

## A PROPOSED NEW GENUS FOR *ELAPHE SUBOCULARIS* AND *ELAPHE ROSALIAE*

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**Summary:** After comparison with other species of the genus *Elaphe* and with allied genera, a new generic name is proposed for *Coluber subocularis* Brown and *Coluber rosaliae* Mocquard. These species differ in relatively minor ways from *Elaphe* and *Pituophis* in general morphology, but data from scanning electron microscopy, karyotype analysis, and immunological comparisons show that they are distinct from the members of both genera.

### Introduction

Recent information on the karyotypes (Baker et al. 1971, 1972; Mengden and Stock, 1980), the ultrastructure of dorsal scales (Price, 1981, 1982), and immunological comparisons (Dowling et al., 1983) support the separation of *Coluber subocularis* Brown, 1901, from other species of the genus *Elaphe*. That the morphological features of this species and of *C. rosaliae* Mocquard, 1899, distinguish them from other American ratsnakes was indicated long ago when they were allocated to a separate "Rosaliae Section" of American *Elaphe* (Dowling, 1952). Since that time it has become clear that they also differ from the Eurasian species of *Elaphe* and other related genera.

This report proposes a new genus for *E. subocularis*. *E. rosaliae*, in spite of some differences in dorsal scale microdermatoglyphics and karyotype, is also tentatively allocated to this taxon because of previously described similarities in body form, scutellation, and hemipenial morphology (Dowling, 1952, 1957). These allocations emphasize the similarities between the two

species and their differences from the other members of the genus *Elaphe*. It also has the advantage of making the latter a more compact and definable taxon.

### Materials and Methods

The morphological data contained herein were obtained through the personal examination of 48 living or preserved specimens of *Elaphe subocularis* and five of *Elaphe rosaliae*. Many of these are listed in Dowling (1957). Additional specimens are: *E. subocularis*: Texas (HISS 532, 72164, 76561; USNM 218931; RMP 14); New Mexico (USNM 147893); *E. rosaliae*: Mexico, Baja California Sur (HISS 76560; USNM 240225, 240680, 248124). Skulls of *Pituophis* examined include AMNH 43294, 57388, 57409, 64357, 68943, 75095, 75544, 75549, 75730, 77635, 81873, and 84560. In addition, more than 1200 specimens of allied species in 29 genera have been examined (data in HISS files). Additional information was derived from the comprehensive files of Herpetological Information Search Systems (HISS) and from the other publications cited. The summary by Worthington (1980) updated information on *E. sub-*

*ocularis*. Live specimens of *E. subocularis* for immunological study were collected in the Trans-Pecos region of Texas by Price.

Museum acronyms are those suggested by Leviton et al. (1985).

**Morphology:** Standard methods previously developed (Dowling, 1952 et seq.) were employed in the study of dentition, scutellation, and osteology. Study and description of hemipenes are as suggested in Dowling and Savage (1960), with lengths indicated as the number of subcaudals subtended.

**Microdermatoglyphics:** The dorsal scale ultrastructure was studied as indicated in Price (1981). Terminology follows Price (1982). Specimen preparation was done by Price or Paul Kelly of New York University. Both the negatives and scales utilized are retained in the HISS collection.

**Karyotypes:** Recent information on the karyotype of *Elaphe rosaliae* is taken from a personal communication from Greg Mengden (1985). The data for *E. subocularis* and allied forms are primarily from Baker et al. (1971, 1972) and Mengden and Stock (1980).

**Immunology:** Data on immunological comparisons of *Elaphe quatuorlineata* (the type species of the genus) with related forms was kindly provided by Mark Hutchinson (personal communication). Other data are derived from the work of Linda R. Maxson and her associates, as was reported in Dowling et al. (1983). As used in our previous works, an estimate of one albumin immunological distance (AID) unit change every 0.58 million years offers a reasonable time scale for estimating times of divergence.

### Observations

#### Similarities of *Elaphe* and *Pituophis*

*Elaphe* and *Pituophis* both belong to the

group of colubrid snakes that lack hypapophyses on the posterior body vertebrae and have a spinose and calyculate (non-capitate) hemipenis with a simple sulcus (= the colubrinae of Dunn, 1928). They are also similar in having maxillary teeth of subequal length that are not interrupted by a diastema, and in having large numbers of keeled scale row reductions that are entirely mid-lateral (= the Lampropeltiini of Dowling and Fries, 1987).

They are similar in most visible features including those of vertebral morphology. Auffenberg (1963) in his study of the vertebrae of these genera stated: "The genus [*Pituophis*] is most easily confused with *Elaphe*. From that genus it can be separated only by the concave zygosphenes from above (only rarely so in *Elaphe*), the somewhat better developed epizygapophyseal spines, and the neural spine, which is usually much higher in *Pituophis*." None of these features was found to be definitive in a recent study (Brummer, 1980).

The distinctive triangular nasal bones that prop the enlarged premaxillary in *Pituophis* were cited as a differentiating feature by Dowling (1958), but are now known to be found only in eastern subspecies of *P. melanoleucus*. The western USA subspecies *P. m. catenifer* and *P. m. affinis* have unmodified nasals, as do *P. deppei* and *P. lineaticollis* (the "Deppei Group"), "Pantherophis" *Elaphe* (*sensu* Dowling, 1952), *E. quatuorlineata*, and members of the "Rosaliae Section" (personal observations).

Both genera have relatively large numbers of low-keeled dorsal scales (usually keeled posteriorly if not at midbody) with small, rounded pairs of apical pits, and having the dorsal scale rows reduced by the loss of mid-lateral rows (Dowling, 1958). Both the "Rosaliae" and "Pantherophis"

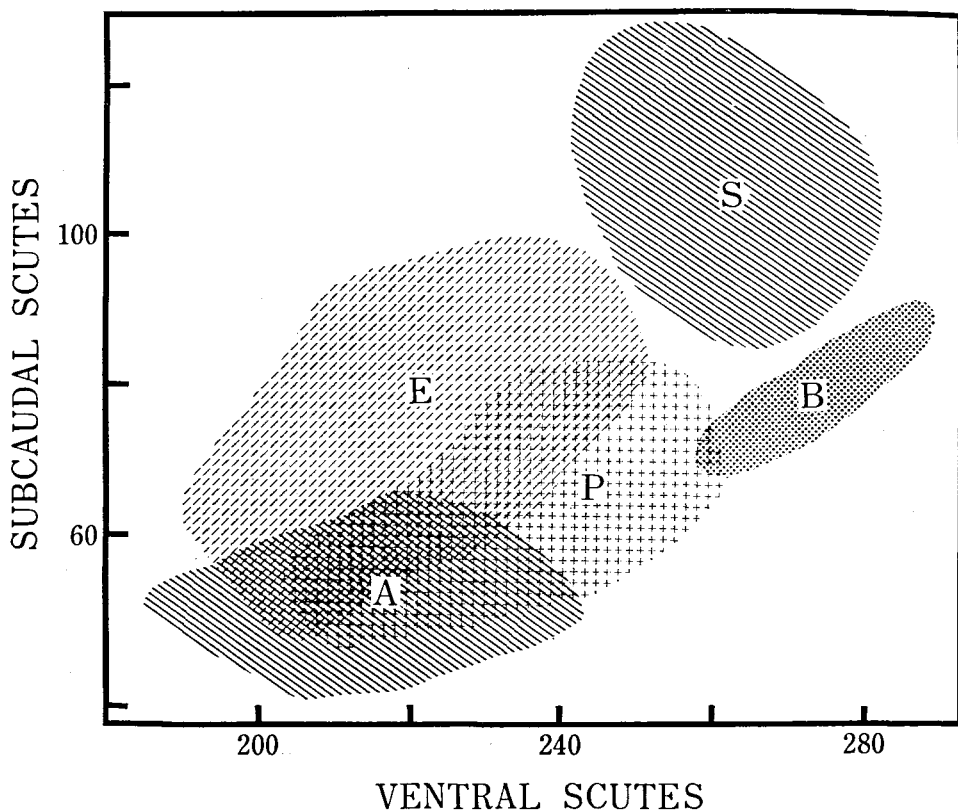


Fig. 1. Plot of ventral versus subcaudal scute numbers in ratsnakes. The range of variation shown for *Arizona elegans* (A) is based on 36 maximum and minimum counts for all subspecies (Klauber, 1946); *Bogertophis* (B) on 37 specimens (6 *rosaliae*, 31 *subocularis*); *Elaphe* (E) on 164 specimens (66 *guttata*, 56 *obsoleta*, 42 *vulpina*) plus maximum and minimum counts for Palearctic species; *Pituophis* (P) on 26 maximum and minimum counts for all species; *Senticollis triaspis* (S) on 84 specimens.

sections of *Elaphe*, as well as *E. quatuorlineata*, have the typical crown scutes and generalized scutellation of unspecialized colubrid snakes. The members of the "Rosaliae Section" differ only in the added lorilabial row of scales. Some Asian species of the genus *Elaphe* (*sensu lato*) have the divided anal scute of typical members of the genus, while others have the single scute found in *Pituophis*.

#### Differentiation of *Elaphe*, *Pituophis*, and members of the "Rosaliae Section"

Part of the difficulty of the generic allocation of these snakes is that the Holarctic

and Oriental genus *Elaphe* remains essentially undefined. For purposes of the comparisons that follow, only the European type species (*E. quatuorlineata*), its apparent close relatives in Japan (*E. climacophora* and *E. quadrivirgata*), *E. longissima* of Europe, and the three Nearctic representatives of the "Pantherophis Section" (*E. guttata*, *E. obsoleta*, and *E. vulpina*) are herein considered true *Elaphe*. Although none of the other Asian ratsnakes resembles the members of the "Rosaliae Section," their generic status is still in question.

Some characteristics that are not wide-

spread or widely studied among colubrid snake genera are, however, possessed either by species of *Elaphe* or *Pituophis*. Further, these two genera differ in their body proportions. Thus the two genera can be distinguished by these criteria, and the relationship of the "Rosaliae Section" to each may be judged.

**Body Proportions:** *Pituophis* and members of the "Rosaliae Section" have relatively shorter tails (as judged by subcaudal counts) than members of typical *Elaphe*, and much shorter than those of the newly described genus *Senticollis* (Dowling and Fries, 1987). As pointed out elsewhere, members of the "Rosaliae Section" differ from species in both genera in lacking any trace of sexual dimorphism in this character. This is reflected in the much narrower vertical variation in these two species as compared with the others (Fig. 1).

**Epiglottal process:** *E. rosaliae* and *E. subocularis* differ from *Pituophis* (in which all species have this feature) and agree with *Elaphe* (in which no member has this feature) (personal observations).

**Osteology:** *Elaphe rosaliae* and *E. subocularis* are not differentiated from either *Elaphe* or *Pituophis* in vertebral characters, but neither can these genera be distinguished in this way (Brummer, 1980). As indicated above, the triangular nasal bones found in eastern United States subspecies of *P. melanoleucus* are not found in the western subspecies, nor in other species of the genus. Thus, they cannot be used in differentiating the two genera. *E. rosaliae* and *E. subocularis* have unmodified nasals.

**Hemipenis:** The hemipenes of *E. subocularis* and *E. rosaliae* are very similar to one another (Dowling, 1957) and closely resemble those of *Pituophis*. The organ is 8–10 subcaudals long, has spinules at the base, and is only slightly expanded apically

in these snakes, as compared with lengths of 12–17 subcaudals with a nude base and distinct bilobation in "Pantherophis" *Elaphe* (Fig. 2), or the greatly expanded clavate structure found in *E. quatuorlineata* (Dowling and Fries, 1987).

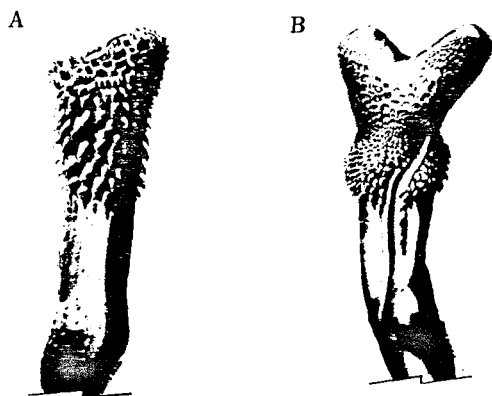


Fig. 2. Hemipenis of (A) *Bogertophis subocularis* (HISS 523); 10 subcaudals in length, compared with that of (B) *Elaphe vulpina* (UMMZ 89894); 13 subcaudals in length. The hemipenes of *E. obsoleta* and *E. guttata* are similar to that of *E. vulpina*, and that of the type species (*E. quatuorlineata*) is not greatly different. The hemipenis of *Bogertophis* resembles that of *Pituophis*.

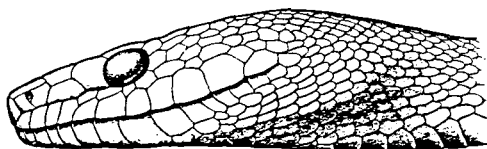
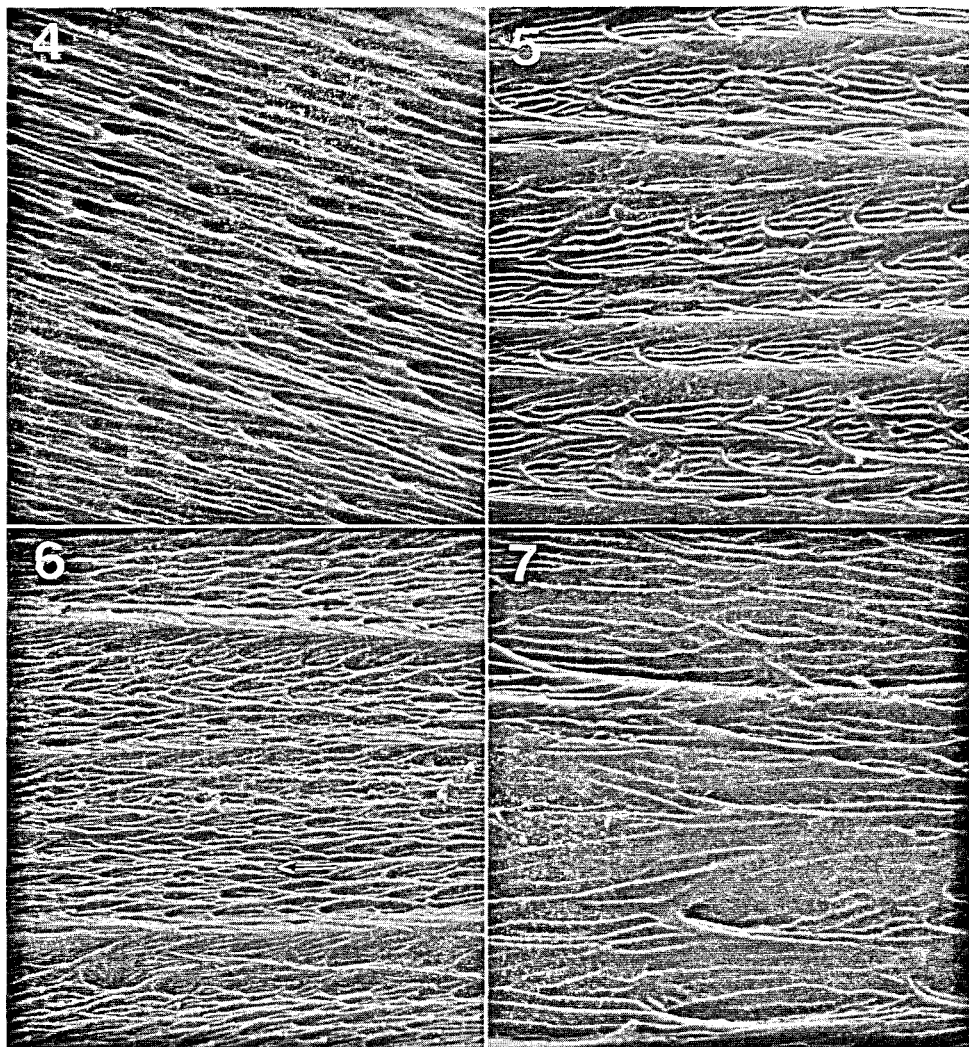


Fig. 3. The head of *Bogertophis rosaliae* showing the distinctive lorilabial scales.

**Scutellation:** Of all the species of *Elaphe*, only *E. rosaliae* and *E. subocularis* possess a lorilabial row of 3–7 scales above the supralabials (Fig. 3). Lorilabials (1–5 in number) are present in some subspecies of *Pituophis melanoleucus* but are lacking in *P. deppei* and *P. lineaticollis* (Stull, 1940), and are presumed to be independent



- Fig. 4. Dorsal microdermatoglyphic pattern of *E. guttata* (HISS 75539). 5000 $\times$ .  
 Fig. 5. Dorsal microdermatoglyphic pattern of *E. obsoleta* (HISS 75031). 5000 $\times$ .  
 Fig. 6. Dorsal microdermatoglyphic pattern of *E. vulpina* (HISS 75362). Arrow indicates papillae. 5000 $\times$ .  
 Fig. 7. Dorsal microdermatoglyphic pattern of *E. quatuorlineata* (HISS 75528). 5000 $\times$ .  
 Fig. 8. Dorsal microdermatoglyphic pattern of *P. deppei* (RMP 077) 2000 $\times$ .  
 Fig. 9. Dorsal microdermatoglyphic pattern of *P. lineaticollis* (RMP 388). 2000 $\times$ .  
 Fig. 10. Dorsal microdermatoglyphic pattern of *P. melanoleucus* (RMP 078). 2000 $\times$ .  
 Fig. 11. Dorsal microdermatoglyphic pattern of *P. melanoleucus* (RMP 078) 5000 $\times$ .  
 Fig. 12. Dorsal microdermatoglyphic pattern of *B. subocularis* (RMP 074). 3800 $\times$ .  
 Fig. 13. Dorsal microdermatoglyphic pattern of *B. rosaliae* (HISS 76570). 5000 $\times$ .

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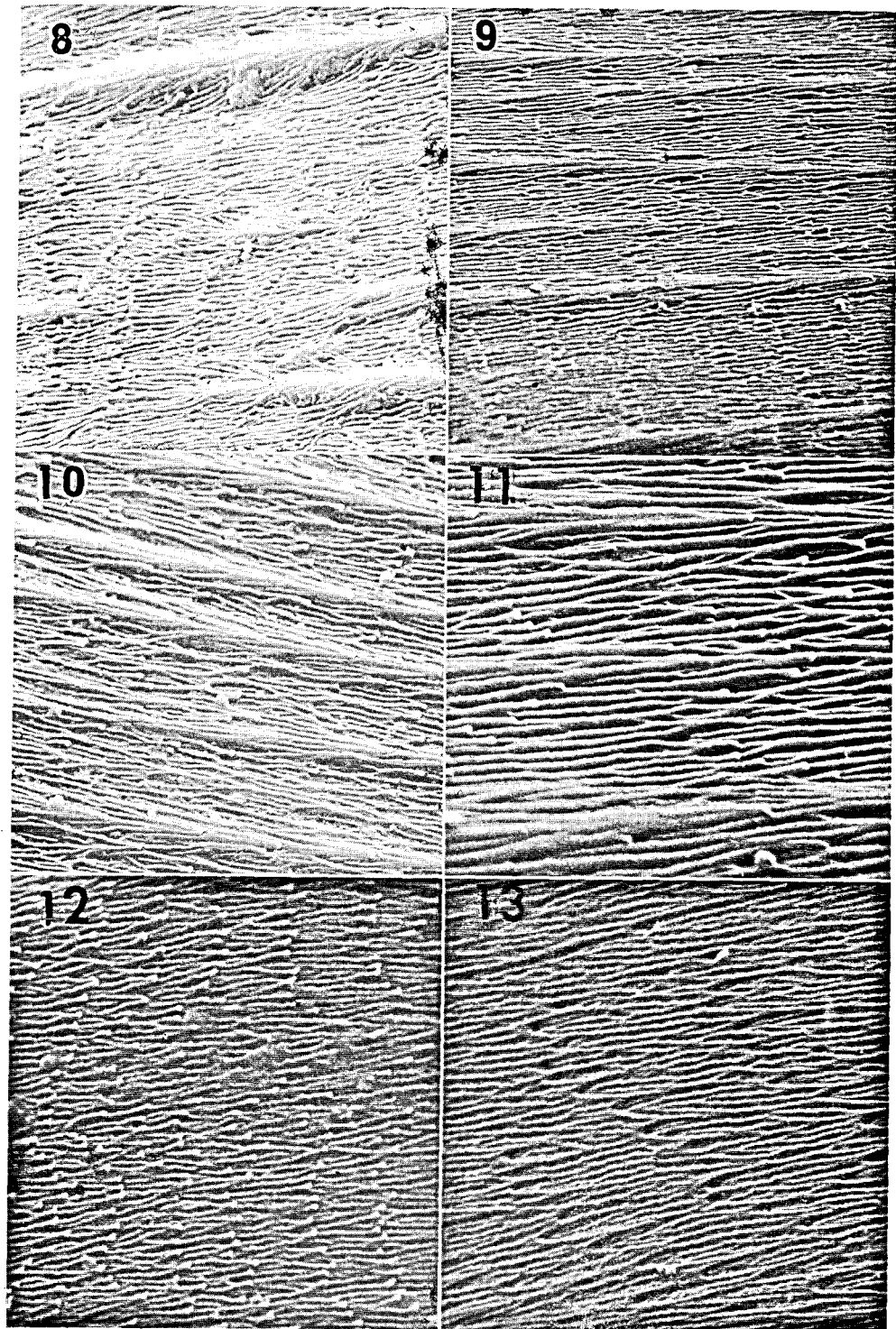
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derivatives in the more specialized *P. melanoleucus*. *E. rosaliae* and *E. subocularis* differ from *Pituophis* and agree with *Elaphe* in having divided anal scutes.

Microdermatoglyphics: Price (1981, 1982, 1987) demonstrated that dorsal scale microdermatoglyphic patterns are very similar among closely related species and that this feature is a valuable generic determinant. The patterns resolvable between 2000 $\times$  and 5000 $\times$  under the scanning electron microscope are echinate in two of the species of "Pantherophis" *Elaphe*: *guttata* and *obsoleta* (Figs. 4, 5). *E. obsoleta* shows reticulations between the echinules. The pattern of *E. vulpina* (Fig. 6) is more complex, having papillae which grade into echinules, as well as reticulations and canaliculi. The patterns of the three American *Elaphe* appear to form a gradient from the simple echinate *E. guttata* to the complexities of *E. vulpina*. The pattern of *E. quatuorlineata* is echinoreticulate and uniform at all magnifications. (Fig. 7).

The microdermatoglyphic patterns of *P. deppei*, *P. lineaticollis*, and *P. melanoleucus* (Figs. 8–10) are indistinguishable from one another. They are papilloreticulate with canaliculi visible at low power and superficially like that of *E. vulpina*, as the arrangement of canaliculi and small elements are similar. *Pituophis* tend to have papillae lined up in fairly regular vertical pleats, as are *E. vulpina* echinopapillae. At high power, however, the nipple like papillae of *Pituophis* species appear considerably duller than echinules (Fig. 11).

The pattern of *E. subocularis* is similar to that of *Pituophis* in that it consists of papillae which are lined up in pleats, but differs in the total absence of canaliculi (Fig. 12). The pattern is uniform over all the exposed part of the scale. The pattern of *E. rosaliae* differs from those of the

above mentioned snakes in that it is strioreticulate with indistinct vertical pleats (Fig. 13). The striae occasionally merge into randomly distributed, poorly formed echinules. No papillae or canaliculi are resolvable, however. The pattern is somewhat reminiscent of that of *E. quatuorlineata*, but is made up of much smaller elements.

Occasional fusion of papillae is seen in *E. subocularis*. A strioreticulate pattern might be derived from this by loss of the nipple-like elements and fusion of the striate portions of adjoining papillae, tending toward a morphological intermediate between papillate and echinate patterns. In any case, the two species differ somewhat in microdermatoglyphic pattern. Both also differ from the patterns found in other American lamppropeltiins, as well as that of the European *E. quatuorlineata*. Both patterns are unique in the Nearctic snake fauna examined to date.

Karyology: *Elaphe guttata*, *E. obsoleta*, and *Pituophis melanoleucus* are known to have a diploid chromosome number of 36 with five or more metacentric or submetacentric macrochromosomes, as do Old World species of *Elaphe* that are related to *E. quatuorlineata* (e.g., *E. climacophora*, *E. longissima*, and *E. quadrivirgata*) and the majority of colubrid snakes (Gilboa, 1975). By contrast, *E. subocularis* has a diploid number of 40 with a single metacentric chromosome (Baker et al., 1971, 1972). In addition, this species has a highly distinctive guaninecytosine banding pattern that is not closely approached by any other colubrine snake tested (Mengden and Stock, 1980). A diploid number of 38 chromosomes has recently been confirmed for *E. rosaliae*, although it is "... not ideally intermediate between *E. subocularis* and other *Elaphe*" (Greg Mengden, *in litt*).

**Immunological Comparisons:** The albumin immunological distances (AID) between representative species of *Elaphe*, *Pituophis*, *Lampropeltis*, and other colubrid snakes have been determined by the technique of microcomplement fixation (Dowling et al., 1983). When tested with antiserum of *Elaphe obsoleta*, the blood sera of *Arizona elegans*, *Pituophis melanoleucus*, *E. guttata*, and *E. vulpina* are found to range 9, 8, 9, and 3 AID from the antiserum. Three Eurasian species are in the range of 18–20 AID (*E. quatuorlineata*, 18 AID; *E. scalaris* 19 AID; *E. quadrivirgata* 20 AID), but *E. subocularis* resembles *Lampropeltis getulus* and *Ptyas mucosus* in being 23 AID from *E. obsoleta*. Tests with antisera of *Lampropeltis* and *Ptyas* show that *E. subocularis* also differs from these genera: 22 AID from the former and 25 AID from the latter.

Our standard calculation of 0.58 million years for each unit of AID suggests that *E. obsoleta* and *E. subocularis* last shared a common ancestor some 13–14 million years ago, at about the same time that *Ptyas* and *Lampropeltis* were diverging from *Elaphe*. This is substantially more than the estimates for the common ancestors of *E. obsoleta* with other Nearctic ratsnakes (2–5 million years) and more than their estimated time of divergence from the Eurasian species of *Elaphe* (10–12 million years) and justifies the taxonomic isolation of *E. subocularis*. Unfortunately, living specimens of *E. rosaliae* are still so rare that we have been unable to obtain a serum specimen for testing.

### Discussion

The present generic allocation of snakes tends to be more the result of historical processes and general agreements on maintaining nomenclatural stability than ex-

pressions of currently recognized relationships. Most snake genera were established long before ideas of generic relationships and evolutionary processes had been developed, and many genera were erected based on "key characters" that are now known to possess little phyletic value.

A number of taxonomic problems result from Boulenger's (1894) allocation of 45 species of generalized colubrid snakes to the comprehensive genus *Coluber*. Although neither of the species under consideration here had been described at that time, there is little question that Boulenger's allocations affected the decisions of Mocquard (1899) and Brown (1901) to place their new species in *Coluber*. Later Stejneger (1907) showed that the proper name for this genus was *Elaphe*, so both of these species, along with many others, were allocated to that genus. Other species of Boulenger's *Coluber* were later allocated to such diverse genera as *Arizona*, *Drymarchon*, *Drymobius*, *Drymoluber*, *Pituophis*, and *Spilotes*.

Some of Boulenger's other comprehensive genera have been partitioned by later workers (e.g. *Natrix* by Malnate, 1960, and Rossman and Eberle, 1977), but *Elaphe*, with eight American and some 30 Eurasian species, has been little changed in the present century. In a study of the American ratsnakes (Dowling, 1952), it was shown that these species fall into three groups. Five species (*E. flavirufa*, *E. guttata*, *E. obsoleta*, *E. phaescens*, and *E. vulpina*) appeared to be closely related to the European type species of the genus, *E. quatuorlineata*, and were allocated to the "Pantherophis Section." One species, *E. triaspis*, has no apparent close relatives and has been allocated to a new genus (Dowling and Fries, 1987). (*Elaphe flavirufa* was later found to differ from typical *Elaphe* more than been recognized in the earlier work and is cur-



rently being reevaluated.)

The two species under consideration here (the "Rosaliae Section") were thought to be rather closely related to the North American genus *Pituophis*. Dowling (1952) emphasized that *E. subocularis* and *E. rosaliae* "are so closely approximated [to *Pituophis*] in numerous characters (those of hemipenis, of body form, and scutellation) that a simple fusion of the two halves of the anal plate in *E. subocularis* would place it, as a distinct species, in the Deppei Group of *Pituophis* if only the usual key characters were observed". The only "key character" left available to differentiate *Pituophis* from the "Rosaliae Section" was the epiglottal cartilage of the former (*vide* Cope, 1900: fig. 202).

### Taxonomic Conclusions

In light of the data presented here, it is apparent that the "Rosaliae Section" of Dowling (1952, 1957) should be removed from the genus *Elaphe*. The historically utilized key mensural and meristic characters (except for the divided anal scute) would place these snakes in *Pituophis*, as would their hemipenial morphology. Dorsal scale microdermatoglyphics also suggest a closer affinity to *Pituophis* than *Elaphe*, although both *E. subocularis* and *E. rosaliae* possess some unique features of pattern. On the other hand, the presence of a specialized epiglottal structure in *Pituophis*, the difference in karyotypes, and the immunological data all point to a different taxon.

Although the data for *E. rosaliae* are scant, this species is clearly the closest living relative of *E. subocularis* (Dowling, 1957). Therefore, we recognize a separate genus of colubrine snakes for these two species.

As the relationships of other members of

the genus *Elaphe* (some of which are poorly known) are currently under investigation by us and others, a definition of this genus is not within the scope of this work. A definition of the genus *Bogertophis* follows:

### *Bogertophis* gen. nov.

*Coluber rosaliae* Mocquard, 1899: 321.

*Coluber subocularis* Brown, 1901: 492.

*Elaphe rosaliae* (Mocquard): Stejneger and Barbour, 1917.

*Elaphe subocularis* (Brown): Stejneger and Barbour, 1917.

Type Species: *Coluber subocularis* Brown, 1901.

Content: Two western North American species, *Coluber rosaliae* Mocquard, and *Coluber subocularis* Brown.

Definition: A genus of colubrid snakes having a small hemipenis (8–10 subcaudals), without basal hooks or distinct distal lobes, and with the basal portion covered by fine spinules. There is a lorilabial row of 3–7 scales, and usually 10–11 supralabials. The ventrals range from 260–287, the anal scute is divided, and the paired subcaudals range from 60–89. The dorsal scale count of approximately 29+35+21 is increased or reduced by the addition or loss of mid-lateral scale rows (Dowling, 1957). The dorsal scales have pairs of small rounded apical pits; they are smooth to Row 5, with rows above generally having low keels, at least posteriorly. The dorsal scale microdermatoglyphics are papillate without canaliculi, the papillae falling into regular vertical pleats (*B. subocularis*), or strioreticulate with indistinct vertical pleats (*B. rosaliae*). There is no apparent sexual dimorphism in any feature of scutellation or pattern.

Diagnosis: The genus *Bogertophis* may be morphologically distinguished from *Pituophis* by its lack of an epiglottal struc-

ture, its paired anal scute, and by the absence of canaliculi in the microdermatoglyphic pattern of its dorsal scales. It is distinguished from *Arizona* by its rounded rostral (slightly pointed, partly separating the internasals in *Arizona*), lorilabial scales, keeled dorsal scales with paired apical pits (vs smooth with single pits), a different hemipenial morphology, paired anal scute, and echinate microdermatoglyphic pattern of *Arizona*. (Price, 1981). It differs from *Senticollis* in the presence of lorilabial scales, a vastly different hemipenis, a much shorter tail (Dowling and Fries, 1987), and lack of regular echinules and the presence of pleating in the microdermatoglyphic pattern of its dorsal scales (Price, 1981).

It may be distinguished from *Elaphe* (*sensu stricto*) by the shorter tail, the smaller, spinulose hemipenis, the presence of lorilabial scales, and in the absence of regular echinules and the presence of pleating in the microdermatoglyphic pattern of its dorsal scales. The two species appear to be unique among colubrine snakes in possessing diploid karyotypes of 38 or 40 chromosomes with few metacentric chromosomes, and in lacking any sexual dimorphism in body proportions or scutellation.

Geographic Range: U.S.A., Texas, west of the Pecos River and southern New Mexico; Mexico, western Nuevo Leon, Coahuila, northeastern Durango, and eastern Chihuahua (*B. subocularis*); Baja California Sur (*B. rosaliae*). [See Fig. 14].

Etymology: Inasmuch as there is no name available for this genus, we name it *Bogertophis* for Charles M. Bogert, Emeritus Curator of the Department of Herpetology of the American Museum of Natural History, in recognition of his many contributions to the knowledge of the relationships of colubrid snakes.

Taxonomic Arrangement: The genus

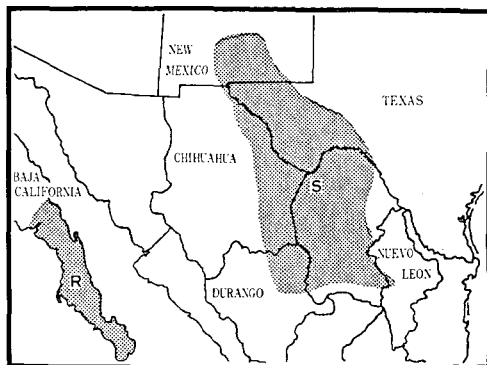


Fig. 14. Map showing general distribution of the genus *Bogertophis* in western North America. (R = *B. rosaliae*, S = *B. subocularis*.)

*Bogertophis* is placed, along with related genera in the "Ratsnake Group" (Dowling and Fries, 1987) of the Lamproleptini as follows:

Family Colubridae Oppel, 1811

Subfamily Colubrinae Dunn, 1928

Tribe Lamproleptini Dowling, 1975

Ratsnake Group

*Arizona* Kennicott, 1859

*Bogertophis* Dowling and Price, 1988

*Elaphe* Fitzinger, 1833

*Pituophis* Holbrook, 1842

*Senticollis* Dowling and Fries, 1987

As yet no data—either morphological or biochemical—are available to provide an adequate phylogeny for this group. In part this is a reflection that the genus *Elaphe* remains a polyphyletic taxon. Although *Arizona* and *Pituophis* are believed to have been derived from the same stock as the American "Pantherophis" species of *Elaphe* in relatively recent times, this does not appear to be the case for *Bogertophis* and *Senticollis*, whose close relatives are as yet undiscovered.

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## 要 約

### *Elaphe subocularis* と *E. rosaliae* のための新しい属

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ナメラ属 *Elaphe* の他の種および近縁属との比較から, *Coluber subocularis* Brown と *C. rosaliae* Mocquard に対して, 新しい属 *Bogertophis* をもうけた。この属は形態的には, *Elaphe* および *Pituophis* とわずかしかわらないが, 鱗表面の微細構造, 核型, 免疫学的な比較では, はっきりと区別される。

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