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A New Species of *Abronia* (Sauria, Anguidae) from the Sierra Madre del Sur of Oaxaca, Mexico

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Three additional species of *Abronia* have been discovered in Mexico since 1949, when Tihen redefined the genus. The two species in Guatemala, and six of the nine species in Mexico, are known only from the vicinity of their respective type localities. The most widely distributed member of the genus is *Abronia taeniata*, restricted to the Sierra Madre Oriental, from central Veracruz and the adjacent portion of Puebla, northward through Hidalgo and San Luis Potosí to southern Tamaulipas. Three species occur in the Sierra Madre del Sur, *A. deppii* in Guerrero, *A. oaxacae* in central Oaxaca, and *A. fuscolabialis* near Cerro Zempoaltepec (or "Cempoaltépetl"), farther east in the same state.

Field work in Oaxaca during the summer of 1963 revealed the existence of an undescribed anguid, the fourth representative of the genus *Abronia* to be found in the Sierra Madre del Sur. The new species was discovered near Tejocotes, a village on the Continental Divide scarcely 40 kilometers west-northwest of the area between El Punto and La Cumbre del Estudiante, which has been the source of most of the specimens of *A. oaxacae* now in museum collections. Despite the proximity of the two populations and evidence of their affinity, they are so strikingly different in other respects that it can scarcely be doubted that two species

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are represented. Moreover, both species are readily separated from all other members of the genus, including *A. deppii*, the only *Abronia* known from the mountains to the west. Other species undoubtedly remain to be discovered in the wide area that now separates the population in Guerrero from the one discovered at Tejocotes.

This mountain village is in the area long occupied by the Mixteca.

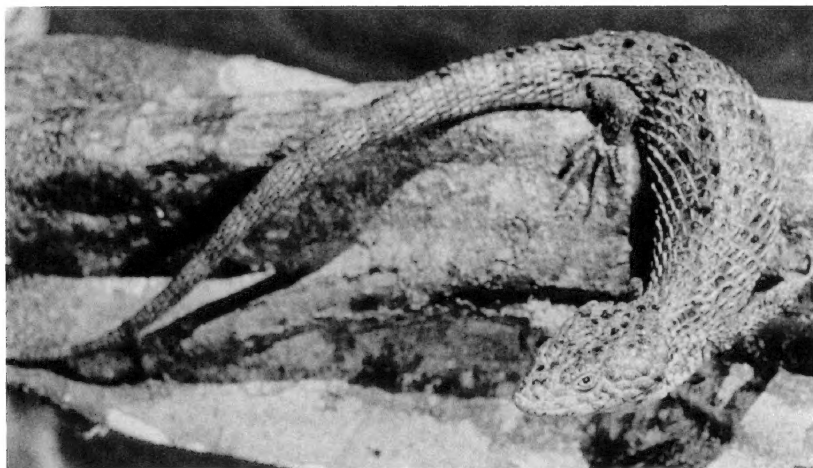


FIG. 1. *Abronia mixteca*, male holotype, in life, now A.M.N.H. No. 91000.

It seems appropriate, therefore, that the species of *Abronia* inhabiting the same region be called

***Abronia mixteca*, new species**

HOLOTYPE: An adult male, A.M.N.H. No. 91000 (figs. 1 and 2) in the collection of the American Museum of Natural History, obtained near Tejocotes, Oaxaca, on August 24, 1963, by Pedro Lopez, C. M. Bogert, Greenfield Sluder, and Nicholas Bucknall. Tejocotes is situated at an elevation of approximately 2400 meters in the Sierra Madre del Sur, near latitude $17^{\circ} 14' N.$, longitude $96^{\circ} 59' W.$ The mountains in this area border the west side of the northern extremity of the Valle de Oaxaca (as mapped in detail by Welte, 1965).

DIAGNOSIS: The species differs from *Abronia oaxacae* in possessing smaller, more numerous scutes on the crown (there are three rows of scutes rather than one row between the three occipitals and the nuchals, as may be seen in figs. 3 and 4), and in having the first superciliary in contact with the cantholoreal instead of being separated from it by the anterior

median supraocular, as it is in 11 of the 12 specimens of *A. oaxacae* examined. The scutes covering the osteoderms on the lateral posterior portions of the head of *A. oaxacae* are knoblike projections, whereas these scutes in *A. mixteca* are smaller, more numerous and rounded in profile, without conspicuous projections. Osteoderms, well developed only in the anterior row of nuchals on *A. mixteca*, are present in the scutes of the

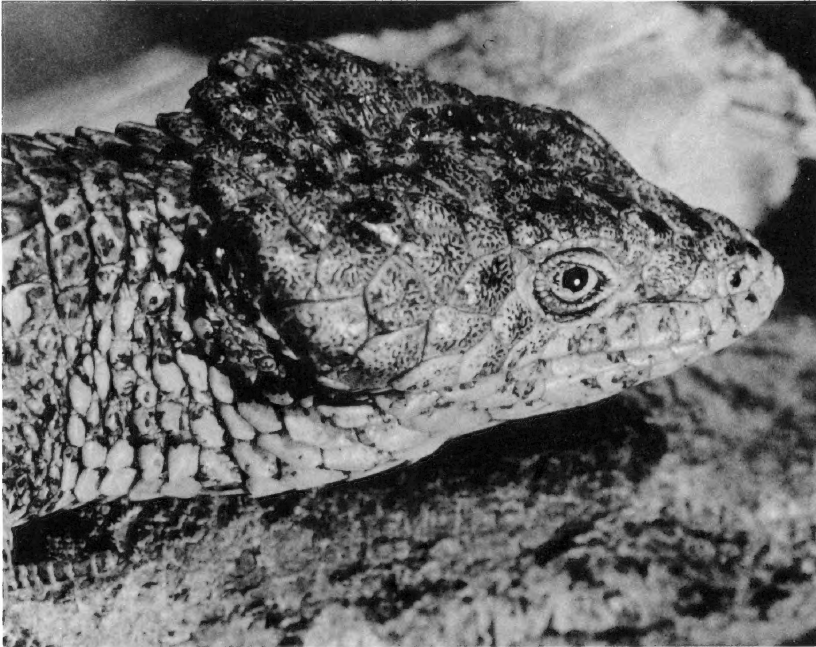


FIG. 2. *Abronia mixteca*, head of holotype, enlarged to show details of the pattern and cephalic scutes.

first four rows on *A. oaxacae*. Three anterior temporals are characteristic of *A. oaxacae*, but four are normally present in *A. mixteca*.

The two species are readily distinguished from all other members of the genus in having the interoccipital flanked by lateral occipitals, which are commonly but not invariably smaller than the median scale. The retention of three occipitals (fig. 5) by these two species may be construed as evidence of affinity, but *A. oaxacae* also has fewer transverse rows of dorsals (from the head, including the nuchals, to the posterior of the thigh), 27 to 29, whereas there are from 28 to 31 on *A. mixteca*. The latter species, however, has fewer whorls of scales on the tail, 77 to 82 in three with unregenerated tails, whereas the number in *A. oaxacae*

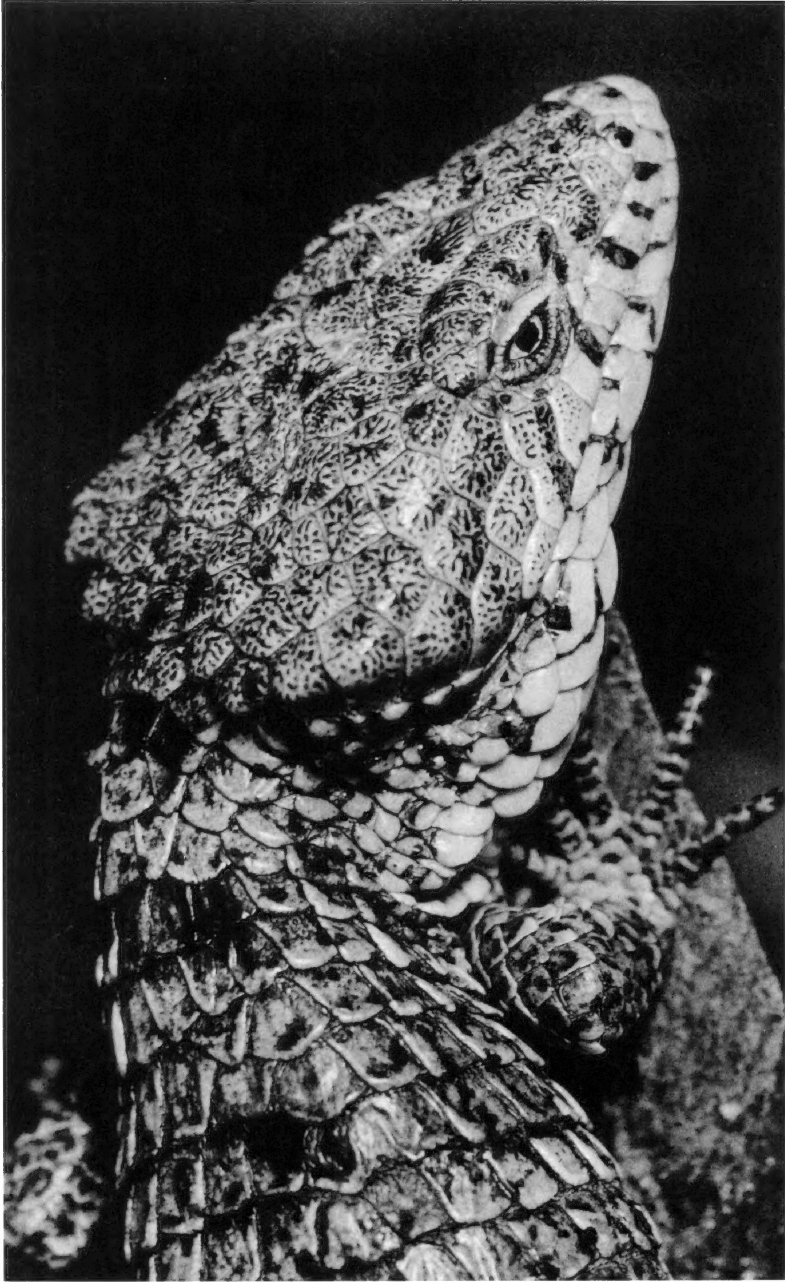


FIG. 3. *Abronia mixteca*, head of paratype, an adult male, A.M.N.H. No. 91001, enlarged to permit detailed comparisons with *Abronia oaxacae* in figure 4.

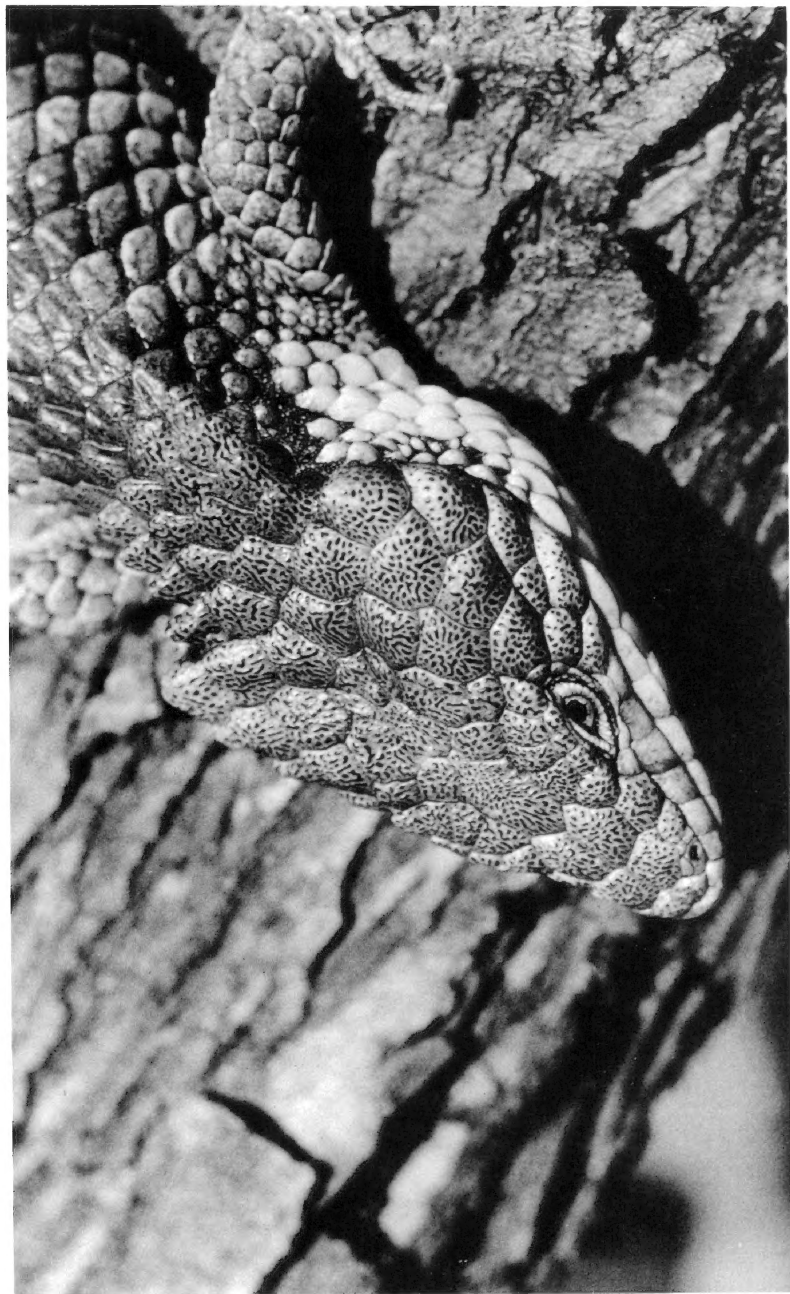


FIG. 4. *Abronia oaxacae*, head of adult male, A.M.N.H. No. 92737, taken north of La Cumbre del Estudiante, Oaxaca, at an elevation of 2700 meters.

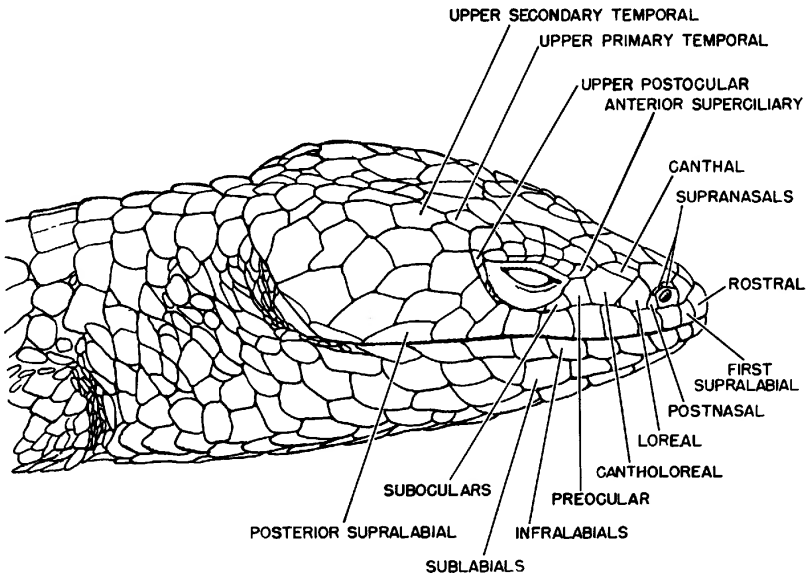
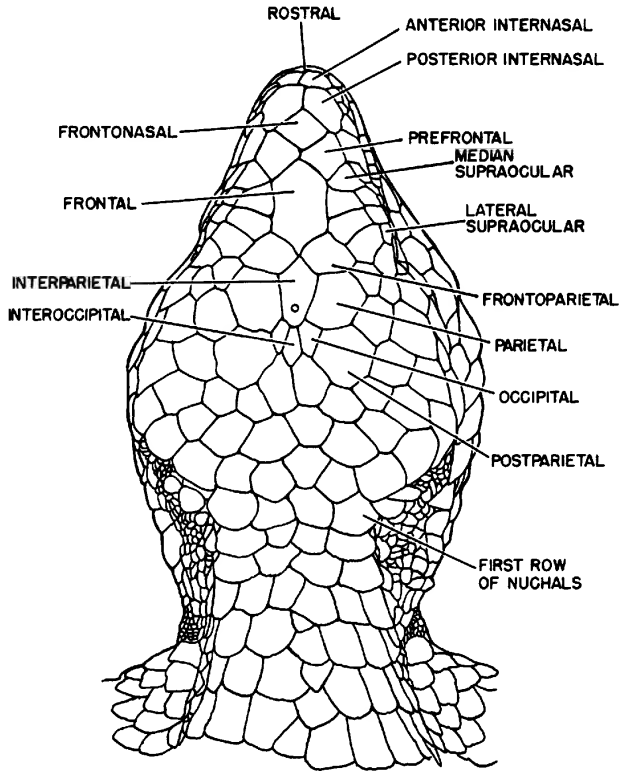


FIG. 5. Terms employed to designate scutes on the top and sides of head of *Abronia mixteca*.

varies from 84 to 92 in eight specimens with unregenerated tails. *Abronia mixteca* also tends to have a shorter tail; it comprises from 55 to 59 per cent of the over-all length in this species, and from 57 to 61 per cent in *A. oaxacae*. The two species also differ in color; the dorsum of *A. oaxacae* may be rather uniformly bronze in color, but more often it is barred or mottled with gray. The enlarged scales on the sides of the neck are invariably white, both in life and in preserved specimens. The dorsal surface of the trunk of *A. mixteca* is yellowish olive (grayish in preserved specimens), with a few small black blotches (fig. 1), and the scales on the lips and the sides of the neck (fig. 3) are yellow in life (but nearly white in preserved specimens). Table 1 summarizes differences between the species from the Sierra Madre del Sur.

DESCRIPTION OF HOLOTYPE: When the holotype was measured prior to being preserved, the length from snout to vent was 103 mm., and the tail measured 142 mm. After being preserved in grain alcohol, however, owing to differentials in shrinkage, the respective measurements are 102 and 136 mm., and the over-all length is 238 mm. The ratio of tail to total length is 0.58.

The rostral is separated from the nasals by the anterior pair of internasals. There are two postnasals and a supranasal on the left, but on the right these three elements are fused. The posterior internasals reach the loreal, the canthal, and, on the right side only, the cantholoreal. The frontonasal is in contact with the frontal, and the prefrontals reach the cantholoreals. There are five median supraoculars, three lateral supraoculars, and six superciliaries. The first superciliary is in broad contact with the cantholoreal and the preocular. There are two suboculars, one preocular, and a series of six postoculars on the right and five on the left. The suboculars are separated from the lowest primary temporal. The frontal reaches the interparietal, the posterior end of which is in contact with three small, elongated scutes, the interoccipital, and occipitals. The occipitals are bordered laterally by the postparietals. Two of the four primary temporals extend to postoculars behind the orbit. A frontoparietal scale separates the upper primary temporal from the interparietal on each side, and the upper primary temporal separates the parietal from the median supraoculars. The secondary temporal series consists of three scales on the right and four on the left. There are 11 supralabials on the right side, and 10 on the left; the antepenultimate supralabial is the posteriormost to reach the orbit. There are nine infralabials on each side. The postmental is divided. The scales in the sublabial series extend to the second infralabial on the right side and to the third on the left.

There are 29 transverse rows of dorsal scales, 87 caudal whorls, and 14 longitudinal rows of ventral scales. Osteoderms are well developed beneath the scales on the upper surface of the head. On the neck osteoderms are present only in the first nuchal row. The minimum number of scales in the transverse rows of nuchals is four. Traces of a median keel are present on the scales of the six median rows of dorsal scales. The scales behind the ear vary in size and shape below the first three rows of scales on the neck, but the fourth row, represented by progressively smaller scales, continues to the ventral surface. The lateral fold is scarcely discernible, marked only by small, irregular scales situated at the edges of the outer row of ventral scales.

The upper surfaces of the head, trunk, and tail are gray, with yellow flecks, most numerous on the sides of the body and tail. The sides of the neck are yellow, flecked with gray, and the skin bordering the eyes is yellow. A few scattered black spots are present on the top of the head (fig. 1). There are five dark gray bars extending obliquely through the supralabials. Black spots on the dorsal surface of the body and tail are about half of the size of the scales. Two dark spots behind the head are followed by an immaculate area that extends beyond the level of the forelimbs. On the dorsal surface of the anterior third of the tail the black spots are separated by five or six caudal whorls. The posterior portion of the tail is indistinctly banded, alternately light and dark gray. The ground color of the ventral surface is whitish, with small, irregularly shaped black spots that are most numerous on the belly. The posterior surfaces of the limbs are covered with small, granular scales. Lamellae on the fourth toe number 18 on the right and 17 on the left. Claws are well developed on all digits.

PARATYPES: Three of the paratypes are in the collection of the American Museum of Natural History. A.M.N.H. Nos. 90999 and 91001, adult males, are topotypic, and A.M.N.H. No. 90098, an adult female, was taken 7 kilometers west of Tejocotes at an elevation of approximately 2350 meters. An immature specimen, M.C.Z. No. 64102 in the collection of the Museum of Comparative Zoology, was obtained slightly below Tejocotes, 6 kilometers to the northwest, where a sharp curve in the road is known as "La Herradura."¹

DESCRIPTION OF PARATYPES: The paratypes agree with the holotype in having the interoccipital flanked by a pair of occipitals, and at least four

¹ Two additional specimens were obtained at Tejocotes on August 7, 1966, by Sherman A. Minton and the senior author.

scales in the transverse row of nuchals. The first superciliary invariably reaches the cantholoreal, two primary temporals extend to the postoculars, and the antepenultimate supralabial is the posteriormost member of the series to reach the orbit. The number of transverse dorsal scale rows varies from 28 to 31. On two specimens the number of longitudinal rows on the dorsum diminishes at intervals to 13. Of the two paratypes with complete tails, one has 77 caudal whorls and the other 82. There are 10 or 11 supralabials and from seven to nine infralabials. The supranasal and postnasal series consists of three scales on three specimens and two on the other. A canthal is present on only one side of one of the paratypes. The frontonasal is separated from the frontal on three specimens, but it reaches the frontal on the fourth. Three of the paratypes have four primary temporals; the other has three on one side and four on the other. There may be either three or four secondary temporals. The snout-to-vent lengths of two males are 103 and 108 mm., and the snout-to-vent length of the female is 110 mm. The immature individual is 55 mm. from snout to vent, and the tail is 78 mm. in length. The lamellae on the fourth toe vary in number from 17 to 19. The median series of dark dorsal spots is present on one paratype, but indistinct on or absent from the others. The supralabials of two adults are indistinctly barred. The head color ranges from gray, with relatively little yellow, to yellow and brown on the thicker portion of the osteoderms. The spots on the head are diffuse in some cases. The venter of the two adult males is thickly flecked with black, but on the belly of the adult female the dots are minute flecks of black pigment, most abundant laterally. The female also differs from adult males in having the dorsal surface of the body covered with minute black spots, from one to three per scale.

OSTEOLOGY, SCUTELLATION, AND RELATIONSHIPS: As Tihen (1949) observed, the lizards of the genus *Abronia* retain characteristics that are perhaps to be regarded as primitive, even though all members of the group are adaptively specialized in some respects. The osteological characters that Tihen used to define the genus are subject to more variation than he anticipated. He depicts the skull of one species, *A. taeniata graminea*. We have examined seven skulls, one removed from a paratype of *A. mixteca* (A.M.N.H. No. 91001), one from a specimen of *A. oaxacae* (A.M.N.H. No. 93208) obtained near Ixtlán de Juárez, Oaxaca, and five skulls from *Abronia t. taeniata* and *A. t. graminea* that were made available by Dr. C. F. Walker. Contrary to what Tihen observed, the otic and occipital elements are not fused; sutures are discernible in all skulls examined. Furthermore, the maxilla reaches the frontal on the skulls of *A. mixteca* and *A. oaxacae*, and, when osteoderms are removed,

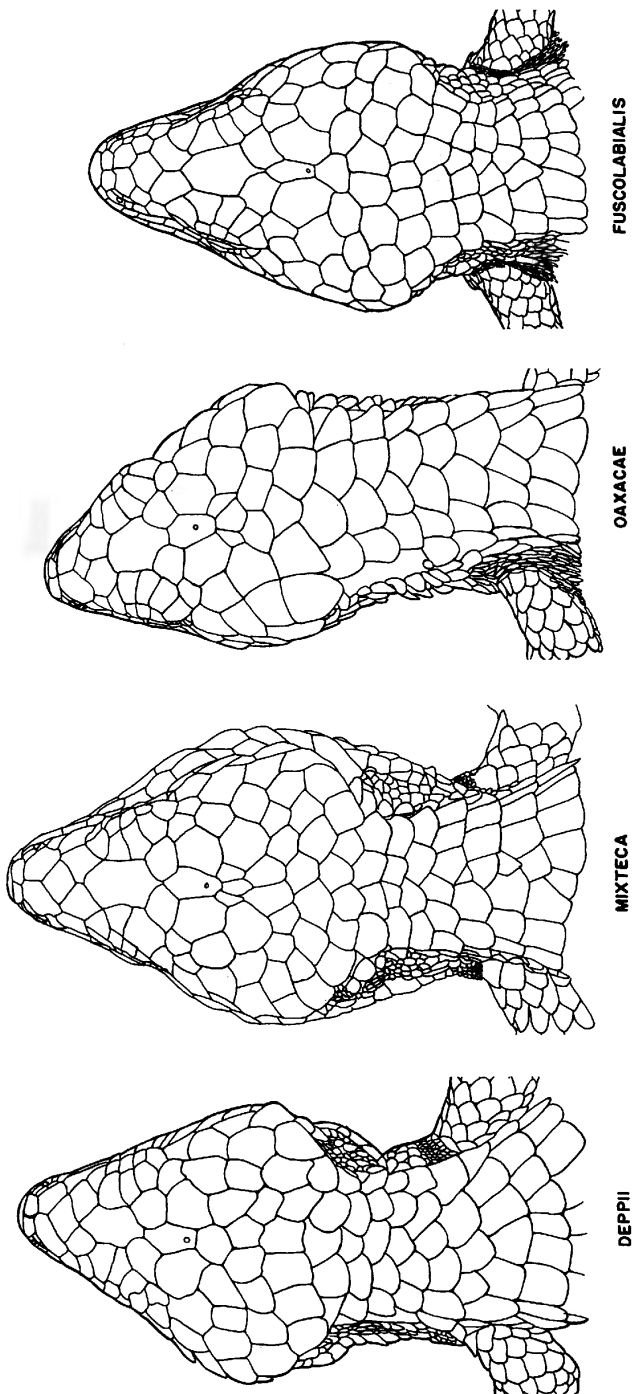


FIG. 6. Dorsal views of the heads of the four species of *Abronia* inhabiting the Sierra Madre del Sur of Mexico, in the order of their occurrence from west to east.

it can be seen that the premaxilla extends posteriorly to the frontal, thereby separating the nasal bones.

Variations of the sort are perhaps to be expected, although on the whole the skulls of the three species examined differ only in minor details. The species differ more extensively in external details, and, if the trend in the evolution of species has been toward a reduction in the number of cephalic scutes, *A. mixteca* would be regarded as more primitive in this respect than other members of the genus. Other species have four primary temporals, but no other member of the genus possesses three rows of scales between the occipitals and the nuchals.

Abronia oaxacae is the only species, in addition to *A. mixteca*, that possesses an interoccipital flanked by lateral occipitals (fig. 6). Such a condition may not have been the primitive one, and our statement that both species have "retained" three occipitals perhaps has implications that are unwarranted. When contiguous populations share a peculiarity of the sort, it is perhaps legitimate to regard this as evidence of affinity. The differences between the two species, however, are at least as striking as their similarity. Though it seems improbable that the presence of three occipitals has any adaptive significance *per se*, the condition may nevertheless be attributable to adaptive convergence if it is a byproduct of some peculiar combination of genes selectively advantageous under the conditions prevailing in the environments of both species. Any explanation for the exceptionally large number of cephalic scutes characteristic of *A. mixteca* is equally conjectural. Nevertheless, it is reasonably certain that most of the differences between species of *Abronia* have arisen as a direct result of natural selection following the ecological and spatial isolation of populations.

Stebbins (1958) has illustrated some of the variations in the cephalic scutes encountered in the species *Gerrhonotus* and *Barisia*. When series become available, similar variations are to be expected in all species of *Abronia*, and they may be more prevalent in one deme than in another. The postmental, for example, is undivided on two of the three specimens of *A. oaxacae* taken near Ixtlán de Juárez, whereas it is divided on nine other specimens from three localities, Luvina, El Punto and vicinity, and Santo Domingo Chontecomatlán. Canthals are present on both sides of the holotype of *A. mixteca*, and present on one side of a paratype, but the other paratypes lack such scales.

Each of the 12 species now recognized, however, can be distinguished by an array of characters, although in some instances populations intermediate in character may be discovered. Tihen (1954) suggested that *A. fuscolabialis* may prove to be a subspecies of *A. taeniata*. Tihen also

placed *graminea* as a subspecies of *taeniata*. The species is represented in collections more adequately than others, and our examination of 20 specimens fails to reveal any dichotomous differences between the two forms. We agree with Tihen, therefore, that *graminea* and *taeniata* are incompletely differentiated, and subspecific status for *graminea* is warranted.

ECOLOGY AND SPECIATION: The village of Tejocotes is a small farm community consisting of a few thatched huts scattered along the sides of ravines. The land has been partly cleared, and corn is cultivated on gently sloping hillsides, but there are small streams in the deeper ravines, and trees and shrubs remain on the steeper slopes. The large trees in the area are pines, oaks, and madroño. Oaks are more abundant in the ravines, but pine is more often the dominant tree on the ridges and the exposed slopes. Manzanita is also present but more abundant in the foothills at lower elevations. Epiphytes, including bromeliads and orchids, thrive on the trees, particularly on the oaks in the ravines where most individuals of *Abronia mixteca* were found. Meteorological information has been recorded since 1953, when a weather station was installed at Tejocotes. The only data readily available, however, are those recorded for the year 1959, when the precipitation totaled 783.6 mm. There was scarcely any precipitation during the winter, from November through March, but the rainfall increased erratically from April until August, when it reached the monthly peak of 185.5 mm. Mist or fog occurred on 34 days, and the sky was overcast on 164 days of the year.

The vegetation at Tejocotes differs little from that in areas occupied by *Abronia oaxacae* near El Punto as well as in the area near Ixtlán de Juárez, to the north of the Continental Divide, where this species has been obtained. The Continental Divide, which reaches an elevation in excess of 3000 meters west of El Punto at the summit of Cerro San Felipe, descends to an elevation scarcely above 1800 meters north of Telixtlahuaca before it rises to the west and reaches an elevation of nearly 2500 meters behind Tejocotes. The pine-oak woodland is discontinuous between the area inhabited by *A. mixteca* and that by *A. oaxacae*. Cerro Zempoaltepec, the source of the two specimens on which Tihen (1944) based his description of *Abronia fuscolabialis*, is roughly 40 kilometers due east of El Punto. Cerro Zempoaltepec, though part of the Sierra Madre del Sur, is slightly north of the Continental Divide but connected to it by a ridge that rises to an elevation scarcely above 2000 meters. The sparse vegetation on the connecting ridge suggests that it is somewhat drier. Perhaps habitats suitable for lizards of the genus *Abronia* are interrupted along the crest of this ridge.

These lizards appear to be largely if not wholly restricted to pine-oak

woodland, which is continuous around the headwaters of the Río Grande (a tributary of the Río Papaloápan) north of the Continental Divide. It is not difficult to account for the presence of *A. oaxacae* at El Punto, as well as in the terrain at the same elevation on the opposite side of the valley, where specimens have been obtained at the Vivero Rancho Teja east of Ixtlán de Juárez. *Abronia oaxacae* has also been taken in the oak belt farther north on the east side of the Río Grande, at Luvina. (Erroneously listed on the label of A.M.N.H. No. 65809 as "Tehuantepec," whereas the collector evidently intended to write "Luvina, Oaxaca." Entries in the catalogues of the American Museum show that the same collector was in the neighboring town of Macuiltianguis on March 3, 1946, the day before he obtained the *Abronia* at Luvina. Hence this specimen of *A. oaxacae* came from pine-oak woodland at approximately the same elevation as others from the region, rather than from the lowlands of Tehuantepec, as Tihen [1954] was led to believe.) The three species, *mixteca*, *oaxacae*, and *fuscolabialis*, therefore, all occur in the same region but appear to have been isolated from one another long enough to have become well differentiated.

It is more difficult to explain the presence of *Abronia oaxacae* in the mountains south of the Sierra Madre del Sur, at Santo Domingo Chontecomatlán, where the species has been reported by Smith and Williams (1963). Through the courtesy of Dr. Hobart M. Smith we have examined the specimen from this locality, and the lizard conforms closely to the lizards taken between El Punto and La Cumbre del Estudiante (which is listed in some accounts by herpetologists as "La Cumbre").

It is improbable that *mixteca*, *oaxacae*, and *fuscolabialis* will prove to be sympatric, although Smith and Alvarez del Toro (1963) report that two specimens described as *Abronia lythrochila* are "apparently sympatric" with *Abronia ochoterennai*. Farther on in their account, however, these authors note that *lythrochila* is confined to the drier pine-oak forests, "whereas *ochoterennai* occurs in the very humid cloud forests." The two species can scarcely be sympatric, even though the area of cloud forest inhabited by *A. lythrochila* lies between the two areas where *A. ochoterennai* has been taken. Stuart (1963) has assigned the Guatemalan species *fimbriata* to the synonymy of *Abronia aurita* (Cope) because he found "it difficult to believe that two species of *Abronia* exist sympatrically in Alta Verapaz." In view of the imprecise type localities and the variations that occur in the pattern and cephalic scutes of other species represented by small samples, there is little reason to believe that the situation in Guatemala is comparable to that in Chiapas where the two species are ecologically as well as spatially isolated.

Tihen (1949) regarded the lizards he grouped in the genus *Abronia* as "an early branch of the gerrhonotine stock" but perhaps no more primitive than the Recent anguids with limbs and a lateral fold that he assigned to other genera. This assumption seems to be valid, and it is probable that the few peculiarities of the lizards in the genus *Abronia* are directly or indirectly associated with arboreal specializations and their adaptation to relatively cool, moist woodland environments. These lizards are largely if not strictly arboreal, and their scarcity in collections is attributable largely to their cryptic coloration, secretive habits, and distributions restricted to montane forests, few of which were easily reached by collectors before roads made them accessible.

Werler and Shannon (1961) noted that the holotype and paratype of *Abronia reidi*, an inhabitant of an isolated cloud forest in Veracruz, were taken near the rim of the Volcan San Martin "under thick layers of moss growing on the trunks of trees" at an elevation of 5370 feet (ca. 1600 meters). Smith and Alvarez del Toro (1963) observed that "*Abronia lythrochila* lives in the largest trees." They added that "on one occasion one fell to the ground a few feet from the junior author, presumably from limbs that were some 40 meters from the ground." *Abronia mixteca* remained undiscovered until we enlisted the cooperation of Señor Pedro Lopez, a professional *carbonero* at Tejocotes, who makes his living largely by felling oaks and converting them into charcoal or *carbon*. Dr. Walter Miller accompanied the senior author to the place near El Punto where a specimen of *Abronia oaxacae* had been taken on the ground. He recalled, however, that *carboneros* were working in the immediate vicinity at the time. The exact source of specimens in collections is seldom recorded, but it should not be assumed that individuals labeled "Cerro San Felipe" came from the summit. It is improbable that *A. oaxacae* occurs much above 2700 meters, though it is to be expected in pine-oak woodland north of Cerro San Felipe.¹

¹ An adult *Abronia oaxacae* was found on the ground in a moist ravine south of El Punto on August 13, 1966, by C. M. Bogert. Trees had recently been felled in the area by Francisco Perez Acevedo, who noted the lizard on the ground and pointed it out to the collector. A juvenile of the same species was discovered in a bromeliad growing on the nearly horizontal limb of an oak 0.3 kilometer west of San Vicente Lachixío, Oaxaca, on August 6, 1966, by William E. Duellman of the University of Kansas. The record extends the distribution of *Abronia oaxacae* farther to the southwest than we have indicated on the map (fig. 7), into the mountains approximately 65 miles due south of the type locality of *Abronia mixteca*.

The occurrence of *Abronia* on the ground is not necessarily accidental but is unusual. It must be assumed that individuals occasionally move from one tree to another. The specimen depicted in figure 4 was discovered a few kilometers north of La Cumbre del Estudiante at an elevation of 2700 meters when Nicholas Bucknall heard it scurrying up the trunk of a relatively small pine.

Such lizards are not restricted to oaks, therefore, but, insofar as we can ascertain, all representatives of the genus inhabit either pine-oak woodland or cloud forests, largely at elevations between 1000 and 2700 meters. Pines, oaks, and other temperate montane plants comprise one element of the Mexican and Guatemalan cloud forests, but many of the trees, shrubs, vines, herbs, and epiphytes are primarily tropical in distribution. Epiphytes occur in lowland habitats, but they are perhaps more abundant in moist environments, particularly in cloud forests. Orchids, bromeliads, and other epiphytic plants closely associated with oaks in Mexico support an extensive invertebrate fauna that includes earthworms, snails, slugs, millipeds, scorpions, spiders, and representatives of several orders of insects. The epiphytes also afford shelter for frogs and salamanders, as well as for small snakes and lizards, including arboreal anguids. *Abronia taeniata* has been found in bromeliads in the Sierra Madre Oriental (Smith, 1941). It seems probable that the invertebrates inhabiting the epiphytes comprise a large percentage of the diet of the anguids that live among them. If so they could forage most effectively in woodland areas where epiphytes were most abundant.

The occurrence of *Abronia* in the cloud forests as far north as southern Tamaulipas may be thus explained. Representatives of the genus are absent from the Pacific side of Mexico north of the Balsas River basin, despite the pine-oak woodland in the Sierra Madre Occidental. As compared with the situation in the mountains bordering the Atlantic coastal plain, there are relatively few epiphytes on the trees in the mountains bordering the Pacific from Nayarit northward. *Abronia* is absent perhaps for the same reason that epiphytes are relatively scarce, namely, the lack of adequate surface moisture, owing to fewer cloudy days, and the relatively infrequent occurrence of fog or mist. Members of the family Anguidae inhabit somewhat arid regions, but few are even moderately well adapted to resist desiccation, even though the range of *Gerrhonotus multicarinatus* extends well onto the peninsula of Baja California. Mr. Charles E. Shaw and the senior author discovered an example of this species beneath a dead *Agave* not far north of the Viscaïno Desert in amazingly dry terrain west of Punta Prieta. Anguids do not inhabit the Mojave or Sonoran deserts, however, although a few colonies survive

in isolated mountains in the deserts of California, Arizona, New Mexico, and Texas. Such mountains are surrounded at present by terrain too dry and barren and seasonally too warm to afford environments suitable for anguids.

It is conjectural whether *Abronia* is less resistant to desiccation than the terrestrial and fossorial members (*Ophisaurus*) of the family in Mexico, or whether the northward dispersal of *Abronia* was halted by dis-

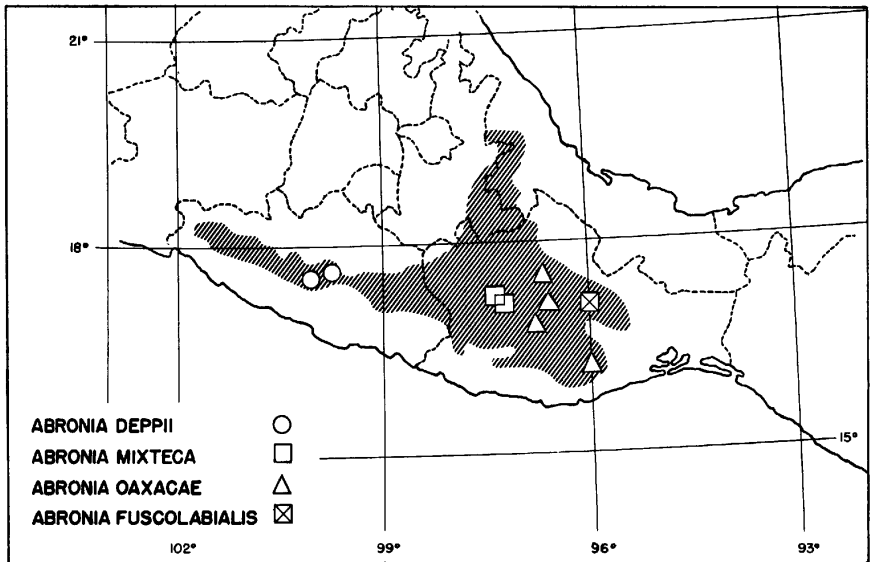


FIG. 7. Map showing the distribution of pine-oak woodland in the Sierra Madre del Sur of Guerrero and Oaxaca in southern Mexico, and the localities where the four species of *Abronia* in the area have been obtained.

junctions in the forested areas or the increasing paucity of epiphytes. In the Sierra Madre del Sur (see map, fig. 7), the occurrence of well-differentiated allopatric populations suggests that more favorable climatic conditions in the past permitted the wide dispersal of a single species, the range of which became fragmented as the region became progressively less humid. The mountains of southern Mexico appear to have been the recent center of dispersal of anguids with limbs and a lateral fold, the so-called "gerrhonotines." At present there appear to be subcenters on opposite sides of the lowlands at the Isthmus of Tehuantepec.

Gerrhonotus liocephalus, perhaps the least-specialized but most widely distributed member of the assemblage, is the only species known to occur

TABLE 1

VARIATIONS OBSERVED IN SAMPLES REPRESENTING THE SPECIES OF *Abronia*
INHABITING THE SIERRA MADRE DEL SUR FROM GUERRERO EASTWARD IN OAXACA
(Means are followed by extremes in parentheses.)

	<i>A. deppii</i> N=6	<i>A. mixteca</i> N=5	<i>A. oaxaca</i> N=13	<i>A. fuscolabiatis</i> N=2
Number of occipitals	1	3	3	1
Rows of scales between occipital, or occipitals, and first row of nuchals	2	3	1	2
Temporals reaching postoculars	1	2	2	2
Anterior superciliary separated from cantholoreal	Usually; variable 6	No 4	Yes 4	No 6
Fewest nuchal scutes in any row	3, rarely 4	4, rarely 3	3, rarely 4	4
Number of anterior temporals	Penultimate	Antepenultimate	Penultimate, or antepenultimate	Antepenultimate
Supralabials reaching orbit				
Whorls of scales on unregenerated tails	79.0 (77-81)	80.0 (77-82)	88.8 (84-92)	88, 1 specimen
Ratio of tail to total length	0.56 (0.54-0.57)	0.57 (0.55-0.59)	0.59 (0.57-0.61)	0.59, 1 specimen
Number of transverse rows of scales on dorsum, from first nuchal row to posterior border of thigh	26.7 (26-28)	29.8 (28-31)	27.8 (27-29)	28.5 (28-29)

both east and west of the lowlands. The majority of the 13 terrestrial species (*Colyptychon*, an obscure gerrhonotine genus restricted to Panama, is beyond the scope of this discussion) are distributed along the Pacific side of the continent west and north of the Isthmus, whereas only three of these, including *G. liocephalus*, are known to the east and south; one species of *Barisia* occurs as far south as Panama. Of the 12 species of *Abronia* thus far discovered, however, six are restricted to the mountains east of Tehuantepec: *bogerti*, *ochoterenai*, *lythrochila*, *matudai*, *aurita*, and *vasconselosi*. There are also six species west of the Isthmus, namely, *reidi*, *taeniata* (with a subspecies, *graminea*), *fuscolibialis*, *oaxacae*, *mixteca*, and *deppii*. Environments suitable for *Abronia* are undoubtedly present on several mountains between the ranges of *A. mixteca* and *A. deppii*, and it is virtually certain that additional species will be discovered, as we note above. Table 1 summarizes the differential characters of the four species inhabiting the Sierra Madre del Sur.

It may be inferred that the progenitors of *Abronia* began to become modified as arboreal inhabitants of cool, moist, oak woodlands as part of an adaptive radiation that also led to diversification among terrestrial forms. Dispersals of the latter were undoubtedly interrupted or even halted from time to time by unfavorable trends in climatic conditions in the lowlands. Barriers to dispersal must have been encountered more often, however, by the anguids that had evolved arboreal specializations, and for this reason their dispersal was probably slower. Discontinuities or sporadic disjunctions of their habitat would have inhibited their dispersal while accelerating their speciation. The progenitors of *Abronia* were perhaps the first secretive insectivorous lizards in the Americas to exploit the invertebrate fauna that evolved in the epiphytes. Arboreal anguids apparently do not compete with the terrestrial members of the family. The evidence is circumstantial but nevertheless convincing when viewed in the light of the arrangement proposed by Stebbins (1958).

Tihen (1949, 1954), whose investigations were hampered by the inadequacy of the samples available, clarified many aspects of the distribution and relationships of the various gerrhonotines. Whereas Tihen advocated grouping the species in five genera, Stebbins (1958) found this arrangement untenable when the variations and distributions of the species were taken into account. Stebbins retained *Abronia* and *Colyptychon*, added another species (*Gerrhonotus panamintinus*, from the Panamint Mountains of California), and rearranged those assigned by Tihen to *Gerrhonotus*, *Elgaria*, and *Barisia*. As revised by Stebbins, the gerrhonotines consist of three genera: *Colyptychon*, *Abronia*, and *Gerrhonotus*, with *Barisia* included as a subgenus of *Gerrhonotus* along with the nominate subgenus.

As regrouped, each of the two subgenera of *Gerrhonotus* consists of a separate series of allopatric species. The distributions of those in the subgenus *Gerrhonotus*, however, widely overlap those of the species assigned to the subgenus *Barisia*.

The arrangement proposed by Stebbins conveys satisfactory implications of relationships within the group. We agree that the two groups of terrestrial species share more features than either group shares with *Abronia*. It is more convenient, however, to consider each group as a separate genus in this discussion. Though Stebbins cautiously stated that the species in each group were "mostly allopatric," field investigations in Oaxaca during five summers have failed to reveal any exceptions. Notes on the habitats of the species taken in three separate mountain areas will illustrate the nature of anguid distributions in Oaxaca:

1. Tejocotes. Three species known; *Abronia mixteca*, *Barisia gadovii laevigata*, and *Gerrhonotus liocephalus liocephalus* inhabit wooded hillsides and ravines at elevations of 2500 meters.
2. El Punto and Cerro San Felipe. Within a radius of 20 kilometers, between elevations of 2100 and 3100 meters, there are three species: *Abronia oaxacae* and *Barisia imbricata planifrons* inhabit pine-oak woodland near El Punto at elevations between 2100 and 2700 meters, but *Barisia viridiflava* occurs only at higher elevations, above 2800 meters on the north slope of Cerro San Felipe in pine-fir forest.
3. Sierra de Juárez and Sierra de Ixtlán (these mountains are contiguous north of the Río Grande). *Abronia oaxacae* at Luvina and east of Ixtlán de Juárez inhabits the pine-oak woodland above 2200 meters, along with *Gerrhonotus liocephalus*, but *Barisia viridiflava* has been found only around the meadow at Llano de las Flores, at an elevation of 2800 meters.

It is of interest to note that in Oaxaca all species of *Barisia* and *Gerrhonotus* are strictly terrestrial, although *Barisia viridiflava* occasionally basks on logs, rocks, or stumps a few centimeters above the ground. These lizards were never seen in trees, even when they might have evaded capture by climbing. In Arizona, however, where no arboreal anguids occur, *Gerrhonotus kingi* does occur in trees, even though it is more often on the ground. Similarly, *Gerrhonotus multicarinatus* in southern California is not restricted to the ground. It often climbs trees as well as fences, walls, or buildings.

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MATERIAL EXAMINED

SPECIMENS FROM THE SIERRA MADRE DEL SUR

(Elevations are approximations, usually altimeter readings)

- Abronia deppei* (Wiegmann). Guerrero: Chilpancingo, A.M.N.H. No. 72543, M.C.Z. No. 33750; Omiltemi, C.N.H.M. No. 105600, M.C.Z. Nos. 42716, 85248, U.S.N.M. No. 113172.
- Abronia mixteca*, new species. Oaxaca: Tejocotes, 2400 meters, A.M.N.H. No. 91000, holotype, A.M.N.H. Nos. 90999, 91001 (paratypes); ca. 7 kilometers west of Tejocotes, 2350 meters, A.M.N.H. No. 90998 (paratype); "La Herradura," 6 kilometers northwest of Tejocotes, 2300 meters, M.C.Z. No. 64102 (paratype).
- Abronia oaxacae* (Günther). Oaxaca: Luvina (Rancho Ocote), A.M.N.H. No. 65809; "Cerro San Felipe," U.I.M.N.H. Nos. 53154, 63720; near El Punto, U.I.M.N.H. Nos. 50156, 50157, 51270; near La Cumbre del Estudiante, ca. 2.7 kilometers south of El Punto, ca. 2550 meters, U.M.M.Z. No. 119672; 5.6 kilometers north of La Cumbre del Estudiante, 2700 meters, A.M.N.H. No. 92737; 3.2 kilometers east of Ixtlán de Juárez, Vivero Rancho Teja, 2200 meters, A.M.N.H. Nos. 90997, 93208, 93209; Santo Domingo Chontecomatlán, U.I.M.N.H. No. 48672.
- Abronia fuscolabialis* (Tihen). Oaxaca: Cerro Zempoaltepec, A.M.N.H. No. 85634, holotype.

