000010010010100
<i>A. reidi</i>	108880010100100000010010010100
<i>A. chiszari</i>	000010111111000010000001000000
<i>A. bogerti</i>	00001011111100001000000100000?
<i>A. mitchelli</i>	000000000000010000010010000000
<i>A. fuscolabialis</i>	0000008010000010000100900001000
<i>A. graminea</i>	0008088080000010000100900008010
<i>A. taeniata</i>	088800808000001000010010008000
<i>A. oaxacae</i>	080108111000021080811022101000
<i>A. mixteca</i>	008800108000021000011012101000
<i>A. deppii</i>	008108101010001088011112108000
<i>A. sp.</i> “Guerrero”	008108101010001010811112108000
<i>A. salvadorensis</i>	000008108000020080110010018000
<i>A. montecristoi</i>	00000010800013001011001001010?
<i>A. matudai</i>	000800100100000180810010018000
<i>A. smithi</i>	000008108000000280810010010010
<i>A. ochoterenai</i>	00000000000000028081001001000?
<i>A. leurolepis</i>	01?80000080000020111001001000?
<i>A. gaiophantasma</i>	000000108080000210810010011000
<i>A. fimbriata</i>	11?100801800000210110010010001
<i>A. lythrochila</i>	080800108800000281810010081001
<i>A. aurita</i>	008000108800000211810010011011
<i>A. anzuetoi</i>	000000108800000211810010011011
Ancestor	0?7000000000000000?70000000000

APPENDIX 3
Matrix Used for the
“Any Instance” Analysis

	00000000001111111112222222223 123456789012345678901234567890
<i>Abronia ornelasi</i>	101110001000100000010010010100
<i>A. reidi</i>	101110010100100000010010010100
<i>A. chiszari</i>	000010111111000010000001000000
<i>A. bogerti</i>	00001011111100001000000100000?
<i>A. mitchelli</i>	000000000000010000010010000000
<i>A. fuscolabialis</i>	000000101000001000010020001000
<i>A. graminea</i>	000101101000001000010020001010
<i>A. taeniata</i>	011100101000001000010010001000
<i>A. oaxacae</i>	010101111000021010111022101000
<i>A. mixteca</i>	001100101000021000011012101000
<i>A. deppii</i>	001101101010001011011112101000
<i>A. sp. “Guer- rero”</i>	001101101010001010111112101000
<i>A. salvadorensis</i>	000001101000020010110010011000
<i>A. montecristoi</i>	00000010100013001011001001010?
<i>A. matudai</i>	000100100100000110110010011000
<i>A. smithi</i>	000001101000000210110010010010
<i>A. ochoterenai</i>	00000000000000021011001001000?
<i>A. leurolepis</i>	01?10000010000020111001001000?
<i>A. gaiophantas- ma</i>	000000101010000210110010011000
<i>A. fimbriata</i>	11?100101100000210110010010001
<i>A. lythrochila</i>	010100101100000211110010011001
<i>A. aurita</i>	001000101100000211110010011011
<i>A. anzueto</i>	000000101100000211110010011011
Ancestor	0??0000000000000??00000000000

APPENDIX 4
Recoded Matrix Used for the “Unscaled” and
“Scaled” Analyses

	00000000011111111112222222223 123456789012345678901234567890
<i>Abronia ornelasi</i>	102110001000100000010010020100
<i>A. reidi</i>	201110010200100000010010020100
<i>A. chiszari</i>	000020212221000020000001000000
<i>A. bogerti</i>	00002021222100002000000100000?
<i>A. mitchelli</i>	000000000000010000010010000000
<i>A. fuscolabialis</i>	000000102000001000010020002000
<i>A. graminea</i>	000101101000001000010020001010
<i>A. taeniata</i>	011100101000001000010010001000
<i>A. oaxacae</i>	010201212000021010111032102000
<i>A. mixteca</i>	001100201000021000011012102000
<i>A. deppii</i>	001201202020001011011112101000
<i>A. sp. “Guer- rero”</i>	001201202020001020111112101000
<i>A. salvadorensis</i>	000001201000020010210010021000
<i>A. montecristoi</i>	000000201000130020210010020100
<i>A. matudai</i>	000100200200000110110010021000
<i>A. smithi</i>	000001201000000210110010020010
<i>A. ochoterenai</i>	00000000000000021011001002000?
<i>A. leurolepis</i>	02?10000010000020221001002000?
<i>A. gaiophantas- ma</i>	000000201010000220110010022000
<i>A. fimbriata</i>	22?200102200000220210010020001
<i>A. lythrochila</i>	010100201100000212110010012001
<i>A. aurita</i>	001000201100000222110010022011
<i>A. anzueto</i>	000000201100000222110010022011
Ancestor	0??00000000000000??0000000000

APPENDIX 5

Change List of Characters for Cladogram Shown in Figure 44

Characters refer to coding in recoded matrix (Appendix 4). Asterisks (*) by changes denote ambiguity due to character optimization of "unknown" cells in the data matrix. Double arrows denote a priori polarity character transformation; single arrows denote reversal.

Character transformation	ci	Steps	Change	Along	Character transformation	ci	Steps	Change	Along
1	0.500	1	0⇒1	stem 22	14	0.600	1	0⇒3	<i>A. montecristoi</i>
		1	1⇒2	<i>A. reidi</i>			1	0⇒2	<i>A. salvadorensis</i>
		2	0⇒2	<i>A. fimbriata</i>			1	0⇒2*	stem 5
2	0.500	1	0⇒1	stem 18			1	2⇒0*	stem 7
		1	1⇒2	stem 19			1	0⇒1	<i>A. mitchelli</i>
		1	0⇒1	<i>A. taeniata</i>	15	1.000	1	0⇒1	stem 3
		1	0⇒1	<i>A. oaxacae</i>	16	1.000	1	0⇒1	stem 13
3	0.400	1	0⇒1	stem 22			1	1⇒2	stem 14
		1	1⇒2	<i>A. ornelasi</i>	17	0.200	1	0⇒1	stem 9
		1	0⇒1	<i>A. aurita</i>			1	1⇒0	stem 22
		1	0⇒1	stem 4			1	1⇒2	<i>A. montecristoi</i>
		1	1⇒0	<i>A. oaxacae</i>			1	1⇒2*	stem 15
4	0.286	1	0⇒1	stem 22			1	2⇒1*	stem 18
		1	0⇒1	<i>A. matudai</i>			1	1⇒0	<i>A. leurolepis</i>
		1	0⇒1	stem 18			1	1⇒2*	<i>A. fimbriata</i>
		1	1⇒2	<i>A. fimbriata</i>			1	1⇒2	stem 10
		1	0⇒1*	stem 3			1	0⇒1	stem 6
		1	1⇒0*	<i>A. fuscolabialis</i>			1	1⇒2	<i>A. sp. "Guerrero"</i>
		1	1⇒2	stem 6	18	0.400	2	0⇒2	stem 16
5	0.667	1	0⇒1	stem 22			2	2⇒0	<i>A. fimbriata</i>
		2	0⇒2	stem 10			1	0⇒1	<i>A. deppii</i>
6	0.250	1	0⇒1	<i>A. salvadorensis</i>	19	0.286	1	0⇒1*	stem 11
		1	0⇒1	<i>A. smithi</i>			1	1⇒0*	stem 22
		1	0⇒1	<i>A. graminea</i>			1	1⇒2	<i>A. montecristoi</i>
		1	0⇒1	stem 6			1	1⇒2	<i>A. salvadorensis</i>
7	0.222	1	0⇒1	stem 2			1	1⇒2	stem 19
		1	1⇒2	stem 9			1	0⇒1*	stem 6
		2	2⇒0	stem 22			1	1⇒0*	<i>A. deppii</i>
		2	2⇒0	<i>A. ochoterenai</i>	20	1.000	1	1⇒0	stem 10
		1	2⇒1	stem 19	21	1.000	1	0⇒1	stem 5
		1	1⇒0	<i>A. leurolepis</i>	22	1.000	1	0⇒1	stem 7
		1	1⇒2	stem 5	23	0.600	1	0⇒1	stem 1
8	0.333	1	0⇒1	<i>A. reidi</i>			1	1⇒0	stem 10
		1	0⇒1	stem 10			1	1⇒2	stem 8
		1	0⇒1	<i>A. oaxacae</i>			2	1⇒3	<i>A. oaxacae</i>
9	0.222	1	0⇒1	stem 2	24	1.000	1	0⇒1	stem 10
		1	1⇒0	<i>A. reidi</i>			1	0⇒2	stem 5
		1	1⇒0	<i>A. matudai</i>	25	1.000	1	0⇒1	stem 5
		1	1⇒0	<i>A. ochoterenai</i>	26	0.667	2	0⇒2	stem 11
		1	1⇒0	<i>A. leurolepis</i>			1	2⇒1	<i>A. lythrochila</i>
		1	1⇒2	<i>A. fimbriata</i>	27	0.222	1	0⇒1	stem 12
		1	1⇒2	stem 10			1	1⇒0	stem 20
		1	1⇒2	<i>A. fuscolabialis</i>			1	1⇒2	stem 15
		1	1⇒2	stem 6			2	2⇒0	stem 19
10	0.286	2	0⇒2	<i>A. reidi</i>			1	0⇒1	stem 3
		2	0⇒2	<i>A. matudai</i>			1	1⇒2	<i>A. fuscolabialis</i>
		1	0⇒1	stem 16			1	1⇒2*	stem 5
		2	0⇒2	stem 10			1	2⇒1*	stem 7
11	0.400	1	0⇒1	<i>A. gaiophantasma</i>	28	1.000	1	0⇒1	stem 21
		2	0⇒2	stem 10	29	0.333	1	0⇒1	<i>A. smithi</i>
		2	0⇒2	stem 7			1	0⇒1	stem 17
12	1.000	1	0⇒1	stem 10			1	0⇒1	<i>A. graminea</i>
13	1.000	1	0⇒1	stem 21	30	1.000	1	0⇒1	stem 16

APPENDIX 6

Lists of Apomorphies by Stems for Cladogram Shown in Figure 44

An asterisk (*) after the hypothesized character change denotes ambiguity due to character optimization or "unknown" cells in the matrix. Double arrows denote transformation along a priori polarity; single arrows denote reversal.

Branch	Charac- ter	Steps	ci	Change	Branch	Charac- ter	Steps	ci	Change
<i>A. aurita</i>	3	1	0.400	0⇒1	stem 5	24	1	1.000	0⇒2
<i>A. deppii</i>	18	1	0.400	0⇒1*		25	1	1.000	0⇒1
	19	1	0.286	1→0		27	1	0.222	1→2*
<i>A. fimbriata</i>	1	2	0.500	0⇒2	stem 6	4	1	0.286	1⇒2
	4	1	0.286	1⇒2		6	1	0.250	0⇒1
	9	1	0.222	1⇒2		9	1	0.222	1⇒2
	17	1	0.200	1→2*		17	1	0.200	0⇒1
	18	2	0.400	2⇒0		19	1	0.286	0→1*
<i>A. fuscolabialis</i>	4	1	0.286	1→0*	stem 7	11	2	0.400	0⇒2
	9	1	0.222	1⇒2		14	1	0.600	2→0*
	27	1	0.222	1⇒2		22	1	1.000	0⇒1
<i>A. gaiophantasma</i>	11	1	0.400	0⇒1		27	1	0.222	2→1*
<i>A. graminea</i>	6	1	0.250	0⇒1	stem 8	23	1	0.600	1⇒2
	29	1	0.333	0⇒1	stem 9	7	1	0.222	1⇒2
<i>A. leurolepis</i>	7	1	0.222	1⇒0		17	1	0.200	0⇒1
	9	1	0.222	1⇒0	stem 10	5	2	0.667	0⇒2
	17	1	0.200	1⇒0		8	1	0.333	0⇒1
<i>A. lythrochila</i>	26	1	0.667	2⇒1		9	1	0.222	1⇒2
<i>A. matudai</i>	4	1	0.286	0⇒1		10	2	0.286	0⇒2
	9	1	0.222	1⇒0		11	2	0.400	0⇒2
	10	2	0.286	0⇒2		12	1	1.000	0⇒1
<i>A. mitchelli</i>	14	1	0.600	0⇒1		17	1	0.200	1⇒2
<i>A. montecristoi</i>	14	1	0.600	0⇒3		20	1	1.000	1⇒0
	17	1	0.200	1⇒2		23	1	0.600	1⇒0
	19	1	0.286	1⇒2		24	1	1.000	0⇒1
<i>A. oaxacae</i>	2	1	0.500	0⇒1	stem 11	19	1	0.286	0→1*
	3	1	0.400	1⇒0		26	2	0.667	0⇒2
	8	1	0.333	0⇒1	stem 12	27	1	0.222	0⇒1
	23	2	0.600	1⇒3	stem 13	16	1	1.000	0⇒1
<i>A. ochoterenai</i>	7	2	0.222	2⇒0	stem 14	16	1	1.000	1⇒2
	9	1	0.222	1⇒0	stem 15	17	1	0.200	1→2*
<i>A. ornelasi</i>	3	1	0.400	1⇒2		27	1	0.222	1⇒2
<i>A. reidi</i>	1	1	0.500	1⇒2	stem 16	10	1	0.286	0⇒1
	8	1	0.333	0⇒1		18	2	0.400	0⇒2
	9	1	0.222	1⇒0		30	1	1.000	0⇒1
	10	2	0.286	0⇒2	stem 17	29	1	0.333	0⇒1
<i>A. salvadorensis</i>	6	1	0.250	0⇒1	stem 18	2	1	0.500	0⇒1
	14	1	0.600	0⇒2		4	1	0.286	0⇒1
	19	1	0.286	1⇒2		17	1	0.200	2→1*
<i>A. smithi</i>	6	1	0.250	0⇒1	stem 19	2	1	0.500	1⇒2
	29	1	0.333	0⇒1		7	1	0.222	2⇒1
<i>A. taeniata</i>	2	1	0.500	0⇒1		19	1	0.286	1⇒2
<i>A. sp. "Guerrero"</i>	17	1	0.200	1⇒2		27	2	0.222	2⇒0
stem 1	23	1	0.600	0⇒1	stem 20	27	1	0.222	1⇒0
stem 2	7	1	0.222	0⇒1	stem 21	13	1	1.000	0⇒1
	9	1	0.222	0⇒1		28	1	1.000	0⇒1
stem 3	4	1	0.286	0→1*	stem 22	1	1	0.500	0⇒1
	15	1	1.000	0⇒1		3	1	0.400	0⇒1
	27	1	0.222	0⇒1		4	1	0.286	0⇒1
stem 4	3	1	0.400	0⇒1		5	1	0.667	0⇒1
stem 5	7	1	0.222	1⇒2		7	2	0.222	2⇒0
	14	1	0.600	1→2*		17	1	0.200	1⇒0
	21	1	1.000	0⇒1		19	1	0.286	1→0*

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