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THE STATUS OF THE GENUS *LEPTODRYMUS* AMARAL, WITH COMMENTS ON MODIFICATIONS OF COLUBRID PREMAXILLAE

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The classification of the Central American colubrid currently known as *Salvadora pulcherrima* (Cope) has been troublesome to taxonomists since its earliest description. Originally described by Cope in 1874 as *Masticophis pulcherrimus* the species has been inadvertently redescribed twice under different generic names and referred to two additional genera. Further confusion has resulted from superficial resemblances of this Central American species with *Salvadora lemniscata* of the Pacific slope in the Tehuantepec region of Mexico; Bocourt (1890), as well as Boulenger (1893) and some recent authors, uses the name *pulcherrimus* for the latter, apparently without having seen the smaller snake to which the name is properly applied. I attempted to clarify the situation in 1939b and placed some of these erroneous citations in the synonymy of *Salvadora lemniscata*. Other references are assigned in the synonymy below.

Although relatively few additional specimens of *pulcherrimus* have come to hand, it is now possible to re-evaluate the status of the form in the light of additional data drawn from other genera. Stuart (1932) was the first to suggest that the species belonged in the genus *Salvadora*, although he presented no data to substantiate the putative relationship. Cope (1887) had placed the species in the genus *Drymobius*, but inasmuch as he included a variety of other species in the group the implications of the action are dubious. Amaral (1927), unaware of the identity of his type specimen with those described by Cope and by Boettger, erected the genus *Leptodrymus* and called the species *clarki*. Amaral asserted that *Leptodrymus* was related to both *Dry-*

mobius Fitzinger and "*Leptophis* Wagler" (now *Thalerophis* Oliver, 1947). Dunn (1931), who pointed out the synonymy of the three specific names, suggested that *Leptodrymus* might be a valid genus. In this view I concur. It is difficult to ascertain which group of colubrids it most closely resembles, although the premaxilla is virtually identical with that of some species of *Thalerophis*. However, the hemipenis differs from that of other American colubrids, and there appear to be scale characters that leave *pulcherrimus* unacceptable in currently recognized genera to which it supposedly might be allied.

Because the species cannot be placed in any group with certainty, the monotypic genus *Leptodrymus* must be recognized; there appears to be no alternative at present, although it is hoped that additional studies of Neotropical colubrids will clarify the relationships of the genera and permit a more satisfactory arrangement of the groups. There would be no objection to the inclusion of *pulcherrimus* in the genus *Salvadora* (even though the range of variation in generic characters would have to be extended to do so), but for the fact that *pulcherrimus* seems to be more closely allied to *Thalerophis*, *Dendrophidion*, *Dryadophis*, and perhaps to other Neotropical colubrids.

Although the genus was diagnosed by Amaral (1927), he failed to include all vacant sockets in his count of the maxillary teeth, the hemipenis is erroneously depicted, and other characters that prove to be of diagnostic significance were omitted. The genus may be redefined with additional characters included, and a summary of variations within the species can be added

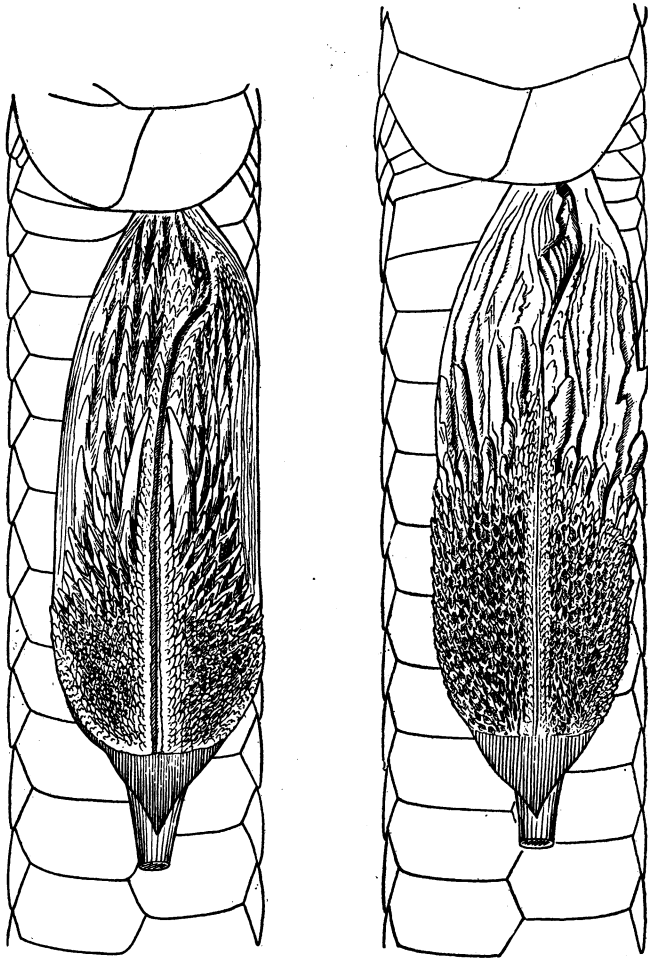
**LEPTODRYMUS PULCHERRIMUS****SALVADORIA LEMNISCATA**

Fig. 1. Left hemipenes of *Leptodrymus pulcherrimus* (M.C.Z. No. 38737, enlarged $\times 4$) and *Salvadoria lemniscata* (U.S.N.M. No. 109245, enlarged $\times 2$), depicted as dissected from the retracted position, slit down the dorsum and spread out on the under surface of the tail. Note the symmetrical arrangement of the spines in *pulcherrimus* in contrast to the asymmetrical condition in *lemniscata*, with only one greatly enlarged spine adjacent to the sulcus.

that will supplement the description previously given (Bogert, 1939a, p. 184).

LEPTODRYMUS AMARAL

Leptodrymus AMARAL, 1927, Bull. Antivenin Inst. Amer., vol. 1, p. 29. Genotype *clarki* = *pulcherrimus*.

DEFINITION: A genus of colubrid snakes with the following characters: Hemipenis with basal spines and distal calyces in symmetrical arrangement flank-

ing an undivided sulcus, one strongly enlarged spine on each side of the sulcus near the middle of the organ (fig. 1). Premaxilla with pronounced lateral projections not strongly recurved (fig. 2). Maxilla (fig. 4) with 17 to 19 subequal teeth followed after a diastema by three enlarged teeth; mandibular teeth 19 to 21. Dorsal scales smooth, with double apical pits, arranged in 17 rows at midbody but reducing to 15 at the base of the tail by sup-

pression of the fourth row in the region of the body between 124th and 136th ventral. Rostral normal, width greater than height. Loreal twice as long as broad. One preocular and three postoculars, strongly pitted, the pitted area extending forward to the loreal, onto the upper portion of the supralabials and posteriorly onto the anterior temporals. (Depending on the manner of preservation these structures, possibly tactile organs, appear as tiny pustules or as pits. On removed epidermal coverings of the scales they appear as holes or transparent dots.)

Leptodrymus pulcherrimus (Cope)

1874. *Masticophis pulcherrimus* COPE, Proc. Acad. Nat. Sci. Philadelphia, vol. 26, p. 65. (Type locality, "Western side of Central America"; cotypes, Academy of Natural Sciences of Philadelphia Nos. 14688 and 5199.)
1887. *Drymobius pulcherrimus* COPE, Bull. U. S. Natl. Mus., no. 32, p. 70.
1894. *Zamenis pulcherrimus*, GÜNTHER (*partim*), Biologia Centrali-Americana, Reptilia and Batrachia, p. 123.
1898. *Zamenis bitaeniatus* BOETTGER, Katalog Reptilian-Sammlung in Museum der Senckenbergischen Naturforschenden Gesellschaft in Frankfurt am Main, pt. 2, p. 42, footnote. (Type locality, Retalhuleu, Guatemala.)
1927. *Leptodrymus clarki* AMARAL, Bull. Antivenin Inst. Amer., vol. 1, no. 1, p. 29. (Type locality, Tela, Honduras; type, Museum of Comparative Zoology No. 20207.) 1929, Mem. Inst. Butantan, São Paulo, vol. 4, p. 160.
1929. *Masticophis bitaeniatus*, AMARAL, Mem. Inst. Butantan, São Paulo, vol. 4, p. 153.
1931. *Leptodrymus pulcherrimus*, DUNN, Copeia, p. 163. STUART, 1933, Copeia, p. 9.
1933. *Salvadora pulcherrimus*, STUART, Copeia, p. 10.
1939. *Salvadora pulcherrima*, BOGERT, Publ. Univ. California at Los Angeles in Biol. Sci., vol. 1, p. 182, pl. 3.
1943. *Salvadora pulchra*, SCHMIDT, Amer. Midland Nat., vol. 30, p. 252.

MATERIAL EXAMINED: Three females and seven males, including M.C.Z. No. 20207, Toloa Creek, Tela, Honduras (type of *clarki*); M.C.Z. No. 38737, Portillo Grande (= El Portillo?), 4100 feet elevation, Honduras; U.S.N.M. Nos. 79965, 79966, Managua, Nicaragua; U.S.N.M. No. 16127, "Nicaragua?"; A.N.S.P. Nos. 5199, 14688, "Western side of Central America," probably Nicaragua (cotypes of *pulcherrimus*); U.S.N.M.

No. 38150, Pacaca, Costa Rica; A.N.S.P. No. 22623, Tileran, Costa Rica; and U.S.N.M. No. 25239, no locality data. The only additional specimen reliably reported is the type of *Zamenis bitaeniatus* taken at the northern extremity of the known range near Retalhuleu, Guatemala.

SUMMARY OF CHARACTERS: Head shields as depicted in figure 5, with minor variations; the supralabials are uniformly nine except on the female from Managua, which has 10 on the left side with the second, third, and fourth reaching the loreal instead of the normal second and third. The infralabials are normally 10 (rarely 12) with the first five in contact with the anterior chin-shields. The preocular is uniformly single, and all specimens examined have three postoculars, although the type of *Z. bitaeniatus* reportedly had but two. The temporals normally are 2+2+2, but any pair is occasionally single, with other modifications such as those seen on the snake depicted in figure 5. Conspicuous pits or pustules are present on the preocular, postoculars, and the adjacent scales.

The ventrals range from 195 to 205 in males, mean 200.8, and from 204 to 210, mean 208, in females. The anal plate is divided. The subcaudals are in two series, ranging from 145 to 152 in males, and from 148 to 152 in females (for three of each sex having complete tails). The dorsal scales are disposed in 19 rows on the neck, 17 at midbody, and 15 at the base of the tail. The reduction from 19 to 17 rows on the neck results from suppression of the fourth row in the region above the seventh to eleventh ventrals. The midbody reduction results from the loss of what has become the fourth row in the region between the 124th and 136th vertebrae in males, and between the 134th and 140th in females. An average difference between the sexes is indicated; the mean number for the vertebra where suppression takes place is 131 in males and 137 in females.

FORM: The body is relatively slender, with the head distinct from the neck. The eye is large, with a diameter equal to approximately three times the height of the fifth supralabial. The ratio of the tail to

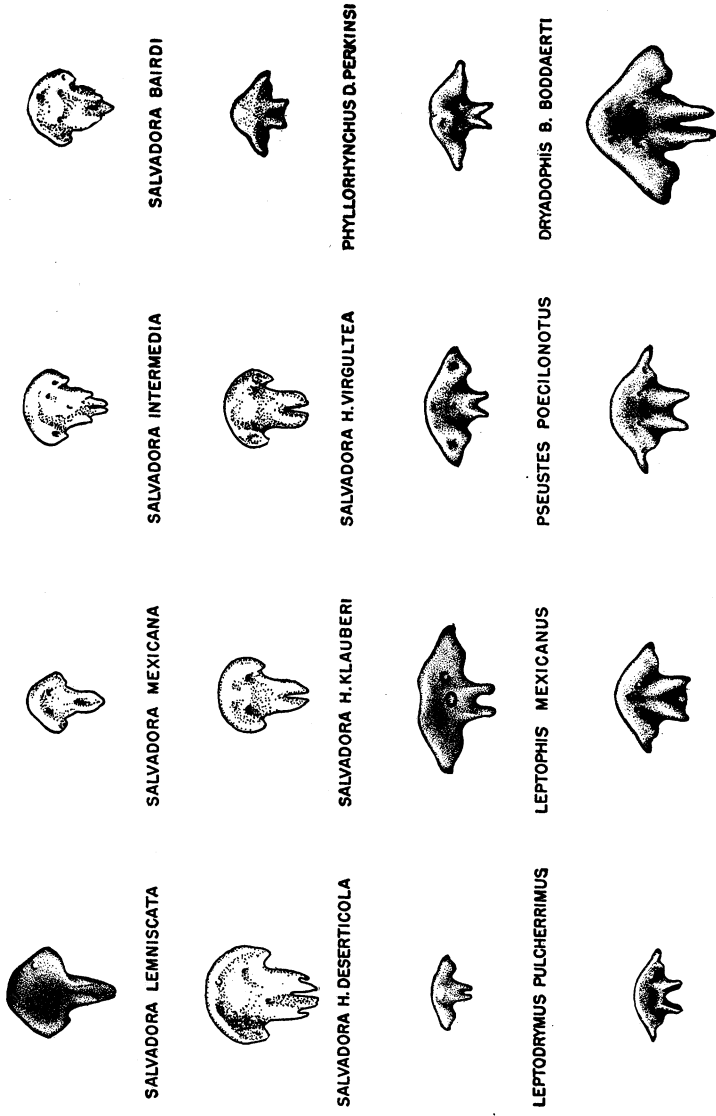


Fig. 2. Ventral views of the premaxillae of representative species of *Salvadora* and other American colubrids (enlarged from $\times 2.5$ to $\times 5$), to show similarities of the bone in representatives of a single genus, and the differences between these premaxillae and the same cranial element in other snakes. Those of *Leptodrymus pulcherrimus* and *Leptophis* (= *Thalerophis*) *mexicanus* are essentially similar, and obviously different from those of *Salvadora*, to which *pulcherrimus* has been assigned.

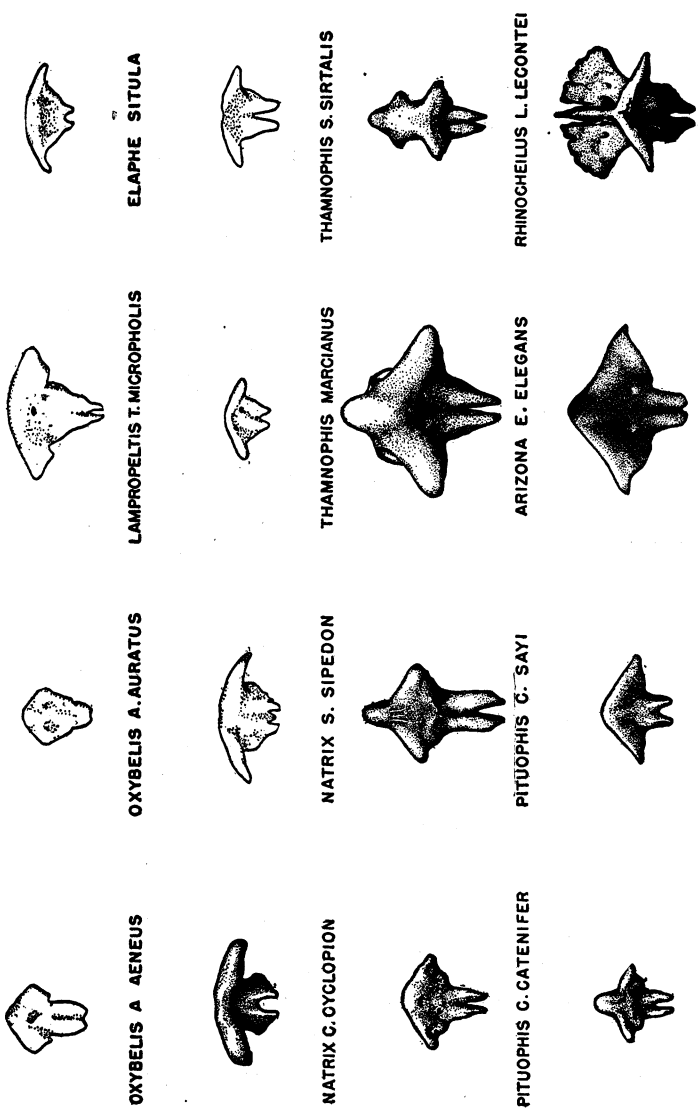
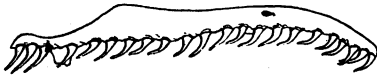


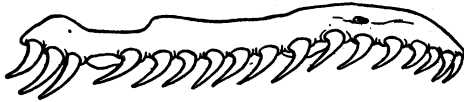
Fig. 3. Ventral views of the premaxillae (enlarged $\times 2.5$ to $\times 5$) of miscellaneous colubrids, including representatives of the subfamilies Natricinae, Xenodontinae, and Colubrinae, including such specialized forms as *Oxybelis* and *Heterodon*. The monotypic genera *Arizona* and *Rhinocheilus*, representing fossorial species, are similar in possessing the projection at the anterior of the bone, a condition approached in *Pituophis*, as well as in the Asiatic *Coluber spinalis*. See text for discussion of parallel modifications.

total length varies from .35 to .36 in males and from .33 to .36 in females. The largest specimen examined is a male (M.C.Z. No. 38737, from Portillo Grande = El Portillo?, Honduras) with an over-all length of 975 mm.

The maxillary contains from 17 to 19 subequal teeth followed after a diastema by three slightly enlarged teeth (fig. 4). Complete tooth counts for one specimen disclose 17+3 on the maxillary, 14 on the



LEPTODRYMUS PULCHERRIMUS



SALVADORA LEMNISCATA

Fig. 4. Lateral view of the right maxilla ($\times 8$) of the slender bodied *Leptodrymus pulcherrimus* compared with the same bone ($\times 5$) from *Salvadora lemniscata*, a larger, stouter species.

palatine, 30 on the pterygoid, and 21 on the dentary. The premaxilla has pronounced lateral projections that are feebly recurved posteriorly (fig. 2).

The hemipenis, as dissected in a preserved specimen, is noncapitate and not bifurcate distally, with a simple sulcus. Basal portion with small spines in about 10 rows; near the middle larger spines are arranged in four rows on either side of the sulcus, with the larger spines flanking the sulcus; two greatly enlarged spines are inserted at the level of the sixth subcaudal. Distally the spines diminish in size and merge with strongly denticulate calyces on the terminus. At the middle an area of longitudinal ridges without spines or calyces lies beyond the outer row of spines. (See fig. 1.)

PATTERN: Dorsum of head greenish. Belly and lips immaculate cream color. Body with middorsal light stripe occupying the median scale row and half of each ad-

jacent scale row, flanked on each side by a black stripe that covers two scale rows and half of each adjacent row (fig. 6). The black stripes extend onto the tail, diminishing in width in proportion to the diameter of the appendage. Anteriorly the stripes extend on the neck and across the temporals to the eye (fig. 5). On some specimens there is a vestige of the stripe on the loreal region in front of the eye.

RANGE: Central America, from approximately 10° N. in Costa Rica, northward to Tela on the Atlantic coast of Honduras, and westward to Retalhuleu in southwestern Guatemala near the Pacific coast. Nothing is recorded concerning the habitat, although the species has a vertical distribution from near sea level to at least 4100 feet elevation.

RELATIONSHIPS: In making comparisons data have been drawn from the papers by Stuart (1932 and 1941), who supplies summaries of characters for the genera *Dryadophis*, *Dendrophidion*, *Drymobius*, and *Drymoluber*. The data for *Masticophis* and *Coluber* are taken from Ortenburger (1928). Summaries of variation for the genus *Thalerophis* (= *Leptophis* auct.) have been generously supplied by my colleague, Dr. James A. Oliver, and those for the genus *Salvadora* have been drawn from my own unpublished data. These genera contain the species that most closely resemble *pulcherrimus*, but the combination of characters found in the latter differs from that of any other group.

First it should be pointed out that *Leptodrymus* differs from these other genera in the structure of the hemipenis. No other group contains species with enlarged basal spines in symmetrical arrangement on the copulatory organ (cf. those in fig. 1). Either basal spines are entirely lacking, or there is one greatly enlarged spine on only one side of the sulcus. In some groups, namely, *Coluber* and *Thalerophis*, the enlarged basal spines may be present or absent, but when present these spines are restricted to one side. *Leptodrymus* seems to be similarly unique in normally having three postoculars. Three scales behind the eye occur in related genera only as an abnormality. Aside

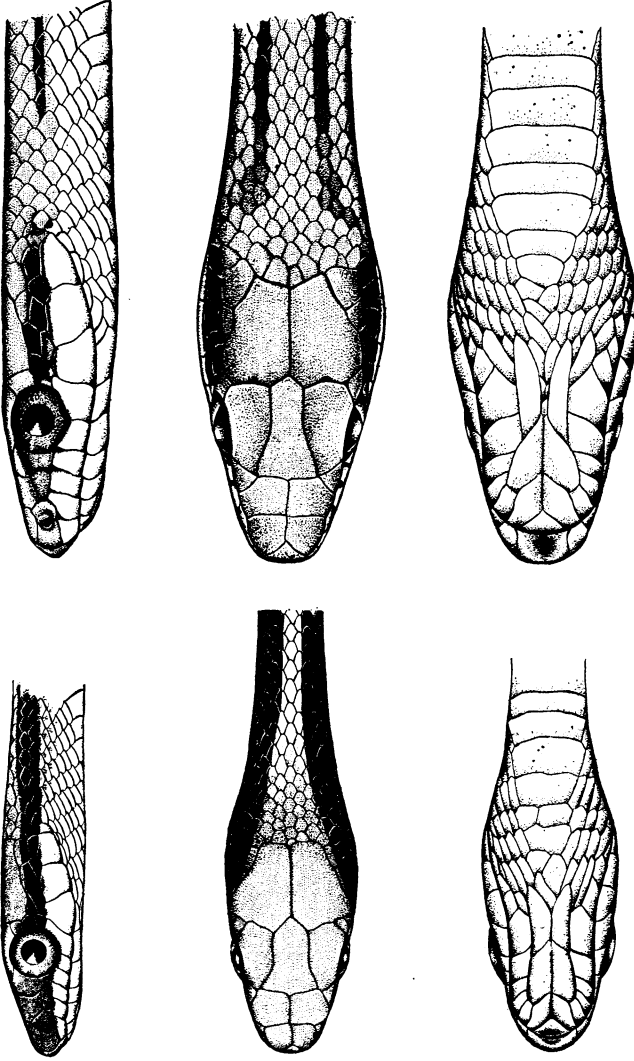
**LEPTODRYMUS PULCHERRIMUS****SALVADORA LEMNISCATA**

Fig. 5. Lateral, dorsal, and ventral views of the heads of adult *Leptodrymus pulcherrimus* and sub-juvenile *Salvadora lemniscata*, to show differences in habitus, sculation, and pattern.

from these characters, the principal differences between *Leptodrymus* and related American colubrid genera can be summarized, taking the various groups one by one, as follows:

1. *Salvadora*: Despite the confusion that existed with reference to *Salvadora lemniscata* and *L. pulcherrimus* the only close resemblance lies in the numbers of ventrals, caudals, and the number of mid-body scale rows. The means for the ventrals and caudals are not identical, however; when only those specimens with complete tails are compared it is evident that the mean number of caudals in *pulcherrimus* closely approaches the maximum for *lemniscata*. In all but one species of *Salvadora* there is a reduction in the number of scale rows to 13 at the vent (in *S. g. lineata* 15 scale rows at the vent occur principally in females, less commonly in males), whereas in *pulcherrimus* all specimens available retain 15 scale rows at the vent. The loreal plate in *pulcherrimus* is normally twice as long as high, the upper edge roughly parallel with the lower; in *Salvadora* the loreal is divided in some species, but when single it is more commonly subtriangular, never twice as long as high. The eye in *pulcherrimus* is proportionately larger than it is in *Salvadora*, with a diameter three times as great as that of the fifth labial; the supralabials in *Salvadora* are not so flat as they are in *pulcherrimus*, and the diameter of the eye is only twice that of the fifth labial. The conspicuous pits or pustules on the scales around the eye of *pulcherrimus* are absent in *Salvadora*.

The habitus of *Salvadora* resembles that of the racers, particularly *Masticophis*, but *Leptodrymus* is a relatively more slender snake, with a mean tail/total length slightly exceeding the average for either of the latter. The slender body and large eye suggest that *pulcherrimus* is primarily an arboreal snake, although this supposition remains to be verified; all *Salvadora* appear to be rather strictly terrestrial.

As may be seen in figure 2, the shape of the premaxilla in *Salvadora* characterizes the snakes in the genus, although the bone in *lemniscata* and *mexicana* differs some-

what from that in the *grahamiae* group, which includes the other species. The lateral projections are greatly reduced and the front of the bone is convex in all *Salvadora*, whereas in *Leptodrymus* the shape of the premaxilla (fig. 2, third row) approximates that of other colubrids. No skull of *pulcherrimus* has been available for detailed comparisons of cranial elements, but there is no species of *Salvadora* with so many maxillary or pterygoid teeth.

Leptodrymus, as well as all *Salvadora*, possesses patterns consisting of a light vertebral stripe flanked by darker stripes. But on all *Salvadora* save *grahamiae* there

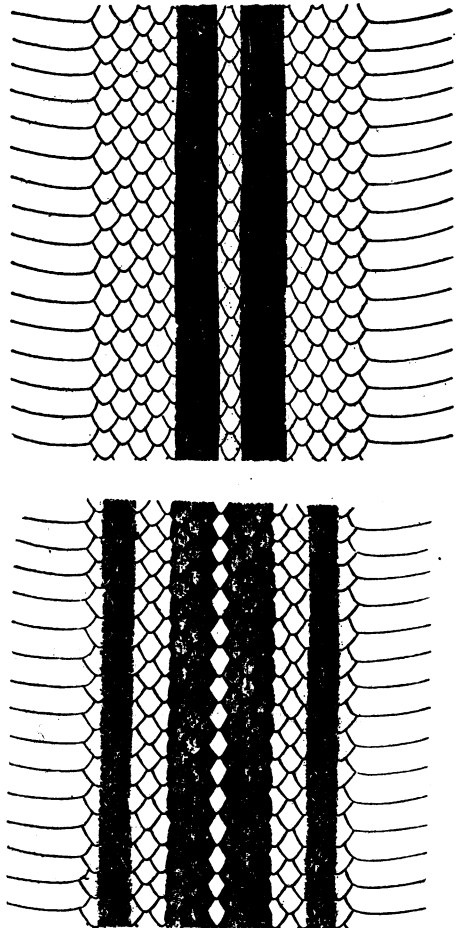


Fig. 6. Midbody patterns of *Leptodrymus pulcherrimus* (upper) and *Salvadora lemniscata* (lower).

are pronounced lateral stripes (cf. drawings in fig. 6), and in the latter the vertebral is three scales wide. Although the pattern fades in preservative to clay white, the middorsal stripe of *pulcherrimus* is reported to be reddish or yellowish in life; anteriorly it is emerald green, this brilliant color extending over the entire top of the head, according to Cope. These colors are unknown in *Salvadora*. Aside from superficial resemblances in pattern, as seen on the preserved snake, *pulcherrimus* has few characters of importance that point to close affinity with the patchnosed snakes in *Salvadora*.

2. *Thalerophis*: The snakes of this genus (long known as *Leptophis*) have not been critically studied until recently. The genus includes a number of species that are characterized by having the dorsal scale formula 15-15-11, some of the dorsal scales with keels, various patterns, most of them either green or comprised of darker longitudinal stripes, invariably involving some green coloration. The green coloration of *Leptodrymus* is not greatly different from that seen on freshly preserved *Thalerophis diploptropis*, for example, a species with a light vertebral stripe flanked by black stripes at the anterior of the body. Snakes of the genus *Thalerophis* more closely approximate *pulcherrimus* in the shape and contours of the head, with the relatively large eye, and the flattened loreal, when this plate is present. The premaxillae of the snakes in the two genera are nearly identical, and they share in common the pitted scales on each side of the eye.

Aside from the differences in the scale reduction formulas and dorsal scales, keeled in *Thalerophis* and smooth in *Leptodrymus*, Dr. Oliver has pointed out to me that in the former two labials reach the eye, and there is but one anterior temporal. While variation in the number of maxillary teeth could include the condition found in *pulcherrimus*, there is no diastema present in snakes of the genus *Thalerophis*. In addition, the relative tail length of *Thalerophis* is greater, there are invariably more caudals, and there is ordinarily no more than one apical scale pit posterior to the point of dorsal scale reduction, whereas in *Leptodrymus*

there are two pits on scales throughout the length of the body.

3. *Drymoluber*: This genus erected by Amaral in 1929 contains but two species, both of them confined to South America. Aside from the gap in the range that would exist if *pulcherrimus* were added to the genus, *Drymoluber* possesses but eight supralabials, and fewer ventrals, fewer caudals, and tails that comprise approximately one-fourth of the total length. In pattern characters there is no resemblance whatsoever to *Leptodrymus*. The body is not so slender as it is in the latter, although the pits on the preoculars and postoculars are present. There is no diastema in the maxillary dentition.

4. *Drymobius*: Four species comprise this genus; all have keeled dorsal scales, and relatively low ventral counts (with a maximum of 170 according to Stuart, 1933). Pits are present on preoculars and postoculars. None of the species possesses a pattern of longitudinal stripes. The maxillary teeth are reported by Stuart to vary from 22 to 34, enlarged posteriorly, although a diastema is lacking. The premaxilla has rather narrow lateral projections (at least in *margaritiferus*), but the shape of the bone suggests that *Drymobius* is not distantly related to *Leptodrymus*. The body is not so slender, however, and the characters of the hemipenis, of the pattern, the keeled dorsal scales, and the presence of but two postoculars, as well as the relatively smaller eye, suggest that the relationship is not close.

5. *Dryadophis*: Snakes of this genus, particularly those in the *boddaerti* group as defined by Stuart (1941), exhibit variations in the normal scalation of species that might include *L. pulcherrimus* except for the presence of only two postoculars. *Dryadophis* contains species with patterns of blotches or stripes, but there is no pattern that closely approaches that of *pulcherrimus*. *Dryadophis* includes species with proportionately shorter tails, and the body is not so slender as it is in *pulcherrimus*. Although the maxillary dentition includes the variations found in *Leptodrymus*, the shape of the premaxilla is modified along somewhat different lines. On the whole, *Leptodrymus* appears to be

about as closely related to *Dryadophis* as it is to *Thalerophis*.

6. *Dendrophidion*: Some species of *Dendrophidion* possess striped patterns not dissimilar from those of *Leptodrymus*, but the keeled scales of the former, the extraordinarily great number of maxillary teeth (33 to 50 according to Stuart), and the differences in the shape of premaxilla do not point to close relationships.

7. *Coluber*: The snakes of this genus, which includes only two species, possess relatively few characters in common with *Leptodrymus*. For *Coluber* Ortenburger (*supra cit.*) reports 16 maxillary teeth as the maximum, and normally there are only seven supralabials. The premaxilla of *Coluber* more nearly resembles that of European racers (which probably can be referred to the genus *Zamenis*) than it does that of *Leptodrymus*, and probably the American species of *Coluber* are as closely related to Old World species as to *Leptodrymus*.

8. *Masticophis*: Recognized by some authors (or placed as a synonym of *Coluber*), this genus differs from *Leptodrymus* in more respects than it differs from the snakes referred to *Coluber*. *Masticophis* and *Salvadora* appear to be the only genera that lack the pits or pustules on the preocular, postocular, and anterior temporals, and the genera have many other features shared by *Salvadora lemniscata* and *S. mexicana*. The dentition is similar, and were it not for the modifications of the rostral and premaxilla, nine supralabials, and slight pattern differences, these two species of *Salvadora* might easily be referred to *Masticophis*, since the hemipenes are virtually identical. Consequently most of the characters that serve to differentiate *Leptodrymus* from *Salvadora* will serve as well to separate it from *Masticophis*.

DISCUSSION: On the basis of this brief review the conclusion may be drawn that *Leptodrymus*, despite its monotypic status, warrants recognition. It cannot be stated with assurance that the single species should be inserted in one or the other of the related genera in preference to another. At the same time it may be observed that it is questionable whether or not we are

dealing with characters of generic importance. It would be superfluous to point out that species have evolved along different lines, perhaps losing ancestral characters or acquiring new ones. Because we do not know, and are unlikely to learn, precisely what characters the ancestral colubrid had, we can do no more than guess whether some characters represent the primitive (or a specialized) condition. The inferences that can be drawn are often obscured by parallel modifications, and it is reasonable to suppose that evolution has been more rapid in some lines than in others. The infrageneric groups in some of the genera currently recognized differ from one another as much as other "full genera" differ. From some standpoints it would be preferable to place the eight New World genera (and perhaps others) in a single genus (*Coluber*), recognizing subgenera as well as species groups.

The state of our knowledge at present does not permit us to set up a phylogenetic arrangement that is very meaningful. The keys that have been constructed are largely artificial even though they serve the useful and practical purpose of simplifying the identification of specimens. In view of the fact that the same structure may be retained in one branch but strongly modified in another branch of the same general stock, it is inevitable that keys very often do not reflect phylogenies. *Salvadora*, *Masticophis*, and most species and subspecies of *Coluber* have similar hemipenes with enlarged basal spines, but one subspecies (*priapus*) of *Coluber constrictor* possesses a copulatory organ without enlarged spines. In this instance a difference exists between subspecies, virtually identical in other characters, that has been widely used as one of generic importance. It is possible, of course, to set up generic classifications on the basis of one character, as Inger and Clark (1943) have done. But the significance of such classifications is open to considerable doubt. On the other hand, a consideration of several characters seems often to complicate the picture to such an extent that conclusions become increasingly difficult.

Because of similarities in scale row reductions (to which they might have added

penial characters) Inger and Clark propose placing the Asiatic species *spinalis* in the genus *Coluber*. Had they examined the maxillary dentition it would have seemed obvious that the snake belonged in the same group as the European snakes they separated as *Zamenis*. Or if they had been basing their conclusions on pattern and coloration they might have felt impelled to lump the form with *Salvadora*. On the other hand, if they had examined the premaxilla (fig. 3) they could easily have shown that the snake was unique in this respect, and a new generic name might have been proposed.

The basic difficulty, of course, lies in

knowing which characters in any species can be given the most weight in setting up a natural classification. Generic names should be used to indicate similarities, but the choice of characters to do this is left to the judgment of the systematist. If he examines only one or two characters per species he is less likely to arrive at sound conclusions than he will if he considers several characters and selects those that seem to be of greatest importance. Analysis must precede synthesis, and however complex the situation may become, there is every likelihood that some useful knowledge will accrue if as many characters as possible are investigated.

PREMAXILLARY MODIFICATIONS

In the survey summarized above attention was directed to the characters of the premaxilla. Little use has been made of such characters in the past, although this element of the skull can profitably be used in defining genera or in working out phylogenies. In this instance I have been concerned primarily with the status of a species that has been assigned to the genus *Salvadora*, a group of snakes that includes species with various degrees of enlargement in the rostral plate. It was of interest, therefore, to ascertain whether osteological modifications accompanied those on the exterior of the snout. To accomplish this purpose it was necessary to examine, not only the premaxilla of all species of *Salvadora* (as well as the species *pulcherrima*, now referred to *Leptodrymus*), but representatives of related genera as well. Because the value of such a study could be enhanced by broadening it beyond the original scope of this note, the project was extended to cover species in other genera. The premaxillae of several colubrids have been depicted in figures 2 and 3, and a few noteworthy observations can be pointed out.

First, it is instructive to note that modifications of the premaxillae are much alike in all species of *Salvadora*. On the basis of proportionate tail length, scale characters, and dentition, two infragenic groups can be segregated in the genus. One of these contains two large species, *lemniscata* and

mexicana, while four smaller species, some of them polytypic, comprise the other group. Even though the premaxillae of all six species are similar, there are minor, but consistent, differences between the snakes in the two groups. The posterolateral projections of the bone are almost completely suppressed in *mexicana* and *lemniscata*, the species with the most poorly developed rostral. Conclusions that may be drawn from a study of premaxillary characters confirm those drawn from other data. It seems clear that the snakes in the genus comprise a natural group that is well differentiated from others.

It may be suggested that the modifications of the rostral that characterize *Salvadora*, the projecting lateral edges and the flattened anterior of the scale, inevitably are accompanied by changes in the premaxillae. It is instructive, therefore, to compare the premaxilla of the patch-nosed snakes (*Salvadora*) with that of the leaf-nosed snakes (*Phyllorhynchus*). The rostral of the latter is flattened in a similar manner and even more strongly enlarged than it is in *Salvadora*. Numerous other scale characters serve to distinguish the genera, although for some years they were believed to be related. *Phyllorhynchus*, however, includes only nocturnal burrowing snakes, whereas the patch-nosed snakes are all diurnal; they are not true burrowers even though most of them are able

to dig in loose soil. But the premaxilla of *Phyllorhynchus* is not modified as it is in *Salvadora*, and shows little departure from what loosely may be referred to as the normal colubrid type.

When other burrowing colubrids are examined, however, some interesting parallels occur. Both *Arizona* and *Rhinocheilus* are crepuscular or nocturnal, and evidently feed while they are on the surface. During the day they presumably remain underground. They glide into loose soil with ease, and are capable of extensive movements beneath the surface. In each of these genera a conspicuous projection that undoubtedly provides support for the snout is present on the middle of the anterior surface of the premaxilla. The bone is strongly attached to the nasal and septomaxillary bones, while the nasals, in turn, are in broad contact with the frontals in *Rhinocheilus*, but somewhat less so in *Arizona*.

In general the modifications of the premaxilla in these burrowing snakes seem to be coupled with the necessity for the firm support of a projecting snout. The lateral projections appear to be retained, or even greatly enlarged, because of the support gained by their attachment to the anterior end of the maxillary bones. This attachment is relatively loose in terrestrial or arboreal snakes, but in burrowers it is more often close, indicating that the maxillae further strengthen the snout. The median projection is essentially hemispherical in *Rhinocheilus*, somewhat less so in *Arizona*, whereas in *Pituophis* the same structure is more like a vertical keel on the premaxilla.

Pituophis is not a burrower, although it is capable of pushing its body through loose earth when this is encountered in the burrows of the pocket gopher, *Thomomys*. Undoubtedly it is closely allied to *Arizona*, as Klauber (1946) infers, and it is not difficult to see how the premaxillary bone evolved from an ancestor not unlike existing *Pituophis*. The median projection of the premaxillae is rather variable in the latter genus, as a matter of fact, and within the species *catenifer* there are various degrees of modification. In the third row from the top in figure 3, two extremes for

Pituophis are represented, with the premaxilla of *Arizona* to the right for comparison. A close parallel in the condition of the premaxilla in *Pituophis* is found in the Asiatic *Coluber spinalis*.

Pope (1935) mentions that this snake inhabits arid regions, despite the fact that it is more abundant in the vicinity of water. It is uncertain whether its habits resemble those of *Pituophis* or *Arizona*, but inferences from the shape of the premaxilla suggest that its ecological requirements might be nearly intermediate between those of the two latter genera. It is virtually certain that *spinalis* is more specialized in its habits than other Eurasian or American snakes currently referred to *Coluber*.

The premaxillary bone of a few natricine snakes has been examined with the hope that it might throw some light on the validity of current arrangements. *Natrix* and *Thamnophis* are readily separable as far as most species are concerned, but a few species are perplexing and could be referred to one genus or the other unless great emphasis is placed on the nature of the anal scute. As so often happens in such instances, however, the variations in the shape of the premaxilla preclude the use of simple statements to describe the differences. The few species of *Natrix* that have been examined tend to have somewhat more pronounced lateral projections on the premaxilla than are usually encountered in *Thamnophis*, but such supposedly annectant species as *rufipunctatus* (long known as *angustirostris*) could as readily be referred to one genus as the other on the basis of premaxillary characters. It is noteworthy, nevertheless, that the premaxilla has a characteristic shape in the two genera, although too few specimens have been examined to warrant the statement that all Natricinae are so characterized. Moreover, something of an approach to the condition seen in *Thamnophis* is observable in *Elaphe*.

Some extremes in specialization are depicted in figure 3, wherein it may be noted, for example, that the lateral processes of the premaxilla are greatly reduced in a South American specimen of *Oxybelis aeneus aeneus*, and virtually lacking in a

Mexican example of the more specialized race *O. a. auratus*. An extreme modification along quite different lines (see fig. 3) is exemplified in the premaxilla of the hog-nosed snake, *Heterodon*.

It is plain, however, that premaxillary characters are useful in elucidating relationships, despite the disadvantages that result from the qualitative nature of the differences. Moreover, there are, of course, individual differences that must be taken into account when comparisons of species or genera are attempted. On the whole the variations, especially at the front of the bone, within a single species are not extensive. The posterior processes, where the premaxilla is attached to the septomaxilla and the nasal, may be single, bifurcated, or even with each branch secondarily bifurcated (as represented by *Salvadora h. deserticola* in fig. 2), and are subject to frequent modification, possibly of ontogenetic but not of phylogenetic significance. All

three conditions occur within a single species.

Needless to say, it is preferable to examine the entire skull rather than a single element of it. Unfortunately it is not always possible to obtain skulls since some museums object to having the entire cranium removed from the skin of preserved specimens belonging to rare species. The premaxilla, however, can be examined from the ventral aspect in most species by the simple expedient of removing the connective tissue that covers the bone behind the rostral at the front of the mouth. In most instances the skin on the snout can be peeled from the premaxilla without seriously distorting the shape of the rostral, and the bone can be examined *in situ*. Often the information gained supplements that derived from a study of the hemipenis, or it may prove to be of greater importance. Premaxillary characters have an additional advantage over the hemipenis in that they are not confined to one sex.

SUMMARY

1. The genus *Leptodrymus* erected by Amaral in 1927 should be reinstated for the species *pulcherrimus*, since its superficial resemblances to snakes in *Salvadora* are not accompanied by similarities in penial, premaxillary, and scale characters. Various peculiarities serve to separate *Leptodrymus* from species in other genera, particularly the symmetrical arrangement of spines on the hemipenis, two of them greatly enlarged with the sulcus spermaticus in the middle. Moreover, the presence of three postoculars in *pulcherrimus* serves to differentiate the species from the allied genera.

2. The results of a brief survey of premaxillary characters point to their usefulness in systematic work. The shape of the premaxilla characterizes the snakes in the genus *Salvadora*, and use of the bone may be of aid in delineating other subfamily, generic, or infrageneric groups. Parallel modifications of the premaxilla in some burrowing snakes are pointed out, although it is plain that these do not seriously obscure the inferences with respect to relationships or phylogenies that may be drawn from comparisons of premaxillae.

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