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INTRODUCTION

ABSTRACT

THE SALIVARY GLANDS of about 180 species, representing some 120 genera, of snakes were examined histologically, those of 71 genera for the first time. The supralabial and glands of Duvernoy are described, and the intraspecific variation within these glands is summarized on the basis of a computer analysis.

The patterns of the similarity matrices were compared with the phylogenetic schemes proposed by various authors for the Colubridae.

The conclusions reached are as follows.

There is a trend toward the reduction of cell height with the development of a large Duvernoy's gland.

Duvernoy's glands in the Natricinae seem to be characterized by mucous cells.

The Xenoderminae have a unique arrangement of the supralabial glands, with an alternation of

The Colubridae are an obviously polyphyletic and unwieldy assemblage. They include some 70 per cent of all ophidian species, generally those forms that are not readily assignable to other families. Thus Romer (1956) recognized approximately 275 genera in the Colubridae. More than 250 of these were in the subfamily Colubrinae, and the remaining 25 were allocated to six other subfamilies. Other workers have subdivided the Colubridae differently, but the essential pattern, of one extremely large subfamily and several small subfamilies, has not varied. Although it was early recognized (Reinwardt, reported by Boie, 1826) that some colubrids are venomous, there are only a few reports (Fitz-Simons, 1921; Pope, 1958; Fitz-Simons and Smith, 1958) of fatal results from the bite of colubrid snakes. Reports by Bragg (1960), Brown (1939), Cowles (1941), Mason (1963), Melamud (MS), and Neill (1954) suggest that certain colubrid salivary secretions have an effect on prey; others (e.g., McAlister, 1963) disagree with such a suggestion.

Two factors have contributed to the confusion on this topic. First is the observation, often disregarded by students of snake venoms, that the venoms of various species possess highly specific, possibly prey-related activities. Next is the difficulty of obtaining adequate quantities of uncontaminated glandular secretions. Thus Alcock and Rogers (1902) attempted to study some of the

serous- and mucous-cell cords along the supralabial ridge.

Duvernoy's glands in the Homolopsinae form a gradually enlarging series, with the largest glands found in *Enhydris*.

The variation of the histological pattern in the Duvernoy's glands of the Colubridae clearly opposes the view that the Boiginae (Dipsadomorphinae of authors) are a natural group. The variation of pattern within the Colubrinae and the Boiginae is so great and the overlap so complete that no difference can be seen in the labial glands of the Colubridae that would support the separation of the Boiginae from the Colubridae in respect to this character.

The gland in *Dispholidus typus* is different from the other colubrid glands examined and can be readily differentiated from all other glands.

effects of colubrid venoms by injecting homogenates of parotid (Duvernoy's) gland. Hegeman (1961) employed oral swabbings to obtain colubrid venoms for study. Melamud (MS) employed both of these techniques and observed the effect of bites on the hind limb of mice. Yet none of these techniques is satisfactory for a detailed analysis of venom, particularly for studies sufficiently comparative to permit taxonomic interpretations. A technique has recently been developed for collecting venom from opisthoglyphous snakes in sufficient quantity and relatively uncontaminated by the secretions of other glands (Taub and Ellison, MS). This has increased the possibility of engaging in comparative chemical and physiological studies, and it is now of renewed interest to consider gland architecture and cell types and their distribution.

The present study was therefore undertaken to furnish a morphological basis for studies on the chemistry and effects of colubrid venoms. The survey includes some 180 species belonging to 120 genera. The histology of the supralabial and glands of Duvernoy was examined in detail, and several of their characteristics were evaluated and ranked on a weak ordered scale. An I.B.M. 7044 computer was used for tabulating those species with identical evaluations of the same criteria. These tabulations form the basis for a discussion of the observed patterns among the colubrid glands.

ACKNOWLEDGMENTS

I wish to thank Dr. Carl Gans for his support and guidance throughout this study. Dr. Elazar Kochva was also of very great assistance. He lent for study serial sections of entire heads of snakes (identified by E.K. preceding his numbers).

I also wish to thank the curators and staffs of the following museums who permitted me to dissect specimens in their care and to remove tissue for histological examination: Dr. Charles M. Bogert and Dr. Richard G. Zweifel, of the American Museum of Natural History (A.M.N.H.); Mr. Neil D. Richmond of the Carnegie Museum (C.M.); Dr. Robert F. Inger and Mr. Hymen Marx, of the Field Museum of Natural History (C.N.H.M.); and Dr. Charles Walker, of the University of Michigan Museum of Zoology (U.M.M.Z.). The majority of the other specimens that were used are deposited in the collection of Dr. Carl Gans (C.G.) at the State University of New York at Buffalo, and a few are in my personal collection (A.M.T.). The Zoological Society of London was kind enough to donate

through Dr. Gans a live specimen of *Homalopsis buccata*.

I am deeply in debt to the staff of the Computer Center, State University of New York at Buffalo, for their assistance, particularly Mr. R. Campbell for the development of the computer program and Mr. D. Didising for general advice.

It is a pleasure to acknowledge the technical assistance of the Misses G. Franklin and R. Dessel. I wish also to thank the many other persons who discussed this problem with me and have given freely of their time to assist me in this project. Mr. Herbert I. Rosenberg has been most helpful, both in discussing various aspects of the work and in giving freely of his time to expedite various phases.

This work was done while I was a graduate student at the State University of New York at Buffalo and was supported by a United States Public Health Service Pre-doctoral Fellowship, GPM 19119, from the Institute of General Medical Sciences, National Institutes of Health.

MATERIALS AND METHODS

Appendix 1 lists the specimens examined, the museum number or the number as catalogued in a personal collection, and the locality data, combined with a species index to literature reports of the histology or anatomy of the colubrid salivary glands. Specimens listed in Appendix 1 from the literature are cited by the name used by the original author, followed by the name in use today. Specimens obtained from museums are generally listed under the name by which they are identified in the museum catalogue, again followed by any nomenclatorial change. Table 1 presents raw data recorded for each gland and used in the computer analysis. References in the text are always to the most nearly current name.

It was also possible to examine the histology of the anterior temporal, Harderian, nasal, posterior, infralabial, sublingual, and temporomandibular glands in a few of the forms that are listed in Appendix 1. The venom glands from representatives of all four groups of venomous snakes were examined

for comparison with the glands of colubrids.

TREATMENT OF FRESH MATERIAL

Glands from freshly killed or recently dead (less than 12 hours) specimens were used, and the specimens were deposited in the collection of Carl Gans at the State University of New York at Buffalo.

Animals to be killed were anesthetized with ethyl ether, chloroform, or Halothane® (Ayerst Laboratories). The glands were exposed through an incision through the oral mucosa between the maxilla and the supralabial scales. The skin was dissected free and reflected over the parietal and supraorbital regions. This operation exposes the gland in those forms in which the Duvernoy's gland is well developed and makes easy the dissection of the gland from the head.

In the forms in which the gland is not well developed and in those forms that lack Duvernoy's gland, the supralabial glands usually are closely attached to the overlying skin but, with care, can be dissected free.

This dissection procedure was adopted to preserve the skin intact, maintaining those meristic characters that form the basis for the usual taxonomic decisions.

The glands, after removal, were fixed in one of the following solutions: freshly redistilled acrolein (10% in xylene); Bouin's fluid; 10 per cent formalin; formal-saline (10% formalin in 0.85% NaCl); Helly's fluid; and Zenker's fluid. The acrolein-fixed materials were postfixed in cold, HgCl₂-saturated xylol and dehydrated in a mixture of equal parts of absolute methyl alcohol and ethylene glycol monoethyl ether at 4° C. The dehydrated tissue was allowed to reach room temperature and then infiltrated with filtered polyethylene glycol 400 distearate (Ruger Chemical Company) dissolved in trichloroethylene. Ten per cent increments of wax concentration were employed, and the tissue was embedded in fresh, pure polyester wax. Sections, 2 μ to 10 μ in thickness, were cut in the cold (10° C.). Most of this material was stained with hematoxylin and eosin, but some sections were stained with Cason's stain.

The tissues from the other fixatives were washed and dehydrated in the usual manner. The tissue was cleared in cedarwood oil for several days before it was infiltrated with 52° to 55° paraffin, and embedded in 60° to 62° paraffin. The paraffin-embedded material was sectioned serially at a thickness of 10 μ. This material was stained with hematoxylin and eosin.

TREATMENT OF MUSEUM SPECIMENS

In order to expand greatly the comparative aspects of the study, a method was selected (see Roth and Gans, 1960) that permitted the sampling of routinely preserved specimens already in museum collections. Permission was obtained from several curators to dissect material in their care and to remove the glands for histological study. All such tissues are here identified by specimen number to permit future workers to verify the identification.

A major difficulty of all comparative studies is the identification of the animal from which the material was obtained. Such identification is particularly important when previous work is being interpreted. Names, particularly of tropical species, are still in a

state of flux, which reflects our inadequate knowledge of the biological situation. Several of the older generic names, such as *Coluber* and *Dipsas*, represent catch-all categories used indiscriminately to include species that are now believed to belong in many distinct genera. The names used by previous workers have been checked, and the currently accepted names are given in Appendix 1. Very probably changes have been made of which I am not aware. Beyond the purely nomenclatorial issue, there is the far more basic question of whether the material was correctly identified originally; generally speaking, there is no way to resolve this question.

Glands from preserved museum specimens were removed as described above, and the tissue was placed in 3 per cent potassium dichromate for two weeks (Roth and Gans, 1960). It was then rinsed with 30 per cent ethyl alcohol and dehydrated over a period of a few days. After dehydration, the tissue was cleared with cedarwood oil for from one to three weeks. The tissue was then infiltrated, embedded, and sectioned as described for the other paraffin-embedded material. All this material was stained with hematoxylin and eosin.

OBSERVATION AND ANALYSIS

Photomicrographs were taken with a 35-mm. camera back for an AO Microstar series 10 microscope. A green (Wratten 58B) filter was used to improve the contrast of hematoxylin- and eosin-stained slides.

Classical terms were most useful in histological definitions of the secretory epithelium. Glands were classified as mucous, serous, or mixed in the sense discussed by Munger (1964). With the stains employed in this study, serous cells had an acidophilic cytoplasm, whereas the cytoplasm in mucous cells was basophilic.

The histological characteristics of each gland were evaluated and ranked on 13 criteria as follows:

I. CAPSULE THICKNESS

1. Thin
2. Moderate
3. Heavy
4. Very heavy

II. NUMBER OF TRABECULAE

1. Few
2. Moderate

TABLE 1
EVALUATIONS OF GLANDS EXAMINED

Specimen	Capsule Thickness	Trabeculae Number	Trabeculae Thickness	Cell Shape	Lumen Frequency	Storage Space	Mucous Cells in Duvernoy's Gland	Mucous Cells Associated with Duvernoy's Gland	Vascularity	Cell Height (Size Class)	Cell Width (Size Class)	Nuclear Height (Size Class)	Nuclear Width (Size Class)	Duvernoy's Gland	Absent
A.M.N.H. No. 88335, <i>Abastor erythrogrammus</i>	2	2	3	2	3	7	8	1	3	44	15	9	8	—	—
U.M.M.Z. No. 123169, <i>Abastor erythrogrammus</i>	3	2	3	2	4	21	4	1	3	54	18	11	8	—	—
A.M.N.H. No. 34620, <i>Achalatus spinalis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	x	x
C.G. No. 2541, <i>Achrochordus javanicus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A.M.N.H. No. 2917, <i>Ahaetulla fasciolata</i>	2	2	2	2	4	18	1	1	3	40	15	8	8	—	—
A.M.N.H. No. 43383, <i>Ahaetulla mycterizans</i>	2	2	3	2	4	17	1	2	3	51	15	8	8	—	—
C.G. No. 2710, <i>Ahaetulla mycterizans</i>	2	2	2	2	4	22	1	1	2	54	17	13	9	—	—
A.M.N.H. No. 71525, <i>Ahaetulla prasina</i>	3	2	2	2	3	22	1	1	3	36	18	9	8	—	—
C.G. No. 2778, <i>Ahaetulla prasina</i>	2	3	2	2	4	29	1	1	3	58	18	11	16	—	—
C.M. No. 1332, <i>Alsophis portoricensis</i>	3	2	3	2	3	—	1	1	4	33	18	11	9	—	—
C.M. No. 28126, <i>Alsophis portoricensis</i>	3	3	3	2	4	20	1	1	2	33	15	11	8	—	—
C.M. No. 34178, <i>Alsophis vudi</i>	3	2	4	2	—	—	1	1	—	—	—	—	—	—	—
A.M.N.H. No. 85686, <i>Amphiesma mairi</i>	1	2	2	2	3	18	8	2	3	51	17	11	15	—	—
C.M. No. 9253, <i>Aparallactus modestus</i>	1	2	2	2	3	—	1	2	3	47	18	11	11	—	—
A.M.N.H. No. 85233, <i>Arizona elegans</i>	—	—	—	—	—	—	6	—	—	—	—	—	—	x	x
U.M.M.Z. No. 71967, <i>Arizona elegans</i>	—	—	—	—	—	—	6	—	—	—	—	—	—	x	x
U.M.M.Z. No. 61199, <i>Boaedon virgatus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C.M. No. 9247, <i>Boiga blandingi</i>	3	3	4	2	2	24	1	2	3	54	15	11	11	—	—
C.M. No. 2138, <i>Boiga dendrophila latifasciata</i>	3	3	2	2	4	42	1	1	3	51	18	8	12	—	—
A.M.N.H. No. 86559, <i>Boiga dendrophila</i>	4	3	4	2	5	20	1	1	3	33	15	8	9	—	—
C.M. No. 22050, <i>Boiga fusca</i>	2	3	3	2	4	20	1	1	3	33	15	11	11	—	—
C.M. No. 6819, <i>Boiga pulverulenta</i>	4	3	4	2	2	23	1	1	3	36	15	8	8	—	—
C.M. No. 9304, <i>Bothrophthalmus lineatus</i>	1	1	1	2	3	8	9	1	2	22	10	8	8	—	—
C.G. No. 2438, <i>Brachyophis revoili</i>	3	2	3	2	5	36	1	1	2	36	15	8	8	—	—
A.M.N.H. No. 2878, <i>Calamaria schlegelii</i>	2	1	2	3	1	—	1	1	—	—	—	—	—	—	—
A.M.N.H. No. 24535, <i>Calamaria septentrionalis</i>	2	2	3	—	—	—	6	1	—	—	—	—	—	—	—
C.G. No. 2715, <i>Cerberus rhynchops</i>	R.	4	3	4	5	41	1	1	3	33	15	9	9	—	—
	L.	4	3	2	4	30	1	1	3	40	15	11	11	—	—
C.M. No. 33770, <i>Chironius carinatus</i>	2	3	3	2	5	62	1	1	3	47	15	9	9	—	—
C.G. No. 2545, <i>Chrysopelea ornata</i>	3	3	3	2	3	16	1	1	3	33	26	8	8	—	—

TABLE 1—(Continued)

Specimen	Capsule Thickness	Taberculae Number	Taberculae Thickness	Cell Shape	Lumen Frequency	Storage Space	Mucous Cells in Duvernoy's Gland	Mucous Cells Associated with Duvernoy's Gland	Vascularity	Cell Height (Size Class)	Cell Width (Size Class)	Nuclear Height (Size Class)	Nuclear Width (Size Class)	Duvernoy's Gland
C.M. No. 2567, <i>Chrysopelea paradisi</i>	2	3	2	2	4	22	1	1	3	40	18	9	11	—
U.M.M.Z. No. 62820, <i>Clelia clelia</i>	4	3	3	2	5	32	1	1	3	47	18	8	11	—
A.M.T. No. 1, <i>Coluber constrictor</i>	2	2	2	2	3	23	1	1	2	33	13	8	9	—
E. K. No. M2, <i>Coluber ravergieri</i>	1	2	2	2	3	8	1	1	2	40	—	—	—	—
U.M.M.Z. No. 84486A, <i>Coniophanes fissidens</i>	3	3	4	2	4	20	8	1	3	47	15	11	11	—
U.M.M.Z. No. 57963, <i>Coniophanes fissidens punctularis</i>	2	2	2	2	4	27	1	2	3	44	15	9	11	—
C.G. No. 2619, <i>Coniophanes imperialis</i>	2	2	3	2	—	—	1	—	3	—	—	—	—	—
A.M.N.H. No. 66337, <i>Conophis vittatus</i>	2	3	2	—	—	—	1	1	4	—	—	—	—	—
A.M.N.H. No. 75874, <i>Conopsis biserialis</i>	2	3	3	2	3	43	1	1	3	47	18	15	8	—
A.M.N.H. No. 21801, <i>Coronella austriaca</i>	2	3	3	2	4	—	1	1	2	—	—	—	—	—
M.C.Z. No. 71870, <i>Crotaphopeltis hotamboia</i>	2	2	2	—	—	—	1	1	3	—	—	—	—	—
M.C.Z. No. 71871, <i>Crotaphopeltis</i> sp.	—	—	—	—	—	—	6	—	—	—	—	—	—	x
A.M.N.H. No. 73419, <i>Cyclocorus lineatus</i>	2	3	3	2	5	37	1	1	3	33	15	8	11	x
C.G. No. 2551, <i>Cylindrophis rufus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A.M.N.H. No. 2835, <i>Dendrelaphis pictus</i>	2	2	3	2	4	22	1	1	3	44	20	11	8	—
U.M.M.Z. No. 124069, <i>Dendrophidion percarinatus</i>	2	3	2	—	—	—	1	—	3	—	—	—	—	—
C.G. No. 162, <i>Diadophis punctatus</i>	2	1	1	2	—	—	7	1	2	—	—	—	—	—
A.M.N.H. No. 75952, <i>Dinodon rufosonatum</i>	2	2	3	2	4	35	1	1	2	36	15	9	8	—
A.M.N.H. No. 12470, <i>Dipsadoboa unicolor</i>	2	3	3	2	5	36	1	1	2	38	15	15	11	—
U.M.M.Z. No. 73030, <i>Dipsas brevifacies</i>	1	1	1	2	1	—	1	1	1	33	18	11	11	—
U.M.M.Z. No. 62794, <i>Dipsas ináica bucephala</i>	3	3	4	2	3	—	6	1	3	—	—	—	—	—
U.M.M.Z. No. 92048, <i>Dipsas latifrontalis</i>	2	2	2	—	—	10	1	3	—	—	—	—	—	—
A.M.T. No. 5, <i>Dispholidus typus</i>	4	4	4	3	5	48	1	1	3	25	18	9	9	—
C.M. No. 6340, <i>Dispholidus typus</i>	1	4	2	2	5	47	1	1	3	22	17	8	8	—
C.M. No. 285, <i>Dromicus andrae nebulatus</i>	2	3	3	—	4	—	1	1	—	—	—	—	—	—
A.M.N.H. No. 51393, <i>Dromicus parvisfrons protenus</i>	2	2	2	2	3	24	1	1	3	33	18	8	8	—
A.M.N.H. No. 51396, <i>Dromicus</i> sp.	1	2	2	2	2	18	1	1	3	36	15	9	9	—
U.M.M.Z. No. 116544, <i>Dryadophis dorsalis</i>	2	2	2	2	3	33	1	1	3	40	15	8	8	—

TABLE 1—(Continued)

Specimen	Capsule Thickness	Trabeculae Number	Trabeculae Thickness	Cell Shape	Lumen Frequency	Storage Space	Mucous Cells in Duvernoy's Gland	Mucous Cells Associated with Duvernoy's Gland	Vascularity	Cell Height (Size Class)	Cell Width (Size Class)	Nuclear Height (Size Class)	Nuclear Width (Size Class)	Duvernoy's Gland
U.M.M.Z. No. 71204, <i>Dryadophis melanolomus alternatus</i>	3	3	4	2	—	—	1	1	3	—	—	—	—	—
A.M.N.H. No. 75965, <i>Drymobius boddaerti</i>	2	3	3	2	2	19	1	1	3	44	15	11	11	—
A.M.N.H. No. 36176, <i>Drymobius margaritiferus</i>	3	3	2	—	—	—	1	1	—	—	—	—	—	—
U.M.M.Z. No. 122050, <i>Drymobius margaritiferus</i>	1	2	2	2	—	—	6	1	2	47	15	8	8	—
U.M.M.Z. No. 67701, <i>Drymarchon corais couperi</i>	1	1	2	2	3	—	8	1	3	—	—	—	—	—
A.M.N.H. No. 2904, <i>Dryocalamus subannulatus</i>	3	3	4	2	4	19	1	2	3	40	11	11	8	—
C.G. No. 2228, <i>Duberria lutrix</i>	2	2	1	2	2	11	1	2	1	39	25	15	17	—
A.M.N.H. No. 39187, <i>Duberria lutrix shirana</i>	1	2	2	2	3	31	1	1	2	47	18	15	13	—
A.M.N.H. No. 68159, <i>Eurenis decemlineata</i>	—	—	—	—	—	—	6	—	—	—	—	—	—	x
C.G. No. 2889, <i>Elaphe carinata</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	x
U.M.M.Z. No. 67239, <i>Elaphe longissima</i>	—	—	—	—	—	—	6	—	—	—	—	—	—	x
C.G. No. 2886, <i>Elaphe mandarinus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	x
C.G. No. 2885, <i>Elaphe moellendorffi</i>	—	—	—	—	—	—	6	—	—	—	—	—	—	x
U.M.M.Z. No. 112068, <i>Elaphe obsoleta</i>	—	—	—	—	—	—	6	—	—	—	—	—	—	x
U.M.M.Z. No. 68341A, <i>Elaphe quadrivirgata</i>	—	—	—	—	—	—	6	—	—	—	—	—	—	x
C.G. No. 2887, <i>Elaphe radiata</i>	—	—	—	—	—	—	6	—	—	—	—	—	—	x
U.M.M.Z. No. 124026, <i>Elaphe subocularis</i>	—	—	—	—	—	—	6	—	—	—	—	—	—	x
C.G. No. 2888, <i>Elaphe taenurus</i>	—	—	—	—	—	—	6	—	—	—	—	—	—	x
U.M.M.Z. No. 118522, <i>Elaphe triaspis intermedia</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	x
C.G. No. 2517, <i>Enhydriis bocourti</i>	4	4	4	2	3	18	1	1	3	44	18	11	11	—
C.G. No. 2550, <i>Enhydriis bocourti</i>	4	4	4	2	3	—	1	1	3	—	—	—	—	—
C.G. No. 2652, <i>Enhydriis enhydriis</i>	3	3	4	2	4	30	1	1	3	26	15	6	8	—
C.G. No. 2653, <i>Enhydriis enhydriis</i>	3	3	4	2	5	24	1	2	3	33	18	6	8	—
C.G. No. 2788, <i>Enhydriis</i> sp.	3	3	4	2	3	22	1	1	3	62	18	9	8	—
C.G. No. 2787, <i>Erpeleon tentaculatum</i>	4	1	3	2	3	—	1	2	1	—	—	—	—	—
C.M. No. 1842, <i>Erythrolamprus aesculapii</i>	2	3	3	2	3	13	8	1	3	44	15	11	11	—
U.M.M.Z. No. 57924, <i>Erythrolamprus bizona</i>	3	3	3	2	4	27	1	1	3	58	15	11	11	—
U.M.M.Z. No. 62728, <i>Erythrolamprus venustusissimus</i>	2	3	3	2	2	—	1	1	2	29	11	9	9	—

TABLE 1—(Continued)

Specimen	Capsule Thickness	Trabeculae Number	Trabeculae Thickness	Cell Shape	Lumen Frequency	Storage Space	Mucous Cells in Duvernoy's Gland	Mucous Cells Associated with Duvernoy's Gland	Vascularity	Cell Height (Size Class)	Cell Width (Size Class)	Nuclear Height (Size Class)	Nuclear Width (Size Class)	Duvernoy's Gland	Duvernoy's Gland Absent
A.M.N.H. No. 88338, <i>Farancia abacura</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x
U.M.M.Z. No. 109335, <i>Farancia abacura</i>	4	3	5	2	3	16	6	1	3	47	15	8	8	1	—
C.N.H.M. No. 71699, <i>Fimbrios klossi</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x
C.N.H.M. No. 67271, <i>Fordonia leucobalia</i>	2	3	3	2	4	19	1	1	3	26	15	9	11	—	—
A.M.N.H. No. 10097, <i>Gastropyx smaragdina</i>	3	3	3	2	4	19	1	1	2	40	11	11	8	—	—
A.M.N.H. No. 19773, <i>Geophis multitorques</i>	2	3	3	—	—	—	6	2	3	—	—	—	—	—	—
C.N.H.M. No. 138677, <i>Gonyophis margaritatus</i>	2	2	3	2	4	19	1	1	2	—	—	—	—	—	—
U.M.M.Z. No. 116111, <i>Haldea striatula</i>	1	1	2	2	4	24	1	1	3	—	—	—	—	—	—
A.M.N.H. No. 81458, <i>Helicops angulatus</i>	3	3	3	—	—	—	1	1	3	—	—	—	—	—	—
C.M. No. 31417, <i>Helicops leopardina</i>	3	3	3	2	4	34	1	1	3	40	18	11	8	—	—
C.M. No. 2038, <i>Helicops polylepis</i>	2	3	3	2	4	29	1	1	3	54	18	11	11	—	—
U.M.M.Z. No. 35126, <i>Heterodon nasicus</i>	2	2	3	2	4	55	9	1	3	62	18	11	8	—	—
U.M.M.Z. No. 70750, <i>Heterodon platyrhinos</i>	3	2	3	2	4	29	1	1	2	—	—	—	—	—	—
C.G. No. 2516, <i>Homalopsis buccata</i>	2	2	3	2	3	12	1	1	3	36	11	10	10	—	—
C.G. No. 2548, <i>Homalopsis buccata</i>	3	3	4	2	4	14	1	1	3	22	11	8	8	—	—
C.G. No. 2857, <i>Homalopsis buccata</i>	2	2	3	2	3	15	1	1	3	33	15	8	9	—	—
A.M.N.H. No. 88401, <i>Hydrodynastes bicincta</i>	2	3	3	2	4	—	1	1	3	—	—	—	—	—	—
A.M.N.H. No. 55299, <i>Hydrops marii callositicus</i>	2	3	4	2	4	31	1	1	3	33	18	11	11	—	—
C.G. No. 2483, <i>Hypsiglena torquata deserticola</i>	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
C.M. No. 25897, <i>Imantodes cenchoa</i>	2	2	3	2	—	—	1	1	3	40	15	8	8	—	—
U.M.M.Z. No. 124170, <i>Imantodes cenchoa semifasciata</i>	2	3	3	2	3	16	1	1	3	44	11	8	6	—	—
A.M.N.H. No. 66555, <i>Lampropeltis calligaster</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x
U.M.M.Z. No. 74928, <i>Lampropeltis dohiana polyzona</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x
A.M.N.H. No. 36719, <i>Lampropeltis getulus boylii</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x
C.G. No. 2757, <i>Lampropeltis getulus holbrooki</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x
A.M.N.H. No. 15086, <i>Lampropeltis pyromelana</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x
C.M. No. 24929, <i>Lampropeltis rhombomaculata</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x
C.M. No. 2968, <i>Leimadophis almadensis</i>	2	2	3	2	3	6	1	1	3	—	—	—	—	—	—

TABLE 1—(Continued)

Specimen	Capsule Thickness	Trabeculae Number	Trabeculae Thickness	Cell Shape	Lumen Frequency	Storage Space	Mucous Cells in Duvernoy's Gland	Mucous Cells Associated with Duvernoy's Gland	Vascularity	Cell Height (Size Class)	Cell Width (Size Class)	Nuclear Height (Size Class)	Nuclear Width (Size Class)	Duvernoy's Gland
U.M.M.Z. No. 124283, <i>Leimadophis melanotus</i>	2	3	2	2	3	17	1	1	3	26	18	8	8	—
U.M.M.Z. No. 92027, <i>Leimadophis reginae</i>	1	3	2	2	2	—	1	1	3	54	15	11	8	—
C.M. No. 34842, <i>Leimadophis typhlus</i>	2	3	3	2	2	10	1	1	2	54	18	9	9	—
U.M.M.Z. No. 121276, <i>Leptodeira annulata</i>	3	3	3	2	4	30	1	1	2	44	13	15	11	—
U.M.M.Z. No. 120223, <i>Leptodeira latifasciata</i>	1	2	2	2	3	17	7	1	3	69	15	11	11	—
U.M.M.Z. No. 121547, <i>Leptodeira splendida</i>	2	3	3	2	4	30	1	1	2	44	18	9	15	—
U.M.M.Z. No. 114585, <i>Leptophis diplothropis</i>	3	3	3	2	4	25	1	1	3	47	15	8	8	—
C.M. No. 37259, <i>Leptophis richardi occidentalis</i>	2	3	3	2	4	36	1	1	3	47	11	11	8	—
U.M.M.Z. No. 51256, <i>Liophis cobella</i>	1	2	2	—	—	—	1	—	2	—	—	—	—	—
A.M.T. No. 4, <i>Liophis militaris</i>	2	3	2	2	2	—	1	—	2	—	—	—	—	—
A.M.N.H. No. 86754, <i>Lycodon aulicus</i>	1	2	2	2	4	39	1	2	3	40	12	11	9	—
C.M. No. 2455, <i>Lycodon aulicus</i>	2	3	3	2	3	—	1	1	3	—	—	—	—	—
C.M. No. 31419, <i>Lystrophis dorbignyi</i>	3	3	3	2	4	28	1	1	3	26	18	8	15	—
A.M.N.H. No. 34520, <i>Macropisthodon rudis</i>	2	1	2	2	3	44	1	1	3	54	15	8	8	—
C.G. No. 2185, <i>Malpolon monspessulana</i>	3	1	2	2	2	9	1	1	3	44	15	8	13	—
U.M.M.Z. No. 69661, <i>Masticophis bilineatus</i>	1	1	2	2	4	28	1	1	2	—	—	—	—	—
U.M.M.Z. No. 116548, <i>Masticophis mentovarius</i>	2	3	3	2	4	34	4	1	3	54	15	11	8	—
U.M.M.Z. No. 123469, <i>Masticophis taeniatus ornatus</i>	2	2	3	2	4	21	7	1	3	47	18	11	11	—
A.M.N.H. No. 63769, <i>Meheyla poensis</i>	2	3	2	2	4	14	1	1	3	44	16	11	8	—
A.M.N.H. No. 12449, <i>Miodon gabonensis collaris</i>	3	2	4	2	—	37	1	1	2	40	15	12	8	—
C.N.H.M. No. 97649, <i>Myron richardsoni</i>	2	2	2	2	2	4	2	1	4	54	15	11	11	—
A.M.N.H. No. 11913, <i>Natriciteres olivacea</i>	2	2	4	2	—	—	2	1	—	47	17	15	11	—
C.M. No. 36936, <i>Natrix cycloption floridana</i>	3	3	3	2	—	—	1	1	—	—	—	—	—	—
U.M.M.Z. No. 106289, <i>Natrix cycloption floridana</i>	3	3	4	2	4	27	8	1	3	40	18	11	11	—
U.M.M.Z. No. 103183, <i>Natrix erythrogaster erythrogaster</i>	3	3	4	2	4	25	9	1	3	62	15	8	8	—
U.M.M.Z. No. 77734, <i>Natrix rhombifera</i>	3	3	4	2	4	27	4	1	3	29	15	9	8	—
U.M.M.Z. No. 84144, <i>Natrix sipedon pleuralis</i>	3	3	4	2	3	22	9	1	3	68	11	8	8	—

TABLE 1—(Continued)

Specimen	Capsule Thickness	Trabeculae Number	Trabeculae Thickness	Cell Shape	Lumen Frequency	Storage Space	Mucous Cells in Duvernoy's Gland	Mucous Cells Associated with Duvernoy's Gland	Vascularity	Cell Height (Size Class)	Cell Width (Size Class)	Nuclear Height (Size Class)	Nuclear Width (Size Class)	Duvernoy's Gland Absent
U.M.M.Z. No. 110420, <i>Natrix taxispilota</i>	2	3	2	2	4	20	2	1	3	68	21	7	15	—
A.M.N.H. No. 34592, <i>Oligodon ornatus musyi</i>	—	—	—	—	—	—	1	—	—	—	—	—	—	—
C.G. No. 2378, <i>Ophedryx vernalis</i>	3	2	3	2	3	—	1	1	3	47	15	11	8	—
A.M.N.H. No. 33928, <i>Opisthotropis latouchi</i>	2	2	2	2	—	—	1	2	3	—	—	—	—	—
C.M. No. 2027, <i>Oxybelis fulgidus</i>	3	2	3	2	4	31	1	1	3	54	18	11	15	—
A.M.N.H. No. 25185, <i>Oxyrhopus petola</i>	3	2	3	2	2	5	1	1	2	47	15	11	11	—
U.M.M.Z. No. 80428, <i>Oxyrhopus petola</i>	1	1	2	2	3	19	1	1	2	36	15	8	8	—
A.M.N.H. No. 34606, <i>Pareus stanleyi</i>	2	2	3	2	—	—	6	1	3	—	—	—	—	—
A.M.N.H. No. 75314, <i>Philodryas schotti</i>	2	3	2	—	—	—	1	1	2	—	—	—	—	—
U.M.M.Z. No. 124606, <i>Pituophis catenifer deserticola</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	x
U.M.M.Z. No. 124765, <i>Pliocercus elapoides</i>	2	2	2	2	2	19	1	1	3	36	15	8	11	—
A.M.N.H. No. 86769, <i>Psammodynastes pulverulentus</i>	2	2	2	2	3	32	2	1	3	54	17	15	8	—
A.M.N.H. No. 81998, <i>Psammophis schokari</i>	2	2	4	2	3	25	1	1	3	58	22	8	11	—
C.M. No. 37529, <i>Psammophis sibilans sibilans</i>	2	3	3	—	2	—	1	1	2	—	—	—	—	—
C.G. No. 2522, <i>Psammophylax triaenatus multisquamis</i>	2	1	2	2	3	17	1	1	1	40	15	6	11	—
A.M.N.H.— <i>Pseudaspis cana</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	x
A.M.N.H. No. 74781, <i>Pseudoeryx plicatilis</i>	5	4	5	2	3	25	1	1	3	36	11	11	6	—
A.M.N.H. No. 27753, <i>Pseudoxenodon bambusicola</i>	1	3	2	2	3	16	1	1	1	44	29	9	8	—
A.M.N.H. No. 12791, <i>Pseudoxenodon sinensis</i>	2	3	4	2	4	17	1	1	3	33	15	8	11	—
A.M.N.H. No. 78990, <i>Pseustes sulphureus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	x
C.G. No. 2786, <i>Ptyas mucosus</i>	4	3	3	2	1	20	1	1	3	47	18	11	11	—
C.G. No. 2658, <i>Rhabdophis subminata</i>	3	2	2	1	2	8	8	1	2	32	15	11	11	—
C.M. No. 34953, <i>Rhabdophis tigrina lateralis</i>	2	3	4	2	4	19	7	1	3	25	15	8	8	—
A.M.N.H. No. 63891, <i>Rhadinaea flavilata</i>	1	2	2	2	4	21	8	1	3	51	8	8	11	—
A.M.N.H. No. 73833, <i>Rhamphophis oxyrhynchus rostratus</i>	2	3	2	2	3	6	1	1	3	34	11	7	9	—
A.M.N.H. No. 55610, <i>Rhinobothryum lentiginosum</i>	3	3	4	2	4	12	1	1	3	—	—	—	—	—

TABLE 1—(Continued)

Specimen	Capsule Thickness	Trabeculae Number	Trabeculae Thickness	Cell Shape	Lumen Frequency	Storage Space	Mucous Cells in Duvernoy's Gland	Mucous Cells Associated with Duvernoy's Gland	Vascularity	Cell Height (Size Class)	Cell Width (Size Class)	Nuclear Height (Size Class)	Nuclear Width (Size Class)	Duvernoy's Gland
A.M.N.H. No. 75177, <i>Rhinocheilus leonti leonti</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	x
A.M.N.H. No. 80181, <i>Salvadora grahamiae</i>	2	2	2	2	2	21	3	1	2	44	18	9	9	—
U.M.M.Z. No. 123474, <i>Salvadora grahamiae</i>	3	3	3	2	2	—	1	1	3	—	—	—	—	—
U.M.M.Z. No. 114427, <i>Salvadora mexicana</i>	1	2	2	2	3	17	1	1	2	51	15	9	9	—
A.M.N.H. No. 12147, <i>Scaphiophis albofuniculatus</i>	—	—	—	—	—	—	6	—	—	—	—	—	—	x
A.M.N.H. No. 70239, <i>Scaphiodontophis annulatus</i>	—	—	—	—	—	—	6	—	—	—	—	—	—	x
A.M.N.H. No. 64479C, <i>Sibon nebulata nebulata</i>	2	2	3	—	—	—	—	—	3	—	—	—	—	—
U.M.M.Z. No. 119749, <i>Sibon nebulata nebulata</i>	2	2	3	2	3	—	6	1	2	—	—	—	—	—
U.M.M.Z. No. 79678, <i>Sibynomorphus mikani newiardi</i>	3	3	4	2	4	24	1	1	3	29	11	8	8	—
A.M.N.H. No. 34534, <i>Sibynophis chinensis chinensis</i>	3	2	3	2	4	27	9	1	3	29	12	8	6	—
A.M.N.H. No. 85458, <i>Spalerosophis diadema</i>	3	1	1	—	—	—	1	2	—	—	—	—	—	—
U.M.M.Z. No. 121141, <i>Spilotes pullatus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	x
A.M.N.H. No. 85714, <i>Stegonotus modestus</i>	2	2	3	2	5	27	8	1	3	51	15	11	11	—
A.M.N.H. No. 69968, <i>Stenorrhina freminivilli</i>	3	3	4	2	4	25	1	1	3	47	26	11	11	—
C.G. No. 2377, <i>Stoeria occipitamaculata</i>	—	—	—	—	—	—	1	—	—	—	—	—	—	—
A.M.N.H. No. 75053, <i>Tachymenis chilensis</i>	2	3	2	—	—	—	1	—	—	—	—	—	—	—
U.M.M.Z. No. 107145, <i>Tamilla rubra</i>	2	2	2	2	4	20	1	2	2	28	22	11	8	—
E.K. No. M3, <i>Telescopus fallax</i>	2	2	3	—	—	—	1	1	2	—	—	—	—	—
A.M.N.H. No. 49926, <i>Telescopus semiannulatus</i>	1	2	2	2	2	17	1	1	1	40	18	8	10	—
U.M.M.Z. No. 69679, <i>Thamnophis cyrtopsis cyrtopsis</i>	3	3	3	2	4	25	5	1	2	61	15	9	8	—
U.M.M.Z. No. 122924, <i>Thamnophis elegans vagrans</i>	3	3	3	2	3	33	9	1	3	72	18	11	9	—
A.M.T. No. 2, <i>Thamophis sirtalis</i>	1	2	1	1	2	6	1	1	2	62	36	18	9	—

TABLE 1—(Continued)

Specimen	Capsule Thickness	Trabeculae Number	Trabeculae Thickness	Cell Shape	Lumen Frequency	Storage Space	Mucous Cells in Duvernoy's Gland	Mucous Cells Associated with Duvernoy's Gland	Vascularity	Cell Height (Size Class)	Cell Width (Size Class)	Nuclear Height (Size Class)	Nuclear Width (Size Class)	Duvernoy's Gland
U.M.M.Z. No. 61241, <i>Thelotornis kirtlandi</i>	3	3	4	—	4	—	1	1	—	—	—	—	—	—
C.N.H.M. No. 109763, <i>Trachischium tenuiceps</i>	2	2	2	—	1	—	1	2	1	—	—	—	—	—
A.M.N.H. No. 81153, <i>Tretanorhinus variabilis</i>	2	2	3	2	3	16	8	1	3	—	—	—	—	—
A.M.N.H. No. 66153, <i>Trimorphodon biscutatus</i>	2	3	3	2	4	42	1	1	4	40	15	11	11	—
U.M.M.Z. No. 123332, <i>Trimorphodon biscutatus</i>	3	3	4	2	4	34	1	1	3	44	13	9	6	—
U.M.M.Z. No. 118949, <i>Trimorphodon lau</i>	2	2	2	2	3	—	1	1	3	—	—	—	—	—
A.M.N.H. No. 56190, <i>Tropidodipsas sartorii sartorii</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	x
A.M.N.H. No. 49090, <i>Trypanurgos compressus</i>	2	3	3	2	3	16	1	1	3	44	18	15	15	—
A.M.N.H. No. 40988, <i>Uromacer catesbyi</i>	2	3	2	2	3	21	1	1	3	44	18	8	9	—
A.M.N.H. No. 84528, <i>Xenochrophis piscator</i>	2	3	3	2	4	23	9	1	2	58	18	11	11	—
C.G. No. 2646, <i>Xenochrophis piscator</i>	3	3	3	—	—	—	8	1	2	—	—	—	—	—
C.G. No. 2708, <i>Xenochrophis piscator</i>	3	2	4	2	—	—	4	1	—	58	15	11	9	—
C.G. No. 2709, <i>Xenochrophis piscator</i>	3	2	4	2	3	—	7	1	2	—	—	—	—	—
C.N.H.M. No. 67427, <i>Xenodermus javanicus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	x
C.M. No. 34818, <i>Xenodon merremi</i>	2	2	3	2	5	25	9	1	3	47	15	8	11	—
U.M.M.Z. No. 62986, <i>Xenodon merremi</i>	2	2	2	—	—	—	6	1	3	—	—	—	—	—
U.M.M.Z. No. 109056, <i>Xenodon newwedii</i>	3	3	4	—	2	—	1	1	3	—	—	—	—	—
A.M.N.H. No. 61598, <i>Zaocys dhumnades</i>	2	3	3	—	—	—	1	—	—	—	—	—	—	—

3. Many
4. Very many
- III. TRABECULAE THICKNESS
 1. Very thin
 2. Thin
 3. Moderate
 4. Heavy
 5. Very heavy
- IV. CELL SHAPE
 1. Pyramidal
 2. Columnar
 3. Cuboidal
 4. Other
- V. LUMEN FREQUENCY
 1. Absent
 2. Present in about 10 per cent of the tubules
 3. Present in about 50 per cent of the tubules
 4. Present in about 90 per cent of the tubules
 5. Present in over 90 per cent of the tubules
- VI. WIDTH OF STORAGE SPACE IN TUBULES
To facilitate comparison by computer all measurements have been expressed as size classes. Each size class is 0.5 μ , e.g., if the average storage space fell between 14.5 μ and 15.0 μ it was recorded as in size class 30. Size class 31 represents all those between 15.0 μ and 15.49 μ .
- VII. MUCOUS CELLS IN GLAND
 1. Absent
 2. Rare (less than one per high dry field)
 3. Occasional (one to two per high dry field)
 4. Few (two to five per high dry field)
 5. Common (seven to 10 per high dry field)
 6. Mixed gland (almost all of the lobules contain both serous and mucous cells)
 7. Mixed lobules—rare (fewer than one out of five lobules which contain both mucous and serous cells)
 8. Mixed lobules—few (one to two containing both serous and mucous cells)
 9. Mixed lobules—common (more than five lobules per high dry field that contain both serous and mucous cells)
- VIII. MUCOUS SUPRALABIAL GLAND ASSOCIATED WITH SEROUS DUVERNOY'S GLAND
 1. Yes
 2. No
- IX. VASCULARITY
 1. Slight
 2. Moderate
 3. High
 4. Very high
- X. CELL HEIGHT
Ranked in same manner as VI
- XI. CELL WIDTH

Ranked in same manner as VI

XII. NUCLEAR HEIGHT

Ranked in same manner as VI

XIII. NUCLEAR WIDTH

Ranked in same manner as VI

Representative examples of the histological patterns and some of the criteria are illustrated in plates 1 through 8. Although many sections gave a great deal of useful information, it was not feasible to illustrate each evaluation of the criteria, because these sections were not suitable for photography.

An I.B.M. 7044 computer was programmed to furnish several stages of data analysis. It tabulated those specimens with identical evaluations of the same criteria, calculated the ratio of cell height to cell width, the ratio of nuclear height to nuclear width, and the ratio of these two ratios.

To cite an example: the computer listed all specimens that had a thin capsule and few trabeculae; those that had a thin capsule and many trabeculae; and those that had a thin capsule and very many trabeculae. It next listed those that had a moderate capsule and few trabeculae, and so on. The ratios were ranked in numerical order in increments of 0.2 unit.

The computer was next used to prepare a series of 29 matrices. Twenty-eight of these matrices tabulated the occurrence of any pair of snakes as well as the occurrence of an unpaired specimen for each of the combinations of the following criteria: capsule thickness, number of trabeculae, trabeculae thickness, cell shape, frequency of lumen, amount of storage space in the tubules, occurrence and distribution of mucous cells in the Duvernoy's gland, and vascularity. One matrix tabulated the occurrence of all those specimens that had identical evaluations of capsule thickness and number of trabeculae. A second matrix was prepared for identical evaluations of capsule thickness and trabeculae thickness, and so on, for all possible combinations of the criteria.

A twenty-ninth matrix (the complete matrix) was the summation of all the previous matrices. This matrix was examined, in order to identify specimens that had been frequently grouped in identical categories. These groupings of species were then compared with the various arrangements of the

Colubridae proposed by Boulenger (1893–1896), Cope (1900), Dunn (1928), and Bogert (1940) and to other groupings that were suggested when this problem was discussed with specialists.

The individual matrices were utilized to permit the subtraction from the complete matrix of the contribution made by any pair or pairs of characters. The new matrices thus formed were compared with the complete matrix to ascertain if the change would allow the emergence of a clearer pattern. They were

also compared with the proposed colubrid phylogenies.

Scatter plots were made of capsule thickness as a function of the number of trabeculae, capsule thickness as a function of the trabecular thickness, and trabecular thickness as a function of the number of trabeculae. Regression lines were calculated by the method of least mean squares. The significance of the coefficient of correlation (r) was evaluated by Student's t -test (Croxtton, 1959, p. 312).

HISTORICAL REVIEW

VENOMOUS SNAKES attracted the early attention of scientists. The dramatic nature of snake bite insured a study of these animals and their venom apparatus. Since the first reports (Redi, 1664; Charas, 1669) on the venom glands of vipers, the venom apparatus of the truly poisonous snakes has been studied by many workers. Fontana (1781), Schlegel (1837), Mitchell (1860), Leydig (1873), Reichel (1883), Mitchell and Reichert (1886), and Noguchi (1909) are but a few of the authors who have considered this problem.

A very incomplete bibliography on animal venoms and venom glands (Harmon and Pollard, 1948) listed more than 4000 titles. A more recent and admittedly selective one restricted to snakes (Russell and Scharffenberg, 1964) listed more than 9000. There have been two recent symposia (Buckley and Porges, 1956; Keegan and Macfarlane, 1963), a major portion of which was devoted to the actions of snake venoms. In view of this volume of material, it became necessary to restrict the literature review in the present article to papers dealing primarily with the anatomy or histology of the glands of colubrid snakes.

Although Sarkar (1923) cited a paper by Thomas Smith (1818) as the earliest description of rear fangs, it is agreed (Stejneger, 1893; Phisalix, 1922) that Reinwardt, in a letter cited by Boïe (1826), was the first person to describe the presence of venom glands and fangs in a colubrid snake (*Homalopsis molurus* = *Cerberus rhynchops*). Thomas Smith (1818) discussed fangs in the cobra and in "a species of hydrus [*sic*] of Schneider." Although Sakar apparently mistook this *Hydrus* as representing a homalopsine rather than a hydrophiid, the description of the fang suggests that Smith probably described a member of the family Hydrophiidae.

The various names and homologies of the ophidian cephalic glands have been previously discussed (Taub, 1966). Taub demonstrated the absence of any possible homology between the mammalian parotid gland and the ophidian glands. Therefore he proposed that the ophidian gland previously called the

parotid be named "Duvernoy's gland" to prevent further confusion in the gland homologies.

Intermittently, there have been other reports on the oral and labial glands of snakes. Schlegel (1828) concluded that, since the structure of the parotid (Duvernoy's gland) of colubrid snakes is similar to the structure of other salivary glands, and since the bites of colubrid snakes are not fatal to man, these snakes are not truly venomous snakes. In a major work (1837) he rejected the separation of the opisthoglyphous Colubridae from the remainder of the family. Since 1837 the opinion of Schlegel has been decisive in relegating any study of these glands to a minor position.

In 1898 Oppel collected and summarized the conclusions of most previous workers (Cloquet, 1821; Meckel, 1826; Dugès, 1827; Duvernoy, 1832; Bachtold, 1843; Leydig, 1873; Reichel, 1883; Neimann, 1892; Bisogni, 1895, 1897; West, 1895; and Kathariner, 1898) on the oral and head glands of snakes. He did not cite the work of Duvernoy (1833) which contained observations on *Dipsas* (*Bungarus interruptus*: Oppel) and *Cerberus rhynchops*. Duvernoy (1833) described and figured the glands *in situ* from the following forms: *Cerberus rhynchops* (Schneider), *Coluber aesculapii* (Linné), *Coluber jaspideus* (Hermann), *Coluber jephrodes* (Hermann), and *Crotaphopeltis hotamboia* (Laurenti). Oppel did not comment on the work of Andrew Smith (1849), who found no evidence of venom or venom glands in *Dispholidus typus* (Smith).

West (1896) examined *Erythrolamprus aesculapii* Günther, and found that it was similar to the other opisthoglyphous snakes he previously (1895) had examined. A second snake was examined which was identified only as "?aglyphous variety of *Erythrolamprus*, Günther, (?*Liophis*, Boulenger)." West found the Duvernoy's gland of this form to be identical to that of the previous species. It is unfortunate that the only difference West mentioned between these two specimens is in the teeth; the identification of the second species is thus vague. West (1898) discussed

the general histology of the head glands of snakes, particularly the venom glands. Kathariner (1898) described the anatomy of the digestive system of *Dasyeltis scabra* and also mentioned a large gland of Duvernoy for this form.

Stejneger (1893) and Cope (1900) gave brief summaries of the knowledge of the colubrid parotid (Duvernoy's) glands and referred to several incidents that illustrate the effectiveness of the venom of opisthoglyphous snakes (*Serpentes suspectum*). Stejneger made the very important and often overlooked observation (1893, p. 350) that the presence of a grooved rear fang is not a necessity for the introduction into the prey of the secretion of Duvernoy's gland.

Noguchi (1909) described the gross appearance of the labial glands primarily from literature reports. He indicated that both *Chironius carinatus* and *Liophis miliaris* lack any portion of "Rudimentary venom gland or the yellowish portion of the *Glandula labialis superior*." Such a statement contrasts with the findings of Phisalix (1922) for *Chironius carinatus* (and to my own results for *Liophis miliaris*).

The major survey of the anatomy and histology of these glands, as well as the physiological effects of the secretions of the oral glands, was provided by Marie Phisalix (1922). She followed Leydig in defining the parotid (Duvernoy's) gland on the basis of its position (1922, p. 338) rather than its histological characteristics. Duvernoy's gland was considered to be a mixed gland because its duct is lined with mucous cells. Many forms were examined (55 genera), but Phisalix unfortunately did not indicate which of these were studied histologically. Only for *Natrix natrix* and *Malpolon* sp. were figures of microscopic sections of the glands given.

Sarkar (1923) examined the buccal glands and teeth of the following forms: *Ahaetulla nasuta*, *Cerberus rhynchops*, *Boiga trigonata*, *Chrysopelea ornata*, *Telescopus variegatus*, *Psammophis sibilans*, *Dendrophis picta*, *Amphiesma stolatus*, and *Lycodon aulicus*; he compared them with those of *Oxybelis fulgida*, from West (1895). Sarkar's (1923) paper was devoted mainly to a description of the dentition. He observed that some teeth are firmly fixed to the maxilla but that others are not

and appear to have only a ligamentous connection with the maxilla. He concluded that these latter teeth do not become ankylosed to the maxilla, and he was apparently of the opinion that these teeth are permanent and may be lost only after death.

His conclusion was entirely erroneous, as may be seen by a comparison with Bogert's (1943) report on the normal pattern of colubrid tooth replacement. What Sarkar called "hinged" teeth are undoubtedly replacement teeth that have not yet been firmly joined to the maxilla, which is confirmed by his statement that the teeth rest at different angles from the fixed teeth and by a comparison of his figures 1 through 4 with figures 42 and 43 of Bogert (1943).

Sarkar concentrated on the relationship between the duct of the parotid (Duvernoy's) gland and the fangs. He did not figure the histology of any venom glands, though he did give several figures that represent his conception of the evolution of the opisthoglyphous Colubridae from a hypothetical ancestor. A presumed morphological series showed a gradual enlargement of the venom gland, the development of grooved rear fangs, and the opening of the duct of the venom gland at the base of the grooved fang. Although this scheme is plausible, there is certainly nothing to recommend it over any other hypothesis.

Radovanović (1932)¹ examined the parotid (Duvernoy's) glands of *Telescopus fallax*, *Malpolon monspessulana*, and *Natrix natrix* and compared these glands with the glands of truly venomous snakes. Radovanović gave measurements for cell height, cell width, and nuclear diameter in the forms that he examined. He concluded that the Duvernoy's glands of the opisthoglyphous snakes represent a position between the relatively simple glands of *Natrix natrix* and the highly advanced glands of the venomous snakes exemplified by *Naja naja*. Experiments showed that the venom of the two opisthoglyphous snakes was effective against small animals.

Smith and Bellairs (1947) studied serial sections of the following forms: *Typhlops diardi*, *Boa constrictor*, *Trachyboa boulengeri*, *Cylindrophis rufus*, *Xenopeltis unicolor*, *Col-*

¹ This paper is in Croato-Serbian; my review of it is based primarily on the German summary.

uber fasciolatus, *Natrix natrix*, and *Thamnophis sirtalis*, but did not examine Duvernoy's gland in any of them. They did, however, dissect preserved specimens of these forms, as well as several other species of snakes, to find the head glands. They, unlike Phisalix (1922), did not find a Duvernoy's gland in *Natrix natrix*. [Egerer (1926) referred to a *glandula venerifera* in *Natrix natrix* as distinct from the supralabial glands.] Smith and Bellairs specifically stated that no attention was paid to gland histology. These au-

thors proposed a scheme of the evolution of the venom gland and illustrated their scheme with drawings of the heads of some specimens for the identification of stages in the development of the venom gland. This scheme was very similar to that proposed by Sarkar (1923). Both schemes assumed a straight path of development for the venom gland. They did not take into consideration the extensive experimentation that must have occurred in the evolution of a highly variable adaptation.

MORPHOLOGICAL ANALYSIS

SOURCES OF VARIABILITY

AS A PRELIMINARY STEP, the glands of some specimens of *Thamnophis sirtalis* were examined to determine the extent of variability of the gland of Duvernoy within a single species. The examination indicated relatively little intraspecific variation. Some of the species that were examined for the main project were represented by two or more specimens to offset the effects of possible individual variation.

The effect of fixation in shrinking or swelling tissues is well known (Baker, 1958; Davenport, 1960). The rate of penetration of fixative may, in part, determine whether the cells will retain the secretion or will pass it into the tubules. Different fixatives have different rates of penetration into a tissue. Post-fixation will also affect the tissue and may cause marked shrinkage.

These variations would be insignificant if the same fixative had been used for all the tissues on which this report is based. However, the material obtained from museum collections had often been indifferently fixed in formalin or alcohol of varying strengths and had often been subjected to long-term storage in weak alcohol. After dehydration all the tissue was treated identically, and it is hoped that no further differences were introduced.

Baker (1958) has pointed out that not only do different fixatives shrink tissue to varying extents, but they markedly affect the amount of shrinkage during infiltration and the embedding in paraffin. Fortunately formalin seems to be almost the best fixative for minimal shrinkage during embedding. Checks generally indicated a fairly good correlation between properly fixed specimens and museum specimens of the same species.

In certain specimens that were known to have been in captivity for a long time, the connective tissue of the gland was considerably thickened. An attempt was made to check the possibility that connective tissue increases with age. The trabecular thickness and the capsule thickness were both estimates of the development of the connective tissue of the gland. The trabeculae and capsule are

continuous, and it was believed that if one increased ontogenetically, the other did also. Therefore a regression line and its coefficient of correlation were calculated for capsule thickness as a function of the thickness of the trabeculae. Regression lines and coefficients of correlation for capsule thickness as a function of the number of trabeculae, and for trabecular thickness as a function of the number of trabeculae, were also calculated. All were very low (-0.002 , 0.036 , and 0.035 , respectively), and the values of t were correspondingly low. There was no evidence that there is any relationship between these parameters.

Of the more than 200 specimens examined, 33 pairs of specimens were conspecific, and 68 other pairs were congeneric. The significance of the comparison made in this study is in part measured by the frequency that conspecific or congeneric specimens were evaluated as being identical or at least very similar. If the large majority of congeneric specimens were given identical evaluations of the criteria used in this study, the premise that the histological appearance of the glands reflected the taxonomic situation would be supported. Text figure 1 gives the percentage of identical evaluations of congeneric forms. Surprisingly the percentage of agreement was much higher for congeneric than for conspecific specimens, possibly owing to the fact that, when the gland of a specimen was poorly preserved or in some other way was unsuitable for study, I attempted to obtain a second specimen of the same species. However, both specimens were utilized in the comparisons. For many of the specimens I was unwilling to give a value to each criterion; thus some data are missing (see table 1). Such missing data would, of course, represent a lack of agreement in these comparisons. These facts were also of some importance in the comparison of the congeneric specimens, but, since this sample was more than twice the size of the conspecific sample and since a second species of a genus would not have been looked for because the first gland was unsuitable, the error was lower.

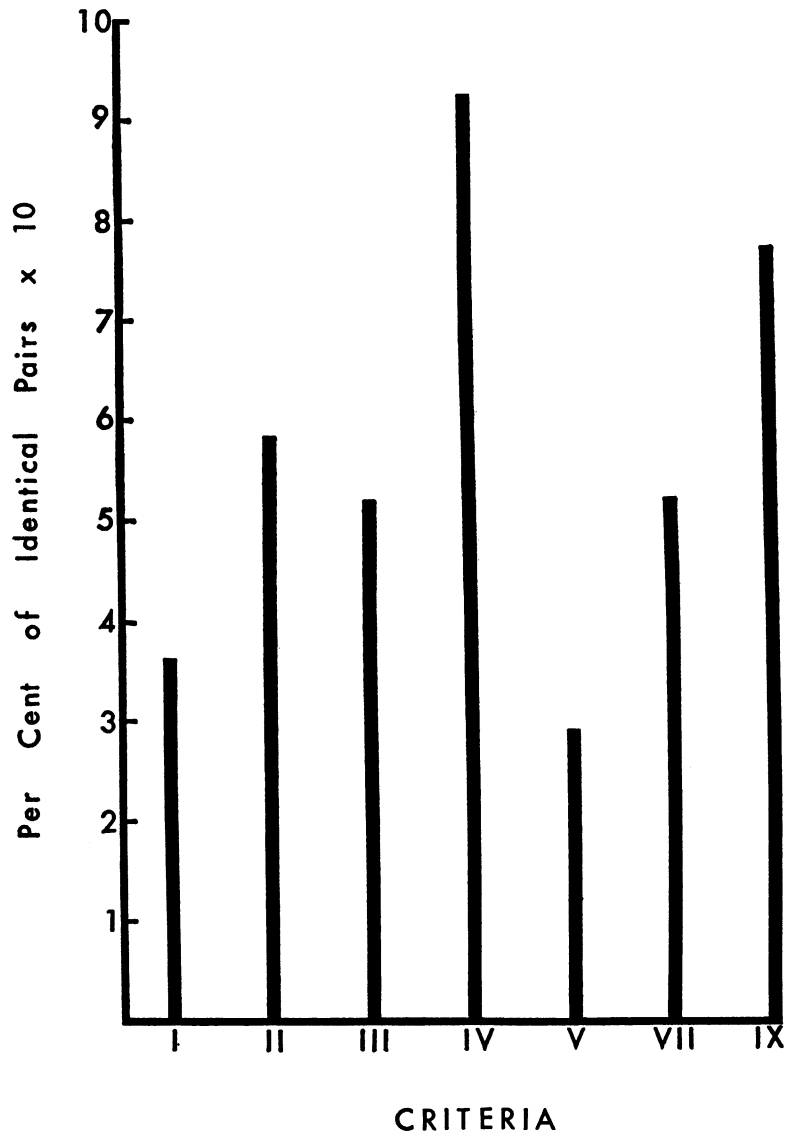


FIG. 1. Comparison of evaluations of conspecific and congeneric specimens. Percentage of identical evaluations of the criteria capsule thickness (I), trabeculae number (II), trabecular thickness (III), cell shape (IV), frequency of lumen (V), distribution and occurrence of mucous cells in Duvernoy's gland (VII), and vascularity (IX) in 33 pairs of conspecific (hatched lines), and 68 pairs of congeneric (solid lines), specimens.

CELL PROPORTIONS

The distribution of cell heights as size classes of 0.5μ is shown in text figure 2. The top histogram shows the data for all the Colubridae. The second gives the distribu-

tion of size classes of the cell height for 11 specimens of the Homalopsinae [*Cerberus rhynchops*, *Fordonia leucobalia*, *Homalopsis buccata* (three), *Enhydriis bocourti* (two),

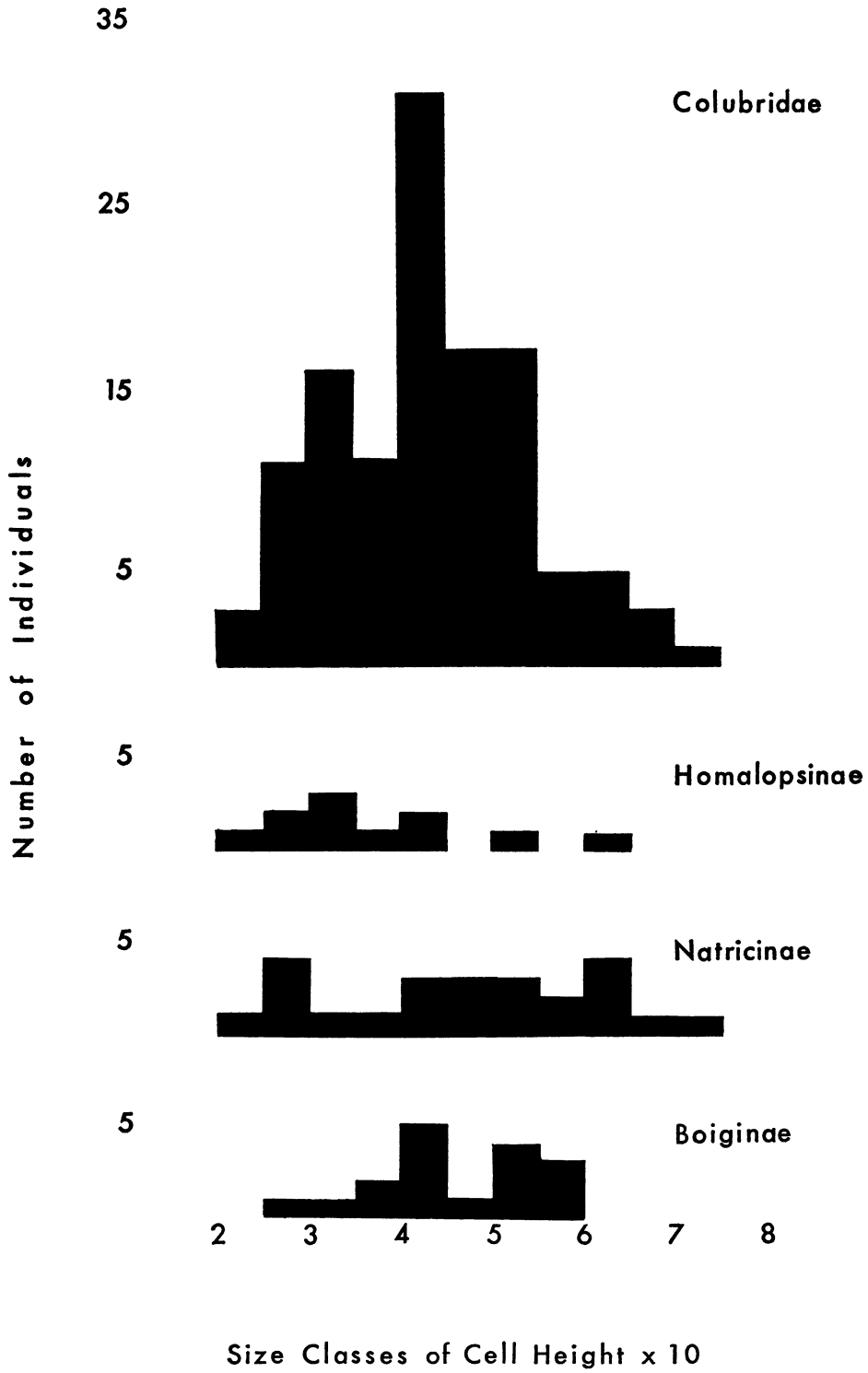


FIG. 2. Distribution of size classes (0.5 μ per class) of cell height for the Colubridae.

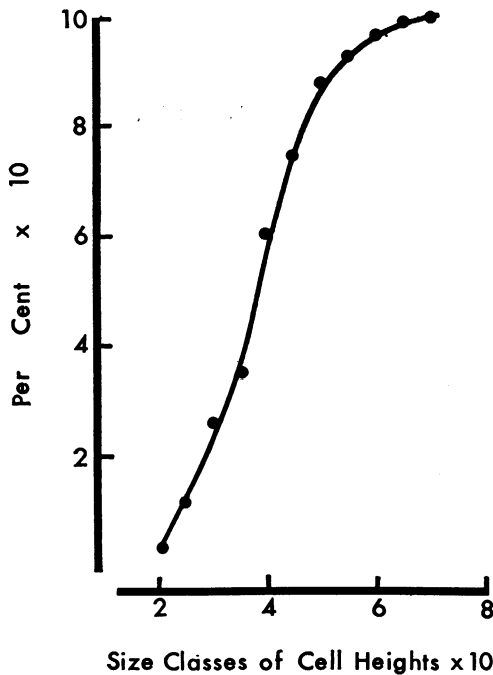


FIG. 3. Cumulative percentage plot of size classes of cell height. The cumulative percentage distribution of all size classes of cell height (0.5μ per class) shows a smooth curve. The absence of multiple inflection points is indicative of a homogeneous population.

Enhydris enhydris (two), *Enhydris* sp., and *Myron richardsoni*].

The third histogram gives the same data for 21 specimens of the Natricinae [*Amphisma mairi*, *Bothrophthalmus lineatus* (two), *Macropisthodon rudis*, *Natriciteres olivacea*, *Natrix cyclopion floridana*, *Natrix erythrogaster*, *Natrix rhombifera*, *Natrix sipedon pleuralis*, *Natrix taxispilota*, *Pseudoxenodon bambusicola*, *Pseudoxenodon sinensis*, *Rhabdophis subminiata* (two), *Rhabdophis tigrina lateralis*, *Thamnophis cyrtopsis*, *Thamnophis elegans vagrans*, *Thamnophis sirtalis* (two), and *Xenochrophis piscator*].

The fourth histogram gives the same data for 17 specimens of the Boiginae [*Ahaetulla fasciolata*, *Ahaetulla nasuta* (two), *Ahaetulla prasina* (two), *Boiga blandingi*, *Boiga dendrophila* (two), *Boiga pulverulenta*, *Clelia clelia*, *Erythrolamprus aesculapii*, *Erythrolamprus bizona*, *Erythrolamprus venustissimus*, *Psammophis schokari*, *Trimorphodon biscutus*

(two), and *Uromacer catesbyi*]. A cumulative percentage plot of these data (text fig. 3) gives no evidence of bimodal distribution of cell height. Those species with lower cell heights include the species that have an effective venom. The cell heights of forms such as *Dispholidus* and the Homalopsinae fall within the range of cell height reported by Radovanović (1928) for *Naja* and *Vipera*. Thus there seems to be a trend toward the reduction of cell height with the development of an effective venom, at least in some lines. The mean size class of cell height for all the Colubridae examined was 40.38 ± 10.4 . This is equivalent to a cell height of $20.5 \pm 5 \mu$. When the size classes of cell height were plotted separately for the Homalopsinae (text fig. 2), an average of 35.0 ± 11.3 , which is equal to a cell height of $17.5 \pm 5.2 \mu$, is obtained; for the Natricinae (text fig. 2), an average of 47.38 ± 10.8 , or a cell height of $22.5 \pm 5 \mu$, is obtained; and for the Boiginae (text fig. 2), an average of 41.76 ± 11 , or a cell height of $20.5 \pm 5.2 \mu$, is obtained.

The means of the size classes of cell heights for the Homalopsinae and for the Natricinae were compared with the use of the equation from Snedecor (1956, p. 97) for Student's t-test. A value of $t = 3.39$ was obtained. For 30 degrees of freedom this corresponds to a P value of 0.005. Thus the probability that the mean cell heights of these two groups have been sampled from the same population is 1/200, whereas the probability is 8/10 for the Homalopsinae and the Colubrinae.

The mean cell height of the Natricinae was also compared with that of the entire sample, and the probability that these were not significantly different was 0.5. Although the mean cell height of neither subfamily is significantly different from that of the entire sample of the Colubridae, the mean cell height of the Natricinae is significantly different from the mean cell height of the Homalopsinae. Neither the mean cell height of the Homalopsinae nor that of the Natricinae is significantly different from the mean cell height of the Boiginae. Such lack of difference is not unexpected, since the Boiginae are generally not considered to be a natural group, and the distribution of the cell heights within this assemblage does not differ from that within the entire colubrid sample (table 2). No

TABLE 2
COMPARISON OF DIFFERENCES IN SIZE CLASSES OF CELL HEIGHT

	Mean Size Class of Cell Height	Colubridae	Significance (P)		
			Homalopsinae	Natricinae	Boiginae
Colubridae	40.38 ± 10.4	—	0.8	0.5	0.9
Homalopsinae	35.0 ± 11.3	0.8	—	0.005	0.8
Natricinae	47.38 ± 10.8	0.5	0.005	—	0.5
Boiginae	41.76 ± 11	0.9	0.8	0.5	—

trends in cell size other than the apparent reduction of cell height with the development of a possibly effective venom could be observed.

In view of this apparent trend, an attempt was made to determine whether any relationship existed between the lumen diameter and the cell height. A scatter plot was made of all the evaluations of lumen diameter as a function of cell height for the Colubridae as a group and separately for the Homalopsinae and the Natricinae. Regression lines were calculated, and the coefficients of correlation were determined (Snedecor, 1956). None of their values differed significantly from zero.

Regression lines were also plotted for cell-height classes as a function of the lumen frequency, and again the value of r (-0.01) was not significantly different from zero. Thus there was no indication of any correlation

between cell height and the frequency of a measurable lumen in the tubules.

The apparent trend toward a decrease in cell height with the development of an effective venom is probably real. Differences in cell height can be the result of many different factors, not the least of which is the secretory state of the cell, e.g., the cell's retention of its elaborated secretion, or its discharge into the lumen of the tubules and ducts. Radovanović (1928) found marked differences in the heights of full and empty cells in the glands of *Vipera ammodytes* and *Naja naja*. Kochva (personal communication) has described the care necessary to retain the venom within the cells for histochemical studies. In most of the specimens studied the snakes were killed under conditions that would favor a release of the venom from the cells, and this may well affect the cell proportions.

HISTOLOGICAL PATTERNS

The supralabial and Duvernoy's glands are easily distinguishable in section, as they are composed of two markedly different types of cell. The supralabial glands are made up wholly of mucous cells, arranged into small multicellular glands which open in the oral cavity via several ducts. Duvernoy's glands are encased in a capsule of connective tissue and are composed primarily of serous cells. In some forms, such as *Thamnophis sirtalis*, these are grouped into cords, but in others, such as *Ahaetulla prasina*, they are in a highly branched tubuloacinous gland. There is a small lumen in the center of each tubule or cord, a lumen that generally leads into a secondary collecting duct. These secondary ducts join to form a collecting or primary duct, which is lined with a mucous epithelium

and leads into the mucous epithelial sheath of the posterior maxillary teeth.

With the exception of those of *Rhabdophis subminiata* and *Thamnophis sirtalis*, the serous cells of the Duvernoy's glands were columnar to cuboidal in shape. In these two species the cells were generally pyramidal in shape.

Primarily four distinct arrangements of glands are recognized in the Colubridae. The most simple and probably the most primitive is only a purely mucous supralabial gland. This gland may be differentiated anteriorly into a premaxillary gland (pl. 1, fig. 3) or may be merely a series of mucous lobules along the supralabial ridge (pl. 1, figs. 1, 4).

The second pattern consists of a mucous

supralabial gland with a predominantly serous Duvernoy's gland, but with some mucous cells present in the Duvernoy's gland, giving the type described as a mixed Duvernoy's gland (pl. 1, fig. 2; pl. 2, figs. 2, 3, 4; pl. 4, fig. 1; pl. 5, figs. 3, 4; pl. 8, fig. 2).

The third pattern may be only a variant of the second, or it may be the precursor of the second pattern. It consists of a mucous supralabial gland with some serous cells included. This is the type that I call the "mixed supralabial gland."

The fourth pattern is represented by the presence of a mucous supralabial gland with a separate, purely serous Duvernoy's gland (pl. 2, fig. 4; pl. 3, fig. 1; pl. 4, fig. 3; pl. 5, fig. 2; pl. 6, figs. 1, 3, 4; pl. 7, figs. 1-4; pl. 8, figs. 1, 3, 4).

The detailed groupings developed by the computer program are presented in Appendix 2. Appendix 2 is deposited with the American Documentation Institute, Washington, D. C., and copies may be obtained from them.¹ The following summary, therefore, only lists the forms in terms of the size and kind of their Duvernoy's glands.

The following forms were found to have a purely mucous supralabial gland, with no trace of serous cells: *Acrochordus javanicus*, *Arizona elegans*, *Boaedon virgatus*, *Cylindrophis rufus*, *Elaphe carinata*, *Elaphe mandarinus*, *Elaphe subocularis*, *Elaphe triaspis intermedia*, *Farancia abcura*,² *Lampropeltis calligaster*, *Lampropeltis doliata polyzona*, *Lampropeltis getulus boylii*, *Lampropeltis g. holbrooki*, *Lampropeltis pyromelana*, *Lampropeltis rhombomaculata*, *Pituophis catenifer deserticola*, *Pseudaspis cana*, *Pseustes sul-*

phureus, *Rhinochelius l. lecontei*, *Spilotes pul-latus*, and *Tropidodipsas s. sartori*.

The following forms also lacked Duvernoy's gland, but some serous cells were observed in the supralabial glands. The gland in these species was classed as a mixed gland rather than a mixed Duvernoy's because of the rarity of serous cells and the absence of a single duct: *Arizona elegans*, *Crotaphopeltis* sp., *Eirinis decemlineata*, *Elaphe longissimus*, *Elaphe moellendorffi*, *Elaphe obsoleta*, *Elaphe quadrevirgata*, *Elaphe radiata*, *Elaphe taeniurus*, *Scaphiodontophis annulatus*, and *Scaphiophis albopunctatus*.

Those forms that lack Duvernoy's gland include widely distributed, generalized colubrid snakes; all species of *Boaedon*, *Elaphe*, and *Lampropeltis* examined in this study fall into this class.

The histology of the supralabial gland varies greatly in the genus *Elaphe*. In some members the glands are purely mucous, whereas in others some serous cells are intermingled with the mucous-cell gland. There are several possible reasons for this variation. It is unlikely that some mucous cells have been mistaken for serous cells, or vice versa, because of the poor preservation of some of the material examined. Why should this occur only in *Elaphe* and not in *Lampropeltis*? A more likely explanation is that the presence of a few serous cells in the supralabial gland is a highly variable character in some genera. Yet another possibility exists. The observed variation may reflect a taxonomic distinction; this is suggested by the distribution of the variability within the genus *Elaphe*. *Lampropeltis* is confined to the New World, and the supralabial glands are similar in all species. On the other hand *Elaphe* is found in both the New World and Old World. With a single exception (*E. obsoleta*), those species of *Elaphe* that possess a mixed gland are from the Old World. With the exception of *E. carinata* and *E. mandarinus*, those species of *Elaphe* with a purely mucous gland are New World forms. This division is suggestive, but these two forms are not generally considered to be more closely related than are other members of the genus.

The glands of *Arizona elegans* and *Farancia abacura* support the hypothesis that the presence of serous cells in the mucous supralabial

¹ The species groupings generated by the computer program (Appendix 2) have been deposited as Document Number 9439 with the American Documentation Institute, Auxiliary Publications Project, Photoduplication Service, the Library of Congress, Washington, D. C., 20540. A copy may be secured by citing the Document number and by remitting \$8.75 for photoprints, or \$3.00 for 35-mm. microfilm. Advance payment is required. Make checks or money orders payable to: Chief, Photoduplication Service, the Library of Congress.

² A second specimen (U.M.M.Z. No. 109335) of this species was found to have a small percentage of serous cells in the supralabial gland. These were organized into a discrete gland at the posterior portion of the supralabial glands. This specimen was included in the analysis as a "mixed Duvernoy's gland."

gland is a highly variable trait. Both of these species were represented in this study by two specimens. The evaluations of the glands in both cases were markedly different. The gland of one specimen of *Farancia abacura* was classed as a mixed Duvernoy's gland, and that of the other as a purely mucous supralabial gland. The gland from one specimen of *Arizona elegans* was also classed as a mixed supralabial gland, and the other specimen was classed as having a mucous supralabial gland. It is of some interest that in *Pituophis catenifer deserticola*, which is considered to be closely related to *Arizona elegans*, no trace of serous cells could be found in the supralabial gland.

The following forms had a Duvernoy's gland with some mucous cells intermingled with the serous cells: *Abastor erythrogrammus*, *Amphiesma mairi*, *Bothrophthalmus lineatus*, *Calamaria septentrionalis*, *Coniophanes fissidens*, *Diadophis punctatus*, *Dipsas indica bucephala*, *Drymobius margaritiferus*, *Drymarchon corais couperi*, *Erythrolamprus aesculapii*, *Farancia abacura*, *Geophis multi-torques*, *Heterodon nasicus*, *Leptodeira latifasciata*, *Masticophis mentovarius*, *Masticophis taeniatus*, *Myron richardsoni*, *Natriciteres olivacea*, *Natrix cyclopion*, *Natrix erythrogaster*, *Natrix rhombifera*, *Natrix sipedon*, *Natrix taxispilota*, *Pareas stanleyi*, *Psammodynastes pulverulenta*, *Rhabdophis subminiata*, *Rhabdophis tigrina*, *Rhadinaea flavilata*, *Salvadora grahamiae*, *Sibon nebulata*, *Sibynophis chinensis*, *Stegonotus modestus*, *Thamnophis cyrtopsis*, *Thamnophis elegans*, *Tretanorhinus variabilis*, *Xenochrophis piscator*, and *Xenodon merremi*.

The following forms had a purely serous Duvernoy's gland: *Ahaetulla fasciolata*, *Ahaetulla mycterizans*, *Ahaetulla prasina*, *Alsophis portoricensis*, *Alsophis vudi*, *Aparallactus modestus*, *Boiga blandingi*, *Boiga dendrophila*, *Boiga fusca*, *Boiga pulverulenta*, *Brachyophis revoli*, *Calamaria schlegeli*, *Cerberus rhynchops*, *Chironius carinatus*, *Chrysopelea ornata*, *Clelia clelia*, *Coluber constrictor*, *Coluber ravergieri*, *Coniophanes fissidens punctigularis*, *Conopsis vittatus*, *Conopsis biserialis*, *Coronella austriaca*, *Crotaphopeltis hotamboiea*, *Cyclocorus lineatus*, *Dendrelaphis pictus*, *Diadophis punctatus*, *Dinodon rufozonatum*, *Dipsadoboa unicolor*, *Dipsas brevifacies*, *Dipsas*

latifrontalis, *Dispholidus typus*, *Dromicus andrae*, *Dromicus protenus*, *Dromicus* sp., *Dryadophis dorsalis*, *Dryadophis melanomus alternatus*, *Drymobius boddaerti*, *Drymobius margaritiferus*, *Dryocalmus subannulatus*, *Duberria lutrix*, *Enhydris bocourti*, *Enhydris enhydris*, *Enhydris* sp., *Erpeton tentaculatum*, *Erythrolamprus bizona*, *Erythrolamprus venustissimus*, *Fordonia leucobalia*, *Gastropyxis smaragdina*, *Gonyophis margaritatus*, *Haldea striatula*, *Helicops angulatus*, *Helicops leopardina*, *Helicops polylepis*, *Heterodon platyrhinos*, *Homalopsis buccata*, *Hydrodynastes bicincta*, *Hydrops marti callosticus*, *Hypsiglena torquata deserticola*, *Imantodes cenchoa*, *Imantodes c. semifasciata*, *Leimadophis almadensis*, *Leimadophis melanotus*, *Leimadophis reginae*, *Leimadophis typhlus*, *Leptodeira annulata*, *Leptodeira splendida*, *Leptophis diplotropis*, *Leptophis richardi occidentalis*, *Liophis cobella*, *Liophis miliaris*, *Lycodon aulicus*, *Lystrophis dorbignyi*, *Macropisthodon rudis*, *Malpolon monspessulana*, *Masticophis bilineatus*, *Meheyla poensis*, *Miodon gabonensis collaris*, *Natrix cyclopion floridana*, *Oligodon ornatus musyi*, *Opheodrys vernalis*, *Opisthotropis latouchi*, *Oxybelis fulgidus*, *Philodryas schotti*, *Pliocercus elapoides*, *Psammophis schokari*, *Psammophis sibilans*, *Psammophylax tritaeniatus multisquamis*, *Pseudoboa petola*, *Pseuderyx plicatilis*, *Pseudoxenodon bambusicola*, *Pseudoxenodon sinensis*, *Ptyas mucosus*, *Ramphiophis oxyrhynchus rostratus*, *Rhinobothryum lentiginosum*, *Salvadora grahamiae*, *Salvadora mexicana*, *Sibynomorphus mikani neuwiedi*, *Spalerosophis diadema*, *Stenorhina freminvilli*, *Storeria occipitomaculata*, *Tachymenis chilensis*, *Tantilla rubra*, *Telescopus fallax*, *Telescopus semiannulatus*, *Thamnophis sirtalis*, *Thelotornis kirtlandi*, *Trachischium tenuiceps*, *Trimorphodon bicutatus*, *Trimorphodon tau*, *Trypanurgos compressus*, *Uromacer catesbyi*, *Xenodon neuweidi*, and *Zaocys dhumnades*.

Xenodermus javanicus has a strikingly different arrangement of the supralabial glands. Instead of the usual conditions, that is, with all the serous cells arranged in a single compact gland at the posterior portion of the supralabial ridge, the serous cells are arranged in cords of cells which alternate with cords of mucous cells along the entire supralabial region (pl. 3, fig. 2).

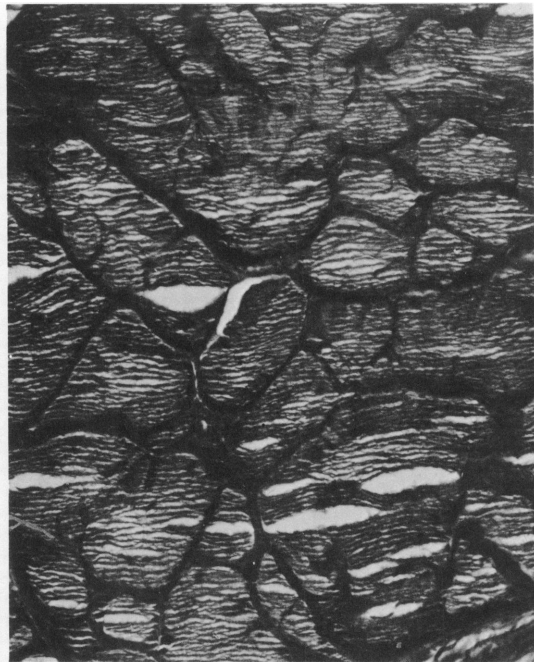
Fimbrios klossi apparently has a similar arrangement of the gland. Because of poor preservation of detail, I am not certain whether the alternation of mucous-cell cords with serous-cell cords extends throughout the entire gland. Only a small portion of the gland gave any recognizable histological detail. That region showed mucous-cell cords interspersed with serous-cell cords. Most of the gland of *Achalinus spinalis* was lost in preparation, and, from the fragments remaining on the slide, little can be deduced. The cells are not typical for Duvernoy's gland, and one lobule resembles serous cells, whereas another may be mucous cells. Thus the pattern, although not clear, does not differ from the gland arrangement seen in other members of the Xenoderminae sufficiently to cause serious doubt that the supralabial glands of the Xenoderminae are markedly different from the supralabial glands of the other Colubridae. The glands seem to be similar within the subfamily.

In view of the recent suggestion of Bogert (1964) that the subfamily Xenoderminae does not represent a natural group and therefore should not be used, this strikingly different arrangement of the labial glands of the

Asiatic forms is of great interest (pl. 3, fig. 2) and suggests that at least these forms are a homogeneous group. Their relationship to the forms of the New World and to those of Africa that have been included in this subfamily is unclear. The labial gland of *Ninia*, which has occasionally been included in this group (see Bogert, 1964), were not included in the present study, but Phisalix (1922) reported no parotid (Duvernoy's) gland in this species. An examination of the labial glands of the members of this group is now in progress and will be reported at a later date.

All other species examined in this study had a distinct Duvernoy's gland.

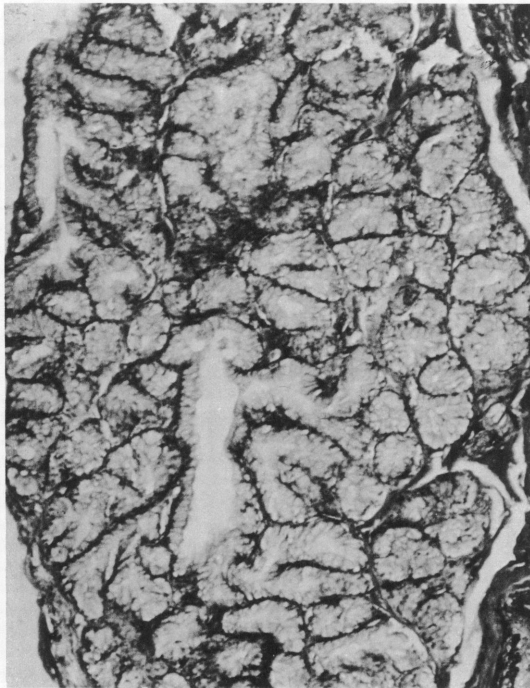
An unusual Duvernoy's gland was found in *Dispholidus typus*. Instead of the usual pattern of a tubuloacinous gland with a moderate amount of storage space provided partly as a result of an increase in the diameter of the tubular lumina, the gland appears to be the result of hypertrophy of a single lobule, or at most only a few lobules. Multiple invaginations and evaginations of the lobule wall provide enormous secretory surface and storage space. The over-all impression is of the folding of the wall of the mammalian gall bladder (pl. 3, fig. 1; pl. 5, fig. 2).



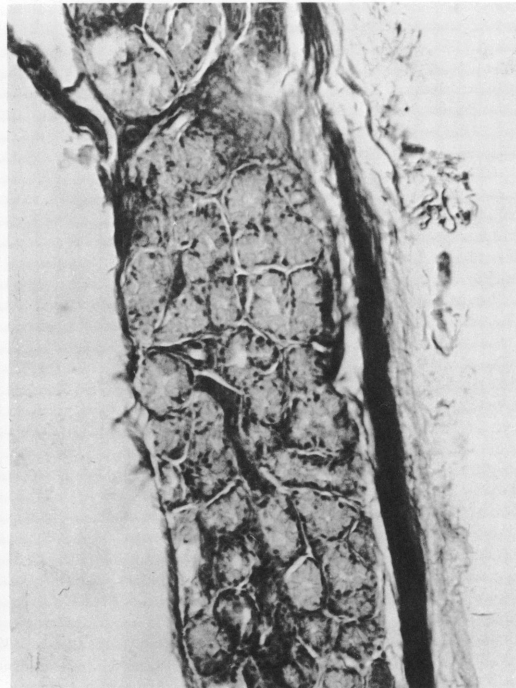
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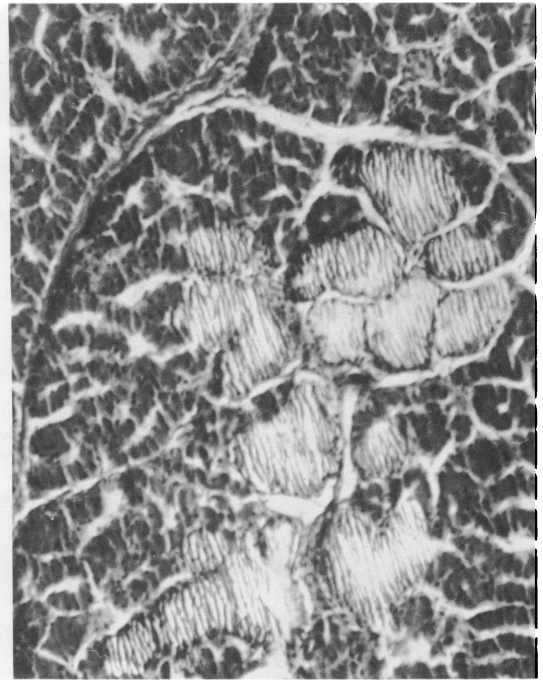


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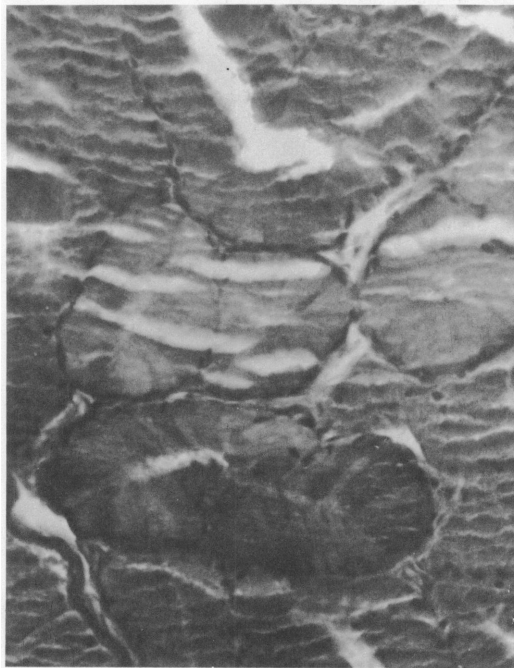
Labial glands. 1. *Drymarchon corais couperi*, U.M.M.Z. No. 67701, mucous supralabial gland. *Ca.* $\times 250$. 2. *Xenodon merremi*, C.M. No. 34818, a mixed Duvernoy's gland. *Ca.* $\times 200$. 3. *Adenorhinos barbouri*, C.N.H.M. Slide No. 2556. The premaxillary gland is a modified supralabial gland. *Ca.* $\times 50$. 4. *Elaphe subocularis*, U.M.M.Z. No. 124026, mucous supralabial gland. *Ca.* $\times 30$



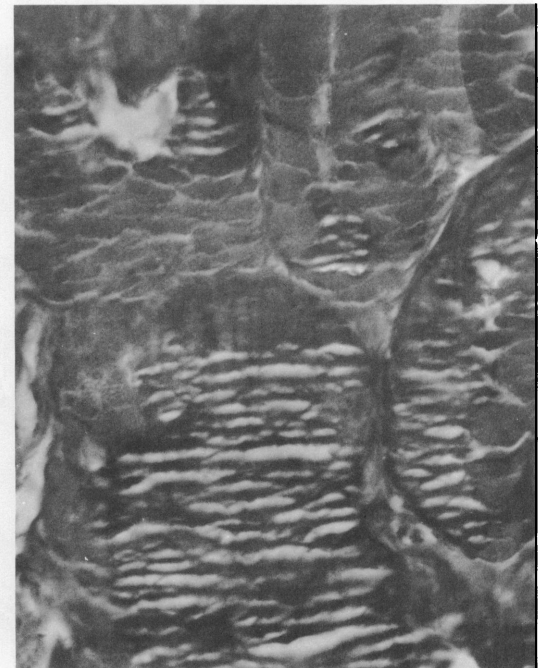
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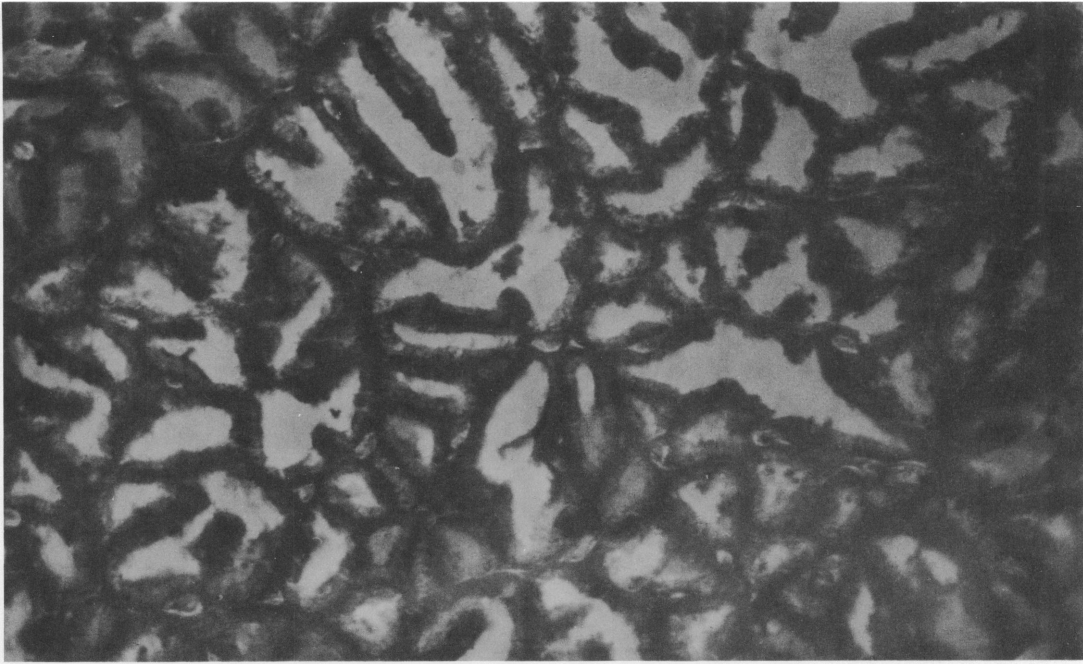


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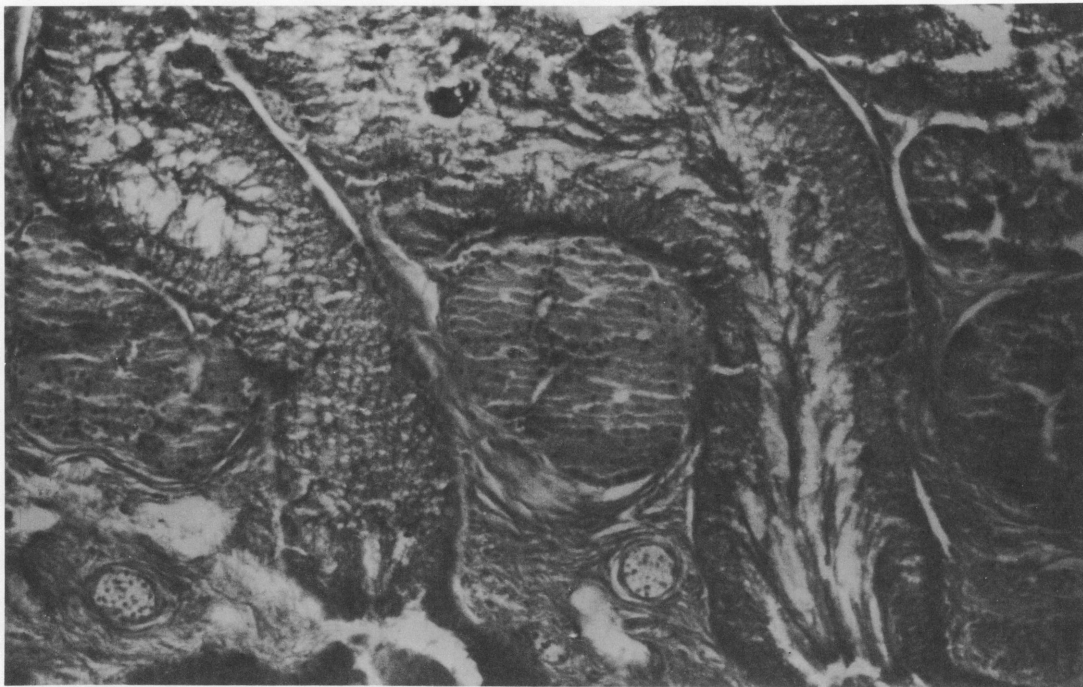


4

Duvernoy's glands. 1. *Ptyas mucosus*, C.G. No. 2786, showing wide distribution of chromatophores. The primary duct is filled with secretory product. Ca. $\times 200$. 2. *Natrix cyclopion floridana*, U.M.M.Z. No. 106289, showing distribution of mucous cells within lobules. Ca. $\times 100$. 3. *Thamnophis cyrtopsis*, U.M.M.Z. No. 69679, showing distribution of mucous-cell lobules. Ca. $\times 300$. 4. *Xenochrophis piscator*, A.M.N.H. No. 84528, showing the relatively few serous cells. Ca. $\times 200$



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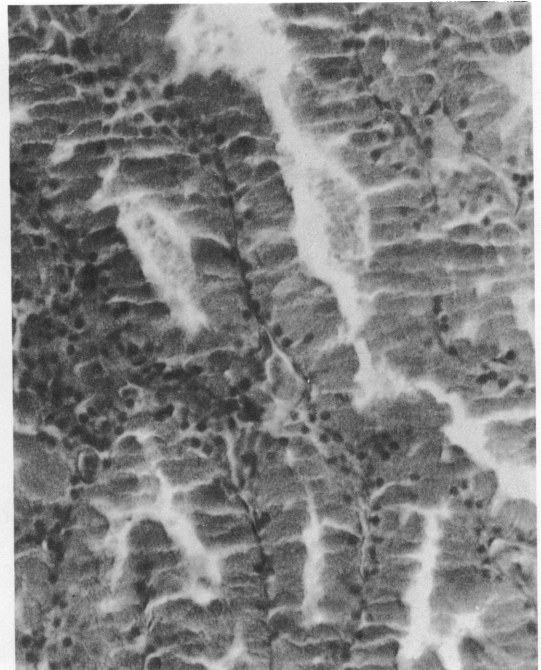


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Unusual glands. 1. Duvernoy's gland in *Dispholidus typus*, C.M. No. 6340, showing highly folded tubule walls and secretion in lumina of peripheral tubules. Ca. $\times 200$. 2. Supralabial glands in *Xenodermus javanicus*, C.N.H.M. No. 62427. The alteration of mucous- and serous-cell cords is clearly shown. The mucous-cell cords empty individually into the oral cavity. Ca. $\times 300$



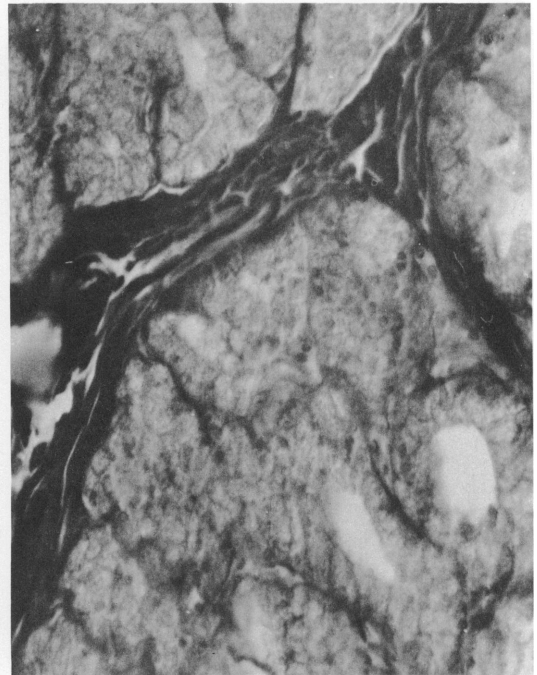
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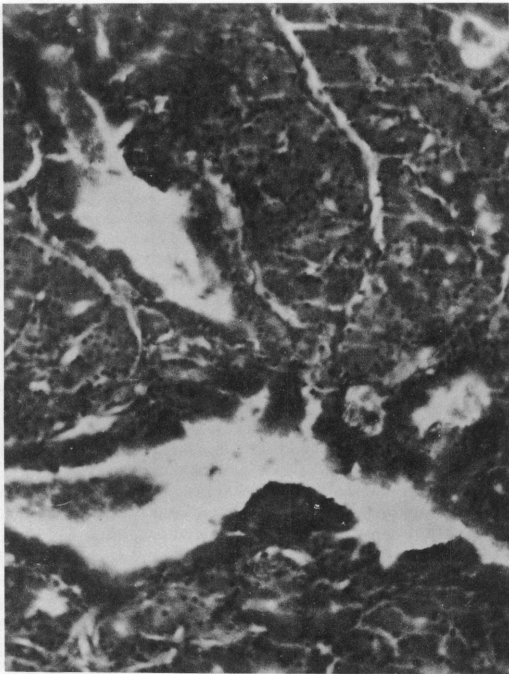


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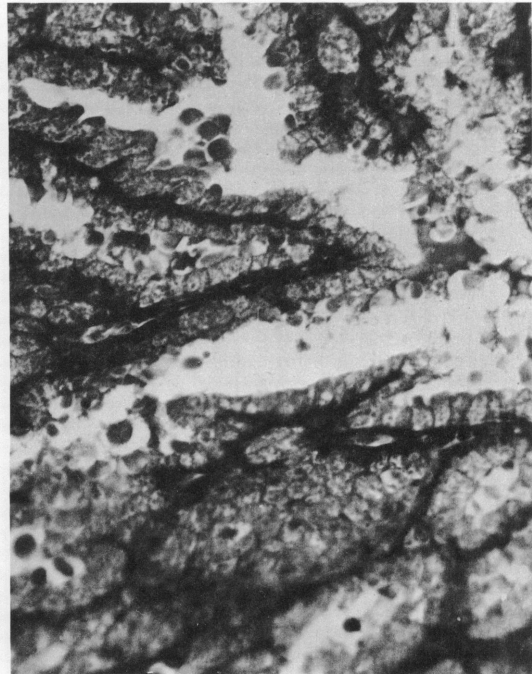


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Duvernoy's glands. 1. *Stegonotus modestus*, A.M.N.H. No. 85714, showing lobulation of gland as well as arrangement of cells within tubules. Ca. $\times 225$. 2. *Stegonotus modestus*, A.M.N.H. No. 85714, showing arrangement of cells within a lobule and presence of secretion product within lumen of a tubule. Ca. $\times 440$. 3. *Boiga dendrophila*, C.M. No. 2138, showing arrangement of tubules and connective tissue separating them. Ca. $\times 225$. 4. *Boiga dendrophila*, A.M.N.H. No. 86559, showing connective tissue separating lobules. Ca. $\times 375$



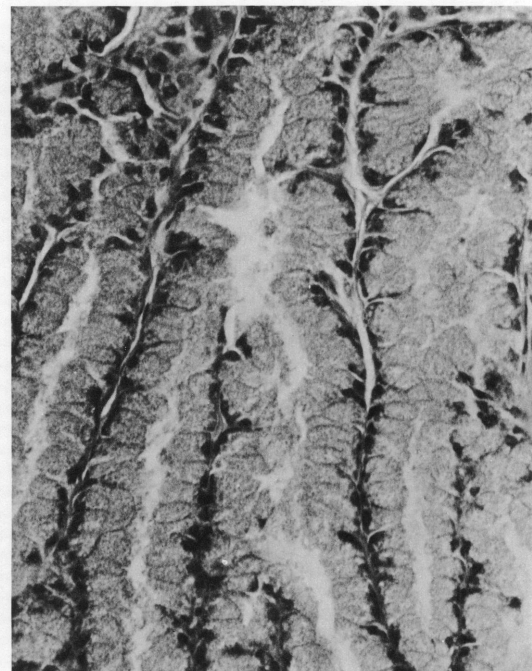
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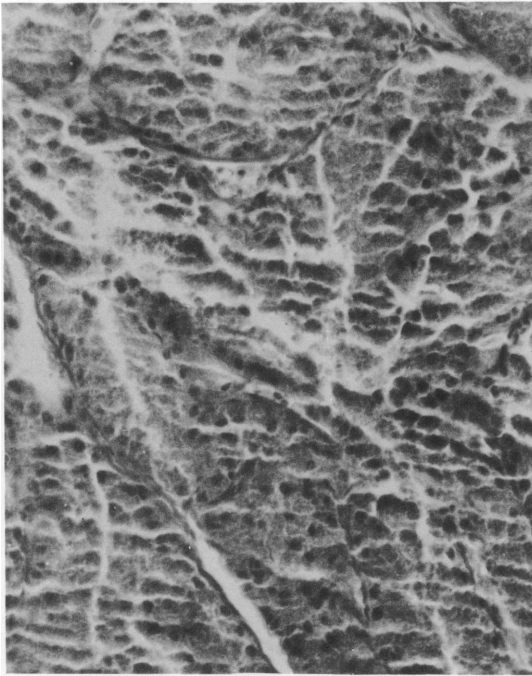


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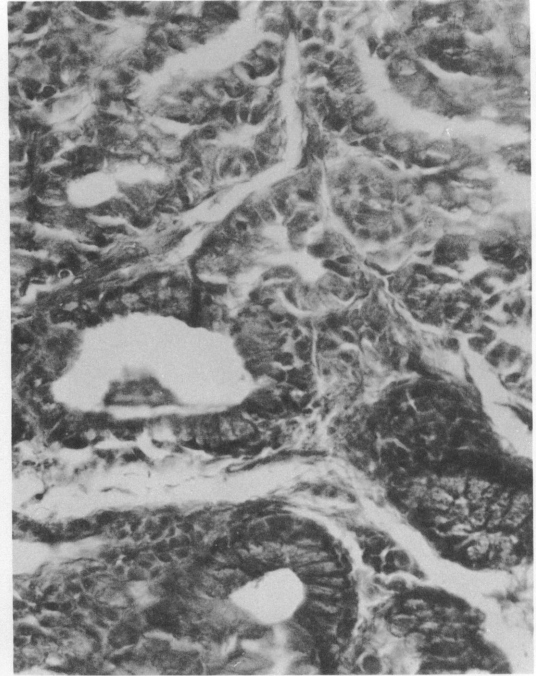


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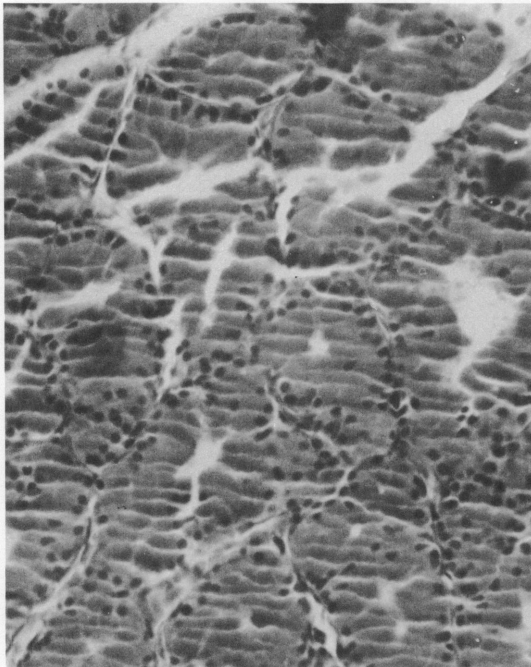
Duct formation. 1. *Rhabdophis tigrina lateralis*, C.M. No. 34953. The secondary duct coalesces to form a primary duct. There is some secretion product in the primary duct. Ca. $\times 280$. 2. *Dispholidus typus*, A.M.T. No. 5. The formation of the primary duct is also typical in this form. There is considerable secretion product in the ducts of this specimen. Ca. $\times 320$. 3. *Masticophis taeniatus ornatus*, U.M.M.Z. No. 123464, showing formation of secondary duct by coalescence of tubular ducts. Ca. $\times 125$. 4. *Masticophis taeniatus ornatus*, U.M.M.Z. No. 123464, showing formation of tubule ducts. Ca. $\times 250$.



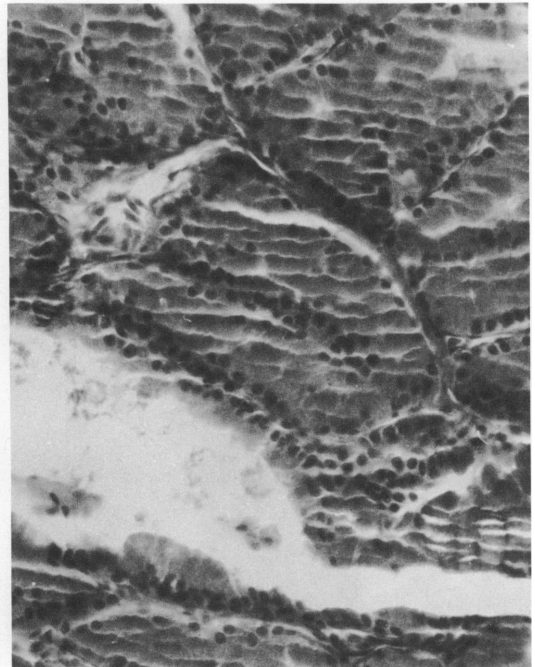
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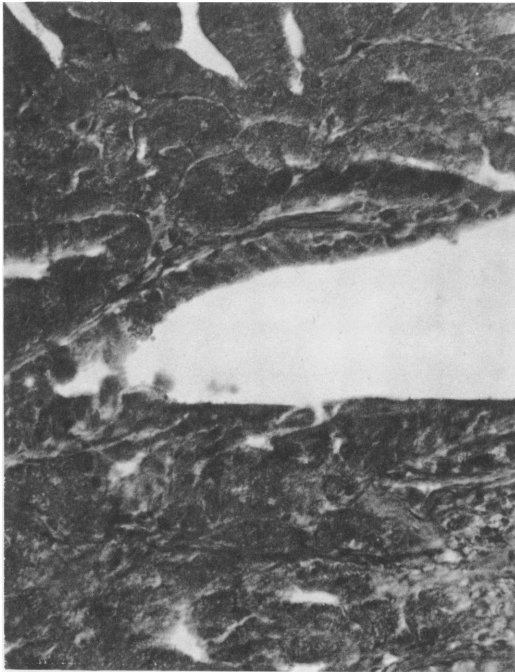


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Duvernoy's glands. 1. *Salvadora grahamiae*, U.M.M.Z. 123474, showing, even in this poorly fixed specimen, over-all arrangement of gland. Ca. $\times 350$. 2. *Bothrophthalmus lineatus*, C.M. No. 9304, showing primary ducts in cross section and mixed nature of lobules. Ca. $\times 350$. 3, 4. *Abastor erythrogrammus*, U.M.M.Z. No. 123169. 3. Contrast between the few small lumina in the tubules. 4. Relatively large primary duct. Both ca. $\times 350$



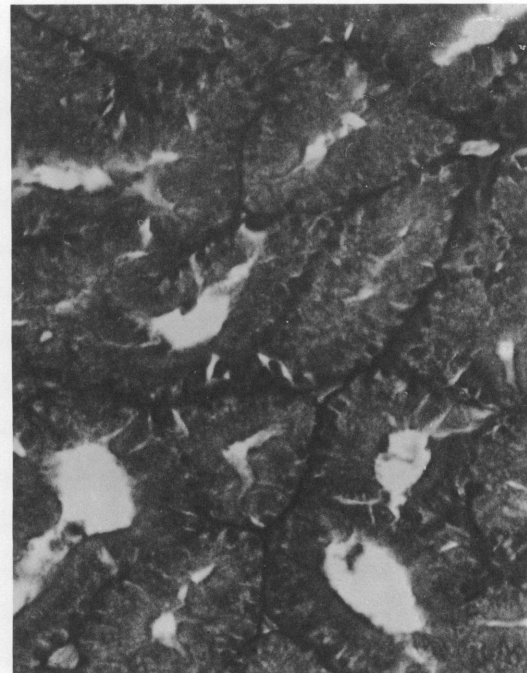
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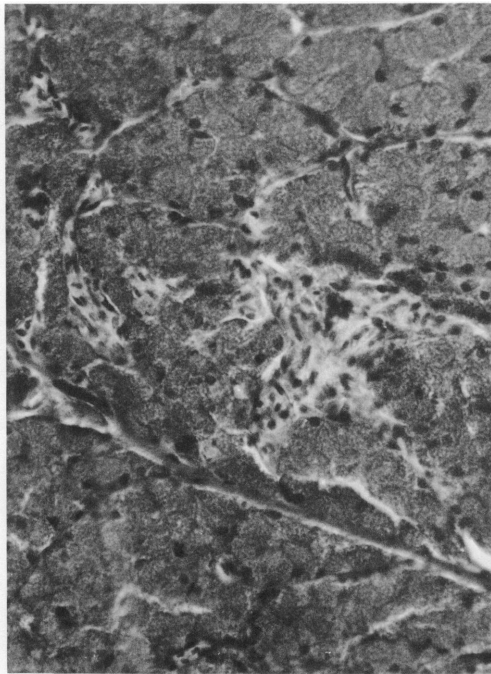


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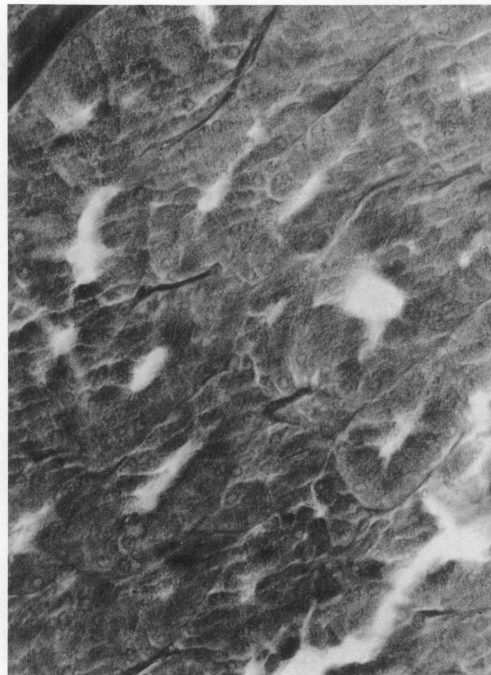
Duvernoy's glands. 1. *Alsophis portoricensis*, C.M. No. 28126, showing very large primary duct. Ca. $\times 380$. 2. *Dendrelaphis pictus*, A.M.N.H. No. 2835, showing very prominent melanocytes in connective tissue separating lobules. Ca. $\times 400$. 3. *Ahaetulla prasina*, C.G. No. 2778. Granular appearance of cytoplasm in this Formal-Zenkers-fixed specimen is characteristic of this tissue in that fixative. Arrangement of tubules of lobules also shown. Ca. $\times 380$. 4. *Helicops leopardina*, C.M. No. 31417, showing arrangement of tubules. Only about half of tubules had a measurable lumen. Ca. $\times 400$



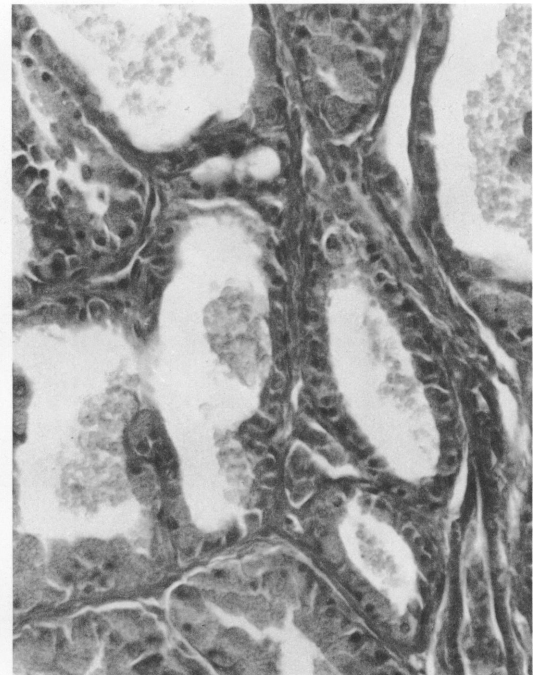
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Duvernoy's glands. 1. *Leimadophis typhlus*, C.M. No. 34842, showing very prominent blood vessels surrounding some of lobules. Ca. $\times 300$. 2. *Natrix rhombifera*, U.M.M.Z. No. 77784, showing blood vessels both in interlobular connective tissue and between some tubules. Ca. $\times 400$. 3. *Dinodon rufozonatum*, A.M.N.H. No. 75952, tangential section showing typical arrangement of tubules. Ca. $\times 330$. 4. *Chironius carinatus*, C.M. No. 33770, a single lobule of gland, showing folding of tubule wall similar to folding in *Dispholidus typus* (cf. pl. 3, fig. 1, and pl. 5, fig. 2). Remaining lobules are representative of arrangement within this gland. Ca. $\times 200$

PHYLOGENETIC ANALYSIS COLUBRID CLASSIFICATIONS

APPROXIMATELY 70 PER CENT of the known snake fauna is lumped into the family Colubridae, an unwieldy assemblage of those snakes that are not readily assignable to other families. The family is thus cosmopolitan and occupies many different ecological niches. It includes such diversely specialized forms as *Dasypeltis scabra*, an almost edentulous, egg-eating species; *Clelia clelia*, an ophiophagous, rear-fanged species; and *Dispholidus typus*, an arboreal rear-fanged form that feeds on birds and mammals and the bite of which has been fatal to human beings.

Both the relationships and the zoogeography of the Colubridae have always presented an extremely confusing problem. The correct relationships of superficially similar forms from different continents remain uncertain. It is, for instance, unclear whether the faunas of North America and Europe, South America and Africa, and Asia and Australia represent parts of the same pattern, or independent diversifications of common ancestral stocks.

Four major attempts have been made at a classification of the colubrids, the cosmopolitan ones of Boulenger (1893-1896) and of Cope (1900), and the work of Dunn (1928) for American species and that of Bogert (1940) for African species. It may be useful to summarize these and some variants thereof and to examine whether any of the groupings suggested show parallel glandular modifications.

Boulenger (1893-1896) subdivided the Colubridae on the basis of the dentition into three series:

Aglypha: All teeth solid, not grooved

Opisthoglypha: One or more of the posterior maxillary teeth grooved

Proteroglypha: Anterior maxillary teeth grooved or perforated

It is generally agreed (e.g., Romer, 1956) that Boulenger's Proteroglypha are distinct from the Colubridae and consist of two related families, the Elapidae and the Hydrophiidae.

Boulenger separated the series Aglypha

and Proteroglypha each into three subfamilies:

AGLYPHA

Acrochordinae: Postfrontal bone (postorbital of Romer, 1956) extending over supraorbital region; scales not or only slightly overlapping

Colubrinae: Postfrontal bone not extending over supraorbital region; scales usually overlapping; teeth on entire length of maxillary and dentary bones

Rachiodontinae (= Dasypeltinae): Rudimentary teeth, maxillary and dentary bones edentulous anteriorly

OPISTHOGLYPHA

Homalopsinae: Nostril valvular, on upper surface of snout

Dipsadomorphinae (= Boiginae): Nostril lateral, dentition well developed

Elachistodontinae: Teeth rudimentary, maxillary and dentary edentulous anteriorly

Boulenger split off the snail-eating snakes, distinguished from the other Colubridae by the absence of a mental groove, into his family Amblycephalidae. It is now considered (Romer, 1956; Peters, 1960) to represent two subfamilies, the Dipsadinae and the Pareinae, within the Colubridae.

Cope (1900) divided the Colubridae mainly on the basis of hemipenial characters, supplementing these by skeletal characters, primarily vertebral and dentitional, and arrived at the following classification of the Colubridae:

AGLYPHODONTA

I. Hypapophyses restricted to anterior part of vertebral column

a. No tracheal lung

Hemipenis spineless, smooth or plicate or papillose only . . . Calamarinae

Hemipenis with apical disc, no calyces, spinous, sulcus furcate

. Xenodontinae

Hemipenis calycalate, spinous; sulcus furcate; no disc Dromicinae

Hemipenis calycalate, spinous; sulcus simple, no disc Colubrinae

aa. With a tracheal lung

Hemipenis calycalate, spinous; sulcus furcate; no disc . . . Leptognathinae

- II. Hypapophyses present to caudal region
 - Hemipenis smooth, not spinous Anoplophallinae
 - Hemipenis spinous, without enlarged basal hook Lycodontinae
 - Hemipenis spinous, with enlarged basal hook or hooks Natricinae

GLYPHODONTA (= DIPSADIDAE)

- I. Hypapophyses on anterior vertebrae only
 - Hemipenis spinous, calyculate; sulcus undivided Dipsadinae
 - Hemipenis spinous, calyculate, sulcus bifurcate Scytalinae
 - Hemipenis spinous, not calyculate, with an apical disc Erythrolamprinae
- II. Hypapophyses extending throughout vertebral column
 - Hemipenis not calyculate; no apical hook on apical disc Homalopsinae

Cope considered the Xenoderminae to represent a subfamily of the family Nothopidae. This family was composed of two subfamilies, the Acrochordinae and the Nothopinae (= Xenoderminae), equivalent to the Acrochordinae of Boulenger.

Dunn (1928) modified the scheme of Cope to take into account some of its defects, particularly Cope's great reliance on the dentition. Dunn gave the following classification for the American subfamilies of the Colubridae:

- Sulcus spermaticus forked Ophiinae (= Xenodontinae)
- Sulcus spermaticus single
 - Hypapophyses absent posteriorly Colubrinae
 - Hypapophyses present posteriorly; dentary free posteriorly; hypapophyses long, narrow, and projecting posteriorly; hemipenis calyculate distally Sibynophiinae
 - Dentary not free posteriorly; hypapophyses short, broad, and not projecting posteriorly, hemipenis spinous, not calyculate distally Natricinae

Dunn's proposed phylogeny of the Colubridae appeared to be supported by the distribution of this group. The Ophiinae were apparently confined to South America, with no near allies. They were aglyphous or opisthoglyphous, possessed or lacked hypapophyses on the posterior vertebrae, and the hemipenis had basal spines and either distal calyces or an apical disk. Dunn considered them to be an old Neotropical group. The

Colubrinae were believed well developed in the Old World and North America, but to have entered South America only slightly. They also included both aglyphous and opisthoglyphous forms, and the hemipenis had basal spines and distal calyces.

The Sibynophiinae were considered to be a monotypic subfamily containing the genus *Sibynophis*. Dunn (1928) examined *S. annulatus* from Mexico and *S. collaris* from China and believed that they were congeneric.

The Natricinae did not enter South America, but they are abundant in North America, Europe, and Asia. Dunn believed that this group did not include any opisthoglyphous forms, but Malnate (1960) reported that *Rhabdophis ceylonensis* possesses two enlarged posterior maxillary teeth, separated from the others by a diastema and grooved on their anterior surface.

Bogert (1940) discussed the inherent difficulties in the phylogeny proposed by Dunn (1928) and gave some evidence that the reproductive structures are not so conservative as originally supposed and, possibly more important, that penial characters are useful for the definition of genera but unsatisfactory when used to define supergeneric groups. Bogert (1940, pp. 11-12) proposed the following arrangement of the African Colubridae:

- A. Hypapophyses present posteriorly
 - B. Sulcus spermaticus forked
 - C. No grooved teeth
 - Group I
 - Glyphoholicus* [= *Lycodonomorphus*]
 - Ablabophis* [= *Lycodonomorphus*]
 - Lamprophis*
 - Bothrophthalmus*
 - Boaedon*
 - Pseudoboodon*
 - Bothrolycus*
 - Group II
 - Hormonotus*
 - Gonionotophis*
 - Mehelya*
 - Lycophilidion*
 - Oophilositum* [= *Chamaelycus*]
 - CC. With grooved posterior maxillary teeth
 - Group III
 - Geodipsas*

- BB. Sulcus spermaticus not forked
 C. No grooved teeth
 Group IV
Natrix
Neusterophis [= *Natriciteres*]
Hydraethiops
Limnophis
- AA. Hypapophyses absent posteriorly
 B. Sulcus spermaticus forked
 C. No grooved teeth
 Group V
Duberria
Grayia
Pseudaspis
- C. With grooved posterior maxillary teeth
 Group VI
Amplorhinus
 Group VII
Aparallactus
Miodon
 [*Macrelaps*]
Calamelaps
Rhinocalamus [= *Calamelaps*]
- BB. Sulcus spermaticus not forked
 C. No grooved teeth
 Group VIII
Coronella
Meizodon
Coluber
Aeluroglena
Spalerosophis
Lytorhynchus
 Group IX
Chlorophis [= *Philothamnus*]
Philothamnus
Hapsidophrys
Gastropyxis
 Group X
Ramnophis
Thrasops
 Group XI
Scaphiophis
 Group XII
Prosymna
- CC. With grooved posterior maxillary teeth
 Group XIII
Boiga
Crotaphopeltis
Chamaetortus
Dipsadoboa
 Group XIV
Tarbophis [= *Telescopus*]
Macroprotodon
 Group XV
Dispholidus
Thelotornis

Group XVI

Hemirhagerrhis
Cerastes [= *Psammophylax*]
Malpolon
Dromophis
Psammophis
Rhamphiophis

Group XVII

Xenocalamus
Chilorinophis
Macrelaps [belongs in Group VII]
Micrelaps

- AAA. Hypapophyses absent posteriorly, strongly enlarged in region of esophagus
 B. Sulcus spermaticus not forked
 C. Teeth vestigial
 Group XVIII
Dasypeltis

Malcolm A. Smith (1943) discussed the Asiatic colubrid fauna. His classification differed slightly from that of Boulenger (1893–1896). Boulenger's Acrochordinae were divided by Smith into the Acrochordinae and the Xenoderminae, the Amblycephalidae were called the Dipsadinae, and the Colubrinae and the Homalopsinae were retained. The Dasypeltinae were treated both as a subfamily of the Colubridae (*op. cit.*, p. 114) and as a distinct family (*op. cit.*, p. 403). Smith also (*op. cit.*, p. 138) suggested the division of the Colubridae into 10 groups, but, like Bogert (1940), he did not assign names to any of them, and, unfortunately, he did not indicate the criteria that he employed to define his groups:

- Group 1: *Elaphe*, *Ptyas*, *Coluber*, *Zaocys*, *Opheodrys*, *Liopeltis*, *Contia*, *Xenelaphis*, *Lytorhynchus*, *Rhynchophis*, *Gonyophis*, and *Phyllorhynchus*
 Group 2: *Coronella*, *Oligodon*, *Calamaria*, and *Lampropeltis*
 Group 3: *Ahaetulla*, *Chrysopelea*, *Chlorophis*, *Philophthalmus*, and *Dryphiops*
 Group 4: *Lycodon*, *Dinodon*, *Cercaspsis*, *Dryocalamus*, *Boaedon*, *Lycophidion*, *Simocephalus*, *Lepurophis*, and *Stegonotus*
 Group 5: *Sibynophis*
 Group 6: *Natrix*, *Pseudoxenodon*, *Macropisthodon*, *Balanophis*, *Pararhabdophis*, *Aretium*, *Xenochrophis*, *Helicops*, and *Liodytes*
 Group 7: *Trachischium*, *Aspidura*, *Blythia*, *Xylophis*, *Haplocercus*, *Plagiopholis*, *Rhabdops*, and *Opisthotropis*
 Group 8: *Psammophis*, *Psammodynastes*, *Trimer-*

orhinus, *Dromophis*, *Rhamphiophis*, and *Mimophis*

Group 9: *Boiga* and *Telescopus*

Group 10: *Dryophis*, *Thelotornis*, and *Dispholidus*

Groups 6 and 7 may be related, as may Groups 8, 9, and 10. Group 5 is considered to have no other close relatives, and Malcolm A. Smith therefore seems to agree with Dunn (1928) about the genus *Sibynophis*.

Romer in 1956 summarized the classification of the Reptilia, both recent and fossil. He considered the Colubridae to be composed of the subfamilies Colubrinae, Xenoder-

minae, Acrochordinae, Dasypeltinae, Dipsadinae, Pareinae (= Amblycephalidae), and Homalopsinae. The Colubrinae remained as by far the largest subfamily. The Acrochordinae (Boulenger) were subdivided by Romer into two subfamilies within the Colubridae, the Acrochordinae and the Xenoderminae.

Table 3 of the present paper summarizes the ways that the genera included in this study have been classified by various workers. Owing to changes in definition, some genera are indicated as being included in two different subfamilies by the same author.

TEST OF GLAND GROUPINGS

RATIONALE OF COMPARISONS

In a study of this nature one can look for two different types of patterns. The first, and certainly the hoped-for, pattern is a distinct series of characters held exclusively in common by limited groups of related forms. Such a pattern was found in the supralabial glands of the Asiatic Xenoderminae (see Histological Patterns, above) and in *Dispholidus typus*.

A second type of pattern to be searched for is a combination of characters held in common with much higher frequencies by the members of one group than by other classes. Such patterns are represented by the trend toward reduction of cell height in the Homalopsinae, by the presence of mucous cells in 70 per cent of the Duvernoy's glands of the Natricinae, and possibly by the absence of Duvernoy's gland from "generalized" colubrids.

To facilitate comparisons the colubrid subfamilies of various authors are considered separately. For reasons that will become obvious the smaller ones are considered first.

COMPARISON OF CATEGORIES

The Sibynophinae (Dunn, 1928) contain a single genus, *Sibynophis*. This form had a Duvernoy's gland of a "typical" pattern, not distinguishable from that of this gland in the Colubrinae.

The Pareinae [Romer 1956; Amblycephalidae (part) Boulenger, 1893-1896] contain the Asiatic snail-eating snakes. The supralabial glands of *Pareas* were of the mixed Duvernoy type and not particularly distinct from any other similar glands.

The Dipsadinae [Romer, 1956; Amblycephalidae (part) Boulenger, 1893-1896; Leptognathinae Cope, 1900] include the American snail-eating forms of the genera *Dipsas*, *Sibon*, and *Sibynomorphus*. The glands in *Dipsas* and *Sibon* were generally mixed Duvernoy's glands, but one species of *Dipsas* and *Sibynomorphus* had purely serous Duvernoy's glands. The infralabial glands of *Dipsas latifrontalis* were found to be enlarged and composed predominantly of serous cells.

The Acrochordinae [Romer, 1956; Acrochordinae (part) Boulenger, 1893-1896] contain only the genus *Acrochordus*. This form lacks a Duvernoy's gland and has purely mucous supralabial glands. The Xenoderminae [Romer 1956; Acrochordinae (part) Boulenger, 1893-1896] were found to have a unique type of supralabial gland. The supralabial glands in this group are characterized by the presence of alternate serous-cell and mucous-cell cords along the supralabial ridge. This marked difference in the supralabial glands further supports the separation of the Acrochordinae and the Xenoderminae.

The subfamily Natricinae of Cope (1900; also Dunn, 1928) shows no differentiating features. The Natricinae of Goin and Goin (1962), defined as having well-developed hypapophyses on the posterior vertebrae, non-valvular nostrils, and wide ventral scales, include part of the Xenodontinae (Cope, 1900; Dunn, 1928). The composition of this grouping has some merit from the point of view of the classification of the salivary glands.

Of species included in the Goin and Goin

TABLE 3—(Continued)

Genus	Colubrinae (BDR C Bogert)	Dipsadomorphae (B)	Xenodontinae (DC)	Acrochordinae (BR)	Xenoderminae (R)	Dipsadinae (CR)	Homalopsinae (BRC)	Natricinae (DC)	Pareinae (BR)	Dromicinae (C)	Erythrolamprinae (C)	Lycodontinae (C)	Leptognathinae (C)	Scytalinae (C)	Sibynophinae (D)	Calamariinae (C)
<i>Pseustes</i>	BDR	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Ptyas</i>	BR	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Rhabdophis</i>	BR	—	—	—	—	—	—	C	—	—	—	—	—	—	—	—
<i>Rhadinaea</i>	BR	—	D	—	—	—	—	—	—	C	—	—	—	—	—	—
<i>Rhamphiophis</i>	R 11	B	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Rhinobothryum</i>	DR	B	—	—	—	C	—	—	—	—	—	—	—	—	—	—
<i>Rhinocheilus</i>	BDR C	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Salvadora</i>	BDR C	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Scaphiodontophis</i>	R	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Scaphiophis</i>	BR 11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Sibon</i>	B	—	—	—	—	RC	—	—	—	—	—	—	C	—	—	—
<i>Sibynomorphus</i>	B	—	—	—	—	R	—	—	—	—	—	—	—	—	—	—
<i>Sibynophis</i>	BR	—	—	—	—	—	—	—	—	—	—	—	—	—	D	—
<i>Spilotes</i>	BDR C	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Stegonotus</i>	BRC	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Stenorhina</i>	DR	B	—	—	—	—	C	—	—	—	—	—	—	—	—	—
<i>Storeria</i>	BR	—	—	—	—	—	—	DC	—	—	—	—	—	—	—	—
<i>Tachymenis</i>	R	B	D	—	—	—	—	—	—	—	—	—	—	C	—	—
<i>Tantilla</i>	DR	B	—	—	—	C	—	—	—	—	—	—	—	—	—	—
<i>Telescopus</i>	R 14	B	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Thamnophis</i>	BR	—	—	—	—	—	—	DC	—	—	—	—	—	—	—	—
<i>Thelotornis</i>	R 15	B	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Trachischium</i>	BR	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Tretanorhinus</i>	BR	—	D	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Trimorphodon</i>	DR	B	—	—	—	C	—	—	—	—	—	—	—	—	—	—
<i>Trypanurgos</i>	R	B	D	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Uromacer</i>	BR	—	D	—	—	—	—	—	—	C	—	—	—	—	—	—
<i>Xenodermus</i>	—	—	—	B	R	—	—	—	—	—	—	—	—	—	—	—
<i>Xenodon</i>	BR	—	DC	—	—	—	—	—	—	—	C	—	—	—	—	—
<i>Zoacys</i>	BR	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

(1962) definition, the following have been included in this study (individuals of species marked with an asterisk had some mucous cells intermingled with the serous cells of Duvernoy's gland): **Amphiesma mairi*, **Bothrophthalmus lineatus*, **Macropisthodon rudis*, **Natriciteres olivacea*, **Natrix cyclopion floridana*, **Natrix e. erythrogaster*, **Natrix rhombifera*, **Natrix sipedon pleuralis*, **Natrix taxipilota*, **Pseudoxenoden bambusicola*, **Pseudoxenodon sinensis*, **Rhabdophis tigrina lateralis*, **Rhabdophis subminiata*, **Thamnophis c.*

cyrtopsis, **Thamnophis elegans vagrans*, **Thamnophis sirtalis*, and **Xenochrophis piscator*. The admixture of mucous cells and serous cells in Duvernoy's gland in the marked species ranged from rare mucous cells to a few mixed lobules. In contrast, less than 10 per cent of the colubrines examined had mucous cells in the Duvernoy's gland. It thus appears highly probable that the presence of mucous cells in Duvernoy's gland is characteristic of the Natricinae and is not an accident of sampling. These forms also have a

mean cell height of $22.5 \pm 5 \mu$, which is different from the mean cell height of the Homalopsinae but not from that of the Colubridae as a whole.

The remaining members of the Xenodontinae (Dunn, 1928) either lack Duvernoy's gland (*Farancia*, *Tropidodipsas*), or have one (*Clelia*, *Rhadinaea*, *Tachymenis*) that is not distinguishable from the gland of other colubrids.

Several of the subfamilies proposed by Cope (1900)—the Calamarinae, the Dromicinae, the Erythrolamprinae, the Lycodontinae, and the Scytalinae—show no consistent pattern of Duvernoy's gland and do not differ in the features of this organ from the Colubridae as a whole. The Calamarinae contain the genera *Calamaria*, *Oligodon*, and *Pareas*. It is generally agreed that the last genus does not belong with the other two (Romer, 1956; Peters, 1960; Goin and Goin, 1962). The other two genera have Duvernoy's glands. The Erythrolamprinae include the genera *Erythrolamprus* and *Philodryas* and cannot be differentiated on the glandular pattern. The Lycodontinae include several diverse genera (*Boaedon*, *Bothrophthalmus*, *Crotaphopeltis*, *Lycodon*, *Oligodon*, and *Pseudaspis*), and the gland architecture reflects the diversity. *Boaedon* and *Pseudaspis* have only a mucous supralabial gland.

The supralabial glands in *Crotaphopeltis* vary markedly. In one specimen (M.C.Z. No. 71870) the glands are typical purely serous Duvernoy's glands, but in another specimen (M.C.Z. No. 71871) the gland is a mixed supralabial gland. These two male specimens (see Gans and Laurent, *in* Gans, Laurent, and Pandit, 1965) were collected in the Somali Republic. They differ strikingly in the structure of the hemipenis, and it has already been suggested that they are not conspecific and possibly not congeneric. *Bothrophthalmus* has a gland of Duvernoy with many mixed lobules; *Lycodon* and *Oligodon* have purely serous Duvernoy's glands.

The Dromicinae are as varied. The Scytalinae contain *Coniophanes*, *Conopsis*, *Oxyrhopus*, *Philodryas*, and *Tachymenis*. Duvernoy's glands in these forms are not different from those of the colubrine pattern.

The Homalopsinae (Boulenger, 1893–1896; Cope, 1900; Romer, 1956) are generally con-

sidered to be distinct. Within this small subfamily there are differences in the structure of the gland, but a morphological series seems to exist. Duvernoy's gland is small and difficult to find in *Erpeton tentaculatum*; it is only slightly larger in *Myron richardsoni*. The gland of the latter species is the only one in the Homalopsinae that has some mucous cells. In *Homalopsis buccata* the gland is well developed and readily seen; it reaches a maximum size in the genus *Enhydris*. *Enhydris bocourti* has the major portion of the head covered by Duvernoy's gland; its gland was the largest seen in this study, and its tubulo-acinous structure can be seen grossly. The gland in *Fordonia leucobalia* is intermediate between the gland of *Myron* and that of *Homalopsis*. The Homalopsinae have a mean cell height of $17.5 \pm 5.2 \mu$ and as a group have the smallest cells of any colubrids. These facts may be related to the development of an effective gland secretion.

The Colubrinae [Boulenger, 1893–1896; Romer, 1956; Dipsadomorphinae (part) Boulenger, 1893–1896] remain a heterogeneous assemblage of snakes. The glandular pattern is highly varied, ranging from purely mucous supralabial glands to well-developed Duvernoy's glands. The Dipsadomorphinae (Boulenger, 1893–1896) are colubrine snakes that have grooved rear teeth and presumably a venom apparatus which is employed in subduing prey. These forms might be expected to have similar patterns of Duvernoy's gland. There is no histological basis for considering the Dipsadomorphinae (= Boiginae) as distinct from the Colubrinae. The highly varied patterns of Duvernoy's glands in these groups support the view that the former group is an artificial division of the latter (Dunn, 1928; Bogert, 1940; Malcolm A. Smith, 1943).

The secretion of the Duvernoy's gland possesses activities presumably related to prey capture, feeding, and the treatment of food. Gans (1961) discussed some of the changes that must have taken place in feeding without limbs, and suggested that even a weakly proteolytic secretion of the parotid (Duvernoy's) gland would have a selective advantage. Stejneger (1893) pointed out that even an enlarged but ungrooved tooth may be able to introduce a significant amount of secretion into a prey animal. With these points in

mind, one may believe it highly probable that the possession of Duvernoy's gland, which produces an effective venom, represents an evolutionary grade and has been reached independently in different groups of the Colubridae.

One group of colubrine snakes with a similar gland pattern may be significant. Those snakes that have only a purely mucous supralabial gland (*Boaedon*, *Elaphe*, *Pituophis*, *Pseudaspis*, *Pseustes*, and *Spilotes*) are for the most part powerful constrictors and presumably do not utilize salivary secretions in prey capture. The absence of Duvernoy's gland may reflect a relationship between these forms. Such a possible relationship may reflect similarities in "making a living" rather than taxonomic similarities. In any case, it is clear that only some colubrine snakes without Duvernoy's gland should be included in this group.

EVOLUTION OF GLAND PATTERNS

The ingestion of food is among the strongest selective pressures on a species. Therefore, there is no reason to believe that any structures that are intimately associated with the capture and digestion of prey will be conservative. Rather it is probable that these structures will reflect great selective pressure.

Text figure 4 shows the phylogeny of the Colubridae as proposed by Boulenger (1893-1896).

Anthony (1955) has supported Boulenger's derivation of the Viperidae from the opisthoglyphous colubrids. Bogert (1940) and Dowling (1959), among others, have suggested that the Colubridae may have been the ancestors of the Elapidae. Elapid stocks are presumed to have differentiated into the Viperidae and the Hydrophiidae. It has also been suggested that the Viperidae and the Elapidae may have been derived in part from the Boidae (Savage, 1957). A recent paper (Marx and Rabb, 1965) supported the thesis that the Viperidae developed from an elapid stock. Because of the possibilities of relationships between these snakes, there arose the hypothesis that the venom gland is nothing more than a specialized "parotid" gland of the Colubridae.

A difficulty of interpretation of the relationships between the colubrid Duvernoy's gland and the venom glands is that, even if colubrids did in fact give rise to the venomous snakes, they have greatly changed and no longer resemble their ancestors. Duvernoy's gland has had as long a period of time to specialize as the venom glands, and differences are to be expected.

Three grades of evolution of the "venom" glands have generally been recognized. Most primitive are the "harmless" colubrid snakes which had no venom apparatus. Next were the rear-fanged colubrids: those colubrids that had a large Duvernoy's gland and a

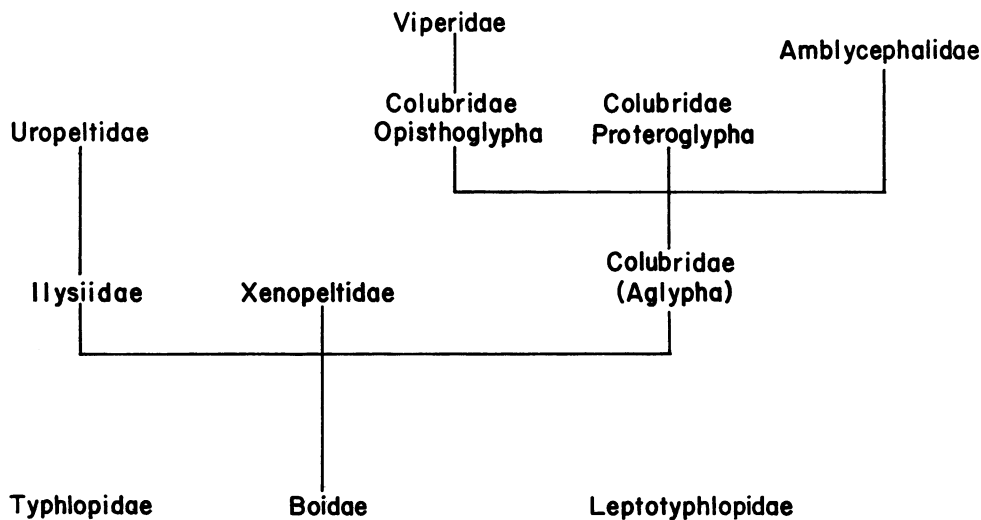


FIG. 4. Phylogeny of snakes, modified from Boulenger (1890-1896).

grooved rear fang. Most advanced were the highly venomous snakes with the fang at the front of the mouth and a large venom gland on the lateral aspect of the head, with a duct leading to the fang.

The here-determined differences in the structure of Duvernoy's glands of the Colubridae do not reflect such a simple sequence. There seem to exist several levels of organization in the structure of the supralabial glands in most lines of the Colubridae. On one level are those forms that lack Duvernoy's gland, *Elaphe*, *Lampropeltis*, and *Tropidodipsas*, to name a few. Next are those genera or species, such as *Farancia* and *Arizona*, that have a mixed supralabial gland and may be in the process of either developing or repressing Duvernoy's gland.

The next recognizable level is that of a small but distinct Duvernoy's gland such as is found in *Thamnophis sirtalis*. At one side, at about this same level of development, are placed the Xenoderminae. They have well-developed serous glands in the supralabial ridge, but the relationship of these many serous cell cords to the Duvernoy's gland of other colubrids is problematical.

The next level of development may include several different degrees of development of the maxillary teeth. There is no evidence that the development of Duvernoy's gland is in any way parallel to the evolution of a grooved fang. The development of a large Duvernoy's gland does not preclude the absence of grooved fangs. Two or more enlarged teeth in the region of the duct of the gland would have much the same effect as a single grooved tooth. A mobile maxilla, such as is found in *Heterodon*, would make a wound that would also permit the inflow of the secretion. Examples of this level of development include *Crotaphopeltis hotamboia*, *Heterodon*, *Homalopsis*, *Enhydris*, *Leptophis*, and *Xenodon newiedi*.

At about the same level, but possibly slightly at one side, are those forms that have a large Duvernoy's gland with mucous cells included in the serous portion of the gland, and those forms that have a mixed Duvernoy's gland. This group would include such forms as *Xenochrophis piscator*, *Rhabdophis subminiata*, *Amphiesma mairi*, *Thamnophis cyrtopsis*, *Dipsas indica*, *Sibon nebulata*, *Xenodon*

merremi, and *Erythrolamprus aesculapii*.

At the end of this arrangement of the glands of the Colubridae is the gland of *Dispholidus typus*. It is of considerable interest that the arrangement of Duvernoy's gland in *Dispholidus* is markedly different from the arrangement found in the presumably closely related *Thelotornis kirtlandi*. This latter species has a typical Duvernoy's gland, with densely packed serous cells in a tubuloacinous arrangement. Duvernoy's gland in *Dispholidus* approaches in organization the gland in the one hydrophiid (*Kerilia jerdoni*) that was available for study.

The gland in *Kerilia jerdoni* is of a simple tubuloacinous type, with the wall of some of the tubules folded into the lumen of the tubule. The suggestion is not made that there is any relationship between *Dispholidus typus* and *Kerilia jerdoni*, but rather it is maintained that these two dissimilar species have solved in a similar manner the problem of increasing the secretory surface of the gland. The folding of the tubule walls also increases the storage space within the gland and may be highly advantageous.

In view of the different levels of complexity of the Duvernoy's gland of the Colubridae, it is probable that a serous-cell supralabial gland has evolved at least twice and possibly four times. The Xenoderminae appear to be the result of an evolutionary line that failed to become very successful. There apparently is a fairly direct line leading from the simple Duvernoy's gland to the large gland of *Enhydris*. *Dispholidus typus* is very probably the result of an offshoot of this line but may represent the single remnant of a different line. Possibly those glands that contain a significant mucous-cell population represent a separate evolutionary line, or possibly they are an intermediate stage in the development of Duvernoy's gland. From the evidence available no decision can be made at this time (see text fig. 5).

An alternate hypothesis to multiple evolution of the serous Duvernoy's gland is that all the ancestral Colubridae possessed a serous portion of the supralabial glands, that in some of the recent Colubridae this has been lost, and that in others it has become a distinct gland.

This hypothesis would not satisfactorily

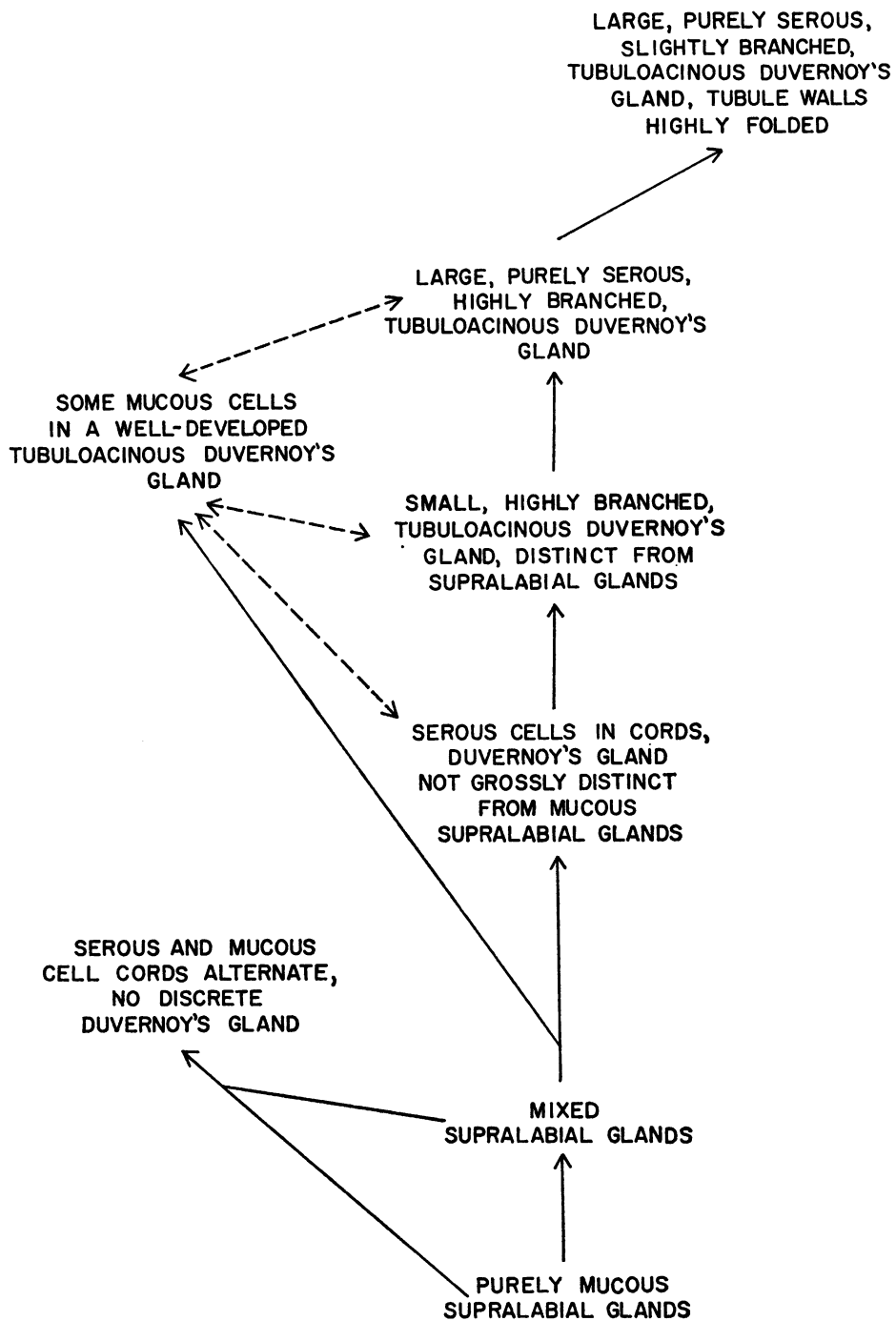


FIG. 5. Tentative scheme of the evolution of the colubrid supralabial glands. The levels of development indicate evolutionary grades rather than taxonomic distinctions. Solid arrows indicate probable lines of development; open arrows, possible alternate variants of these.

explain the arrangement of the glands in the Xenoderminae. A comparative study of the supralabial glands of the Lacertilia, and in particular of the Varanidae (cf. McDowell and Bogert, 1954), would be of importance in an evaluation of this hypothesis. In the single lacertilian supralabial gland (*Agama* sp.; C.G. No. 2229) that was examined, the supralabial gland was a purely mucous-cell gland.

The complexity of organization of the venom glands and the relationship of head muscles to the venom glands in the four groups of venomous snakes suggest that any relationship between the Colubridae and the venomous snakes is, as suggested by Haas (1952) and Anthony (1955), through the protocolubrids rather than through any of the existing lines.

SUMMARY AND CONCLUSIONS

A HISTOLOGICAL SURVEY of the oral glands of the Colubridae was made. Capsule thickness, trabeculae thickness and number, cell shape, the occurrence, distribution, and abundance of mucous cells, and the vascularization were evaluated and classified on a weak order ranking. Cell height, cell width, nuclear height, nuclear width, and the mean diameter of the lumen in the tubules were measured and divided into size classes of 0.5μ . Specimens with identical evaluations of the same criteria were tabulated by an I.B.M. 7044 computer, and the number of times that two species were grouped together was tabulated in a matrix.

The salivary glands of the Colubridae include supralabial and Duvernoy's gland. Duvernoy's gland is a tubuloacinous gland composed of predominantly serous cells. The secretion enters the oral cavity via a single duct which generally opens in the oral mucosa near the posterior maxillary teeth. The supralabial glands are generally smaller and are composed of mucous cells. These glands open into the oral cavity via several ducts.

Glands from 71 of the genera included in this study and about 25 other species represent forms of which the labial gland histology has not been previously described.

There is an apparent trend toward the reduction of cell height in those colubrids that possess a well-developed Duvernoy's gland. None of the other criteria evaluated could be correlated with the development of this gland.

The absence of Duvernoy's gland may be significant. Those genera that have a purely mucous supralabial gland or a mixed supralabial gland are for the most part generalized colubrids.

The Duvernoy's glands in 70 per cent of the examined species of the Natricinae (*sensu* Goin and Goin, 1962) have some mucous cells intermingled with the serous in contrast to about 10 per cent of the other Colubrinae.

The glands in the three Asiatic species of Xenoderminae that were examined are very similar and distinctly different from any glands of any other colubrid studied. The alternation of serous-cell and mucous-cell cords along the supralabial region is found only in this subfamily.

The arrangement of the gland in *Dispholidus typus* was also unusual and different from that of any other colubrid. The highly folded walls, the relatively little branching of the tubules, and the large amount of storage space within the gland permit easy identification of this gland.

This study supports the suggestion that the Boiginae (= Dipsadomophinae) are not a natural group.

The variation of the histological structure of Duvernoy's gland within the Colubridae and particularly within the Colubrinae both suggests that this gland is highly labile and also reflects a strong selective pressure on the feeding apparatus of snakes.

APPENDIX 1: SPECIMENS EXAMINED

A LIST BOTH OF THE SPECIES that were examined for the present work and of those that were examined for the same kind of studies by previous workers follows. The museum catalogue number follows the name of a species from which tissue was examined for the present study. Names of species examined by previous workers are listed by the name used in the original citation, followed by the currently accepted name, and a citation of an author's work in the literature. The currently accepted name is cross referenced to the synonyms. "See also" indicates that I, as well as a previous worker, examined material from the species mentioned, although under a different name. Phisalix (1922) named the species that she examined. It is not possible to determine which forms were examined grossly by her and which were examined histologically, and it is not certain that all were indeed examined histologically. An asterisk indicates those species in which Phisalix did not find a "parotid" gland.

- Abastor erythrogrammus* Latreille: A.M.N.H. No. 68335, United States, South Carolina, Jasper County; U.M.M.Z. No. 123169, United States, Georgia.
- **Ablabes badiolurus* Boë: *Lapsus* for *Ablabes baliodurus*; Phisalix, 1922.
- **Ablabes major* Günther: Phisalix, 1922.
- Ablabes porphyriacus* (Boulenger): See *Coluber prophyriacus* Cantor.
- Ablabes punctatus* Duméril: See *Coronella punctata* (Linné).
- Achalinus spinalis* Peters: A.M.N.H. No. 34620, China, Fukien, Chungan-Hsien.
- **Achrochordus javanicus* Hornstedt: C.G. No. 2541, Thailand, 15 kilometers from Bangkok; Phisalix, 1922.
- Ahaetulla fasciolata* (Fischer): A.M.N.H. No. 2917, Indonesia, Sumatra.
- Ahaetulla mycterizans* (Linné): A.M.N.H. No. 43383, "India"; C.G. No. 2710, Thailand. See also *Dryophis mycterizans* Linné.
- Ahaetulla prasina* (Boë): A.M.N.H. No. 71525, Territory of New Guinea, Borneo, Buntok; C.G. No. 2778, Thailand, 800 kilometers south of Bangkok. See also *Dryophis prasinus* (Boë).
- Alsophis portoricensis* Reinhardt and Lütken: C.M. No. 1332, United States, Puerto Rico, Utuado; C.M. No. 23126, United States, Puerto Rico, Humacao.
- Alsophis vudi* Cope: C.M. No. 34178, West Indies, North Bimini, Easter Key.
- Amphiesma mairi* (Gray): A.M.N.H. No. 85686, Territory of New Guinea, Eastern Highlands District, Krathke, Mt. Arau.
- Amphiesma parallela* (Boulenger): See *Tropidonotus parallelus* Boulenger.
- Amphiesma stolata* (Linné): See *Tropidonotus stolatus* (Linné).
- Amphiesma subminiatus* Duméril and Bibron: See *Macropisthodon subminiatus* Schlegel.
- Aparallactus modestus* (Günther): C.M. No. 9253, Cameroon, Lolodorf.
- Arizona elegans* Kennicott: A.M.N.H. No. 85233, Mexico, Nuevo Leon; U.M.M.Z. No. 71967, United States, Texas.
- Atractus badius* Boë: Phisalix, 1922.
- Atractus latifrontalis* Garman: Phisalix, 1922.
- Atretium schistosus* (Daudin): See *Helicops schistosus* Daudin.
- Boa constrictor* Linné: Smith and Bellairs, 1947.
- Boaedon fuliginosus* (Boë): See *Boodon fuliginosus* Boë.
- Boaedon lineatus* Duméril and Bibron: See *Boodon bilineatus* Duméril and Bibron; *Boodon quadrilineatus* Duméril and Bibron.
- Boaedon virgatus* (Hallowell): U.M.M.Z. No. 61199, "Africa."
- Boiga blandingi* (Hallowell): C.M. No. 9247, Cameroon, Ripindi.
- Boiga ceylonensis* (Günther): See *Dipsas ceylonensis* Günther.
- Boiga dendrophila* (Boë): A.M.N.H. No. 86559, Indonesia, Java. See also *Dipsas dendrophila* Boë.
- Boiga dendrophila latifasciata* (Seba): C.M. No. 2138, Philippines, Agusan, Bunawan.
- Boiga fusca* (Gray): C.M. 22050, no data. See also *Dipsas fusca* (Gray).
- Boiga irregularis* (Merrem): See *Dipsas irregularis* Merrem.
- Boiga pulverulenta* (Fischer): C.M. No. 6819, Cameroon, Sangrelina, Foulassi.
- Boiga trigonata* (Schneider): See *Dipsas trigonata* (Schneider).
- **Boodon bilineatus* Duméril and Bibron = *Boaedon lineatus* Duméril and Bibron: Phisalix, 1922.
- **Boodon fuliginosus* Boë = *Boaedon fuliginosus* (Boë): Phisalix, 1922.
- **Boodon quadrilineatus* Duméril and Bibron = *Boaedon lineatus* Duméril and Bibron: Phisalix, 1922.
- Bothrophthalmus lineatus* (Peters): C.M. No. 9304, Cameroon, Lolodorf.

- Brachyophis revoili* Mocquard: C.G. No. 2438, Somali Republic.
- Calamaria schlegeli schlegeli* Duméril and Bibron: A.M.N.H. No. 2878, Indonesia, Sumatra.
- Calamaria septentrionalis* Boulenger: A.M.N.H. No. 24535, China, Fukien, Chungan-Hsien; Phisalix, 1922.
- Cerberus rhynchops* (Schneider): C.G. No. 2715, Thailand, 38 kilometers from Bangkok at river mouth; West, 1895; Sarkar, 1923. See also *Coluber cerberus* (Daudin).
- Chironius carinatus* (Linné): C.M. No. 33770, Brazil, Rio de Janeiro, Vassouras. See also *Herpetodryas carinatus* (Linné).
- Chlorophis emini* Günther = *Philothamnus irregularis* (Leach): Phisalix, 1922.
- Chlorophis heterodermus* Hallowell = *Philothamnus heterodermus* (Hallowell): Phisalix, 1922.
- Chrysopelea ornata* (Shaw): C.G. No. 2545, Thailand, 300 kilometers south of Bangkok.
- Chrysopelea paradisi* (Boie): C.M. No. 2567, Philippines, Balabac.
- Clelia clelia* (Daudin): U.M.M.Z. No. 62820, "Brasil."
- Coelopeltis insignitus* Wagler (*sic*) = *Malpolon monspessulanus* (Hermann): Viaud-Grand-Mairais, 1880a; 1880b.
- Coelopeltis lacertina* Schlegel = *Malpolon monspessulanus* (Hermann): West, 1895.
- Coelopeltis monspessulana* (Hermann) = *Malpolon monspessulanus* (Hermann): Radovanović, 1932.
- Coluber aesculapii* (Linné): Duvernoy, 1833. See also *Coluber esculapii*.
- Coluber austriacus* Laurenti = *Coronella austriaca* (Laurenti): Duvernoy, 1832.
- Coluber cerberus* (Daudin) = *Cerberus rhynchops* (Schneider): Duvernoy, 1833.
- **Coluber conspicillatus* Boie = *Elaphe conspicillata* (Boie): Phisalix, 1922.
- Coluber constrictor* Linné: A.M.T. No. 1, no data.
- **Coluber deppei* (Duméril and Bibron) = *Pituophis deppei* (Duméril and Bibron): Phisalix, 1922.
- **Coluber esculapii* Lacépède: *Lapsus* for *Coluber aesculapii* (Linné); Phisalix, 1922.
- Coluber fasciolatus* Shaw: Smith and Bellairs, 1947.
- Coluber gemonensis* (Laurenti): See *Zamenis gemonensis* (Laurenti).
- **Coluber helena* Daudin = *Elaphe helena* (Daudin): Phisalix, 1922.
- Coluber hippocrepsis* Linné: See *Zamenis hippocrepsis* (Linné).
- Coluber jaspideus* (Hermann): Duvernoy, 1833. (Unable to identify this species.)
- Coluber jepitrodes* (Hermann): Duvernoy, 1833. (Unable to identify this species.)
- **Coluber melanurus* Schlegel = *Drymarchon corais melanurus* Schlegel: Phisalix, 1922.
- **Coluber phyllophis* Boulenger = *Elaphe carinata*: (Günther): Phisalix, 1922.
- Coluber porphyriacus* Cantor = *Ablabes porphyriacus* Boulenger: Phisalix, 1922.
- Coluber radiatus* Schlegel = *Elaphe radiata* (Schlegel): Phisalix, 1922.
- Coluber ravergieri* Ménetriés: E.K. No. M2, Israel.
- **Coluber scalaris* Schinz = *Elaphe scalaris* (Schinz): Phisalix, 1922.
- **Coluber taeniurus* Cope = *Elaphe taeniurus* (Cope): Phisalix, 1922.
- Coluber viridiflavus* Lacépède: Leydig, 1873.
- Coluber viridiflavus* var. *carbonarius* Schreiber: Leydig, 1873; Oppel, 1898; Noguchi, 1909.
- Coniophanes fissidens* (Günther): U.M.M.Z. No. 84486A, Mexico, Oaxaca.
- Coniophanes fissidens punctigularis* Cope: U.M.M.Z. No. 57963, Panama.
- Coniophanes imperialis* (Baird and Girard): C.G. No. 2619, no data.
- Conophis vittatus* Peters: A.M.N.H. No. 66337, Mexico, Guerrero, near La Union.
- Conopsis biserialis* Taylor and Smith: A.M.N.H. No. 75874, Mexico, Michoacan.
- Conopsis nasus* (Günther): See *Contia nasus* Günther.
- Contia nasus* Günther = *Conopsis nasus* (Günther): Phisalix, 1922.
- Coronella austriaca* (Laurenti): A.M.N.H. No. 21801, Austria, Fleishling; Phisalix, 1922. See also *Coluber austriacus* Laurenti; *Coronella laevis* Lacépède.
- Coronella girondica* (Daudin): Phisalix, 1922.
- Coronella laevis* Lacépède = *Coronella austriaca* Laurenti: Leydig, 1873; Oppel, 1898.
- Coronella laevis* Merrem [*sic*]: Noguchi, 1909, probably = *Coronella austriaca* (Laurenti).
- Coronella punctata* Linné = *Ablabes punctatus* Duméril: Phisalix, 1922.
- Coryphodon korros* (Schlegel) = *Ptyas korros* (Schlegel): Neimann, 1892; Oppel, 1898; Noguchi, 1909.
- Crotaphopeltis hotamboeia* (Laurenti): M.C.Z. No. 71870, Somali Republic. See also *Leptodeira rufescens* (Gmelin); *Ophis albocinctus* Duvernoy; *Ophis heterurus* Duvernoy.
- Crotaphopeltis* sp. (see Gans, Laurent, and Pandit, 1965): M.C.Z. No. 71871, Somali Republic.
- Cyclocorus lineatus* (Reinhardt): A.M.N.H. No. 73419, Philippines, Mindoro Island, San José.
- Cylindrophis rufus* Laurenti: C.G. No. 2551, Thailand, Bangkok; Smith and Bellairs, 1947.
- Dasypeltis scabra* Linné: Kathariner, 1898; Oppel, 1898; Noguchi, 1909; Phisalix, 1922.
- Dendrelaphis caudolineatus* Gray: Phisalix, 1922.
- Dendrelaphis pictus* (Gmelin): A.M.N.H. No. 2835, Philippines, Mindanao; Neimann, 1892; Oppel, 1898; Phisalix, 1922; Sarkar, 1923.

- Dendrophidion percarinatus* (Cope): U.M.M.Z. No. 124069, Venezuela.
- Diadophis punctatus* (Linné): C.G. No. 162, United States, Florida.
- Dinodon rufozonatum rufozonatum* Cantor: A.M.N.H. No. 75952, Taiwan, mountains near Taipei; Phisalix, 1922.
- Dipsadoboa unicolor* Günther: A.M.N.H. No. 12470, Congo, Medje.
- Dipsas annulata* (Linné) = *Leptodeira annulata* (Linné): Neimann, 1892; Oppel, 1898.
- Dipsas brevifacies* (Cope): U.M.M.Z. No. 73030, Mexico, Yucatan.
- Dipsas ceylonensis* Günther = *Boiga ceylonensis* (Günther): West, 1895; 1898.
- Dipsas dendrophila* Boë = *Boiga dendrophila* (Boë): West, 1895.
- Dipsas fusca* (Gray) = *Boiga fusca* (Gray): West, 1895.
- Dipsas indica bucephala* Shaw: U.M.M.Z. No. 62794, Brazil.
- Dipsas irregularis* (Merrem) = *Boiga irregularis* (Merrem): West, 1895.
- Dipsas latifrontalis* (Boulenger): U.M.M.Z. No. 92048, Ecuador.
- Dipsas trigonata* (Schneider) = *Boiga trigonata* (Schneider): Sarkar, 1923.
- Dispholidus typus* (Smith): A.M.T. No. 5, no data; C.M. No. 6340, Southern Rhodesia, Mt. Selinda.
- Dromicodryas bernieri* Duméril and Bibron: Phisalix, 1922.
- Dromicus andreae nebulatus* (Barbour): C.M. No. 285, Cuba, Isle of Pines, Los Indios.
- Dromicus parvifrons protenus* Jan: A.M.N.H. No. 51393, Dominican Republic, Valle de Polo.
- Dromicus temminckii* Schlegel: Phisalix, 1922.
- Dromicus* sp.: A.M.N.H. No. 51396, Dominican Republic, Las Baotess.
- Dryadophis bifossatus* (Raddi): See *Drymobius bifossatus* (Raddi).
- Dryadophis boddaerti boddaerti* (Sentzen): A.M.N.H. No. 75965, Trinidad, Arima Valley, St. Patis Estate.
- Dryadophis dorsalis* (Bocourt): U.M.M.Z. No. 116544, Nicaragua.
- Dryadophis melanolomus alternatus* (Bocourt): U.M.M.Z. No. 71204, Costa Rica.
- Drymobius bifossatus* (Raddi) = *Dryadophis bifossatus* (Raddi): Phisalix, 1922.
- Drymobius margariiiferus* (Schlegel): A.M.N.H. No. 36176, "Panama"; U.M.M.Z. No. 122050, Mexico, Veracruz; Phisalix, 1922.
- Drymarchon corais couperi* Holbrook: U.M.M.Z. No. 67701, United States, Florida.
- Drymarchon corais melanurus* Schlegel: See *Coluber melanurus* Schlegel.
- Dryocalamus nympa* Daudin: Phisalix, 1922.
- Dryocalamus subannulatus* Duméril and Bibron: A.M.N.H. No. 2904, Indonesia, Sumatra.
- Dryophis mycterizans* Linné = *Ahaetulla mycterizans* (Linné): West, 1985; 1898; Sarkar, 1923.
- Dryophis prasinus* (Boë) = *Ahaetulla prasina* (Boë): Neimann, 1892; West, 1895; 1898; Oppel, 1898.
- Duberria lutrix* (Linné): C.G. No. 2228, Kenya, Lumbwa; A.M.N.H. No. 39187, Tanzania, Rungwe Mountains.
- Eirenis decemlineata* (Duméril and Bibron): A.M.N.H. No. 68159, Israel, west of Jordan River.
- Elaphe carinata* (Günther): C.G. No. 2889, "China." See also *Coluber phyllophis* Boulenger.
- Elaphe climacophora* (Boë): See *Elaphis virgatus* Schlegel.
- Elaphe conspiciolata* (Boë): See *Coluber conspiciolatus* Boë.
- Elaphe helena* (Daudin): See *Coluber helena* Daudin.
- Elaphe longissimus* Laurenti: U.M.M.Z. No. 67239, Austria.
- Elaphe mandarinus* (Cantor): C.G. No. 2886, "China."
- Elaphe moellendorffi* (Boettger): C.G. No. 2885, "China."
- Elaphe obsoleta* Say: U.M.M.Z. No. 112068, United States, Ohio.
- Elaphe quadrivirgata* Boë: U.M.M.Z. No. 68341A, Japan.
- Elaphe radiata* (Schlegel): C.G. No. 2887, "China." See also *Coluber radiatus* Schlegel.
- Elaphe scalaris* (Schinz): See *Coluber scalaris* Schinz.
- Elaphe subocularis* Brown: U.M.M.Z. No. 124026, United States, New Mexico.
- Elaphe taeniurus* (Cope): C.G. No. 2888, "China." See also *Coluber taeniurus* Cope.
- Elaphe triaspis intermedia* (Boettger): U.M.M.Z. No. 118522, Mexico, Guerrero.
- Elaphis virgatus* Schlegel = *Elaphe climacophora* (Boë): Neimann, 1892; Oppel, 1898; Noguchi, 1909.
- Enhydris bocourti* (Jan): C.G. No. 2517, Thailand, Bangkok; C.G. No. 2550, Thailand, Bangkok.
- Enhydris enhydris* (Schneider): C.G. No. 2652, Thailand, Bangkok; C.G. No. 2653, Thailand, Bangkok.
- Enhydris* sp.¹: C.G. No. 2788, Thailand, suburb of Bangkok.
- Erpeton tentaculatum* Lacépède: C.G. No. 2787, Thailand, 285 kilometers south of Bangkok.

¹ This specimen is deposited in the collection of the American Museum of Natural History. It could not be identified through any available key and may represent a new form.

- Erythrolamprus aesculapii* Linné: C.M. No. 1842, "South America"; West, 1896.
- Erythrolamprus bizona* Jan: U.M.M.Z. No. 57924, Panama.
- Erythrolamprus venustissimus* Bocourt: U.M.M.Z. No. 62728, no data.
- Eteirodipsas colubriens* = *Eteirodipsas colubrina* (Schlegel): West, 1895.
- Farancia abacura* (Holbrook): A.M.N.H. No. 88338, United States, South Carolina, Jasper County; U.M.M.Z. No. 109335, United States, Florida.
- Fimbrios klossi* Smith: C.N.H.M. No. 71699, "Indochina."
- Fordonia leucobalia* Schlegel: C.N.H.M. No. 67271, Borneo, Sarawak.
- Gastropyxis smaragdina* (Schlegel): A.M.N.H. No. 10097, "French Congo"; Phisalix, 1922.
- Geophis multitorques* Günther: A.M.N.H. No. 19773, Mexico.
- Gonyophis margaritatus* (Peters): C.N.H.M. No. 138677, Borneo, Sarawak.
- Grayia smithii* (Leach): Phisalix, 1922.
- Haldea striatula* (Linné): U.M.M.Z. No. 111611, United States, Texas.
- Hapsidophrys lineata* Fischer: Phisalix, 1922.
- Helicops angulatus* (Linné): A.M.N.H. No. 81458, Trinidad, Sangre Grande, Rio Grande Forest.
- Helicops leopardina* (Schlegel): C.M. No. 31417, Argentina, Sante Fe, La Capital, Rio Colastino.
- Helicops polylepsis* Günther: C.M. No. 2038, Brazil, Sao Antonio de Guapore.
- Helicops schistosus* Daudin = *Atretium schistosus* (Daudin): Phisalix, 1922.
- Herpetodryas carinatus* (Linné) = *Chironius carinatus* (Linné): Neimann, 1892; Opper, 1898; Noguchi, 1909; Phisalix,¹ 1922.
- Heterodon nasicus* Baird and Girard: U.M.M.Z. No. 35126, United States, Iowa; Phisalix, 1922.
- Heterodon platyrhinos* Latrielle: U.M.M.Z. No. 70750, United States, Michigan.
- Heterodon* sp.: West, 1898.
- Homalopsis buccata* (Linné): C.G. No. 2516, Thailand, 20 kilometers south of Bangkok; C.G. No. 2548, Thailand, Bangkok; C.G. No. 2857, Thailand, Bangkok; West, 1895.
- Hormonotus modestus* (Duméril and Bibron): Phisalix, 1922.
- Hydrodynastes bicincta* (Hermann): A.M.N.H. No. 88401, Colombia, Raudal de Yurupari, Rio Vaupes.
- Hydrops marti callostictus* Günther: A.M.N.H. No. 55299, Peru, Loreto, Iquitos, Rio Itaya.
- Hypsiglena torquata deserticola* Tanner: C.G. No. 2483, no data.
- Imantodes cenchoa* (Linné); C.M. No. 25897, "Central America," banana import; U.M.M.Z. No. 124170, Panama.
- Lamprophis rogeri* Mocquard: Phisalix, 1922.
- Lampropeltis calligaster* (Harlan): A.M.N.H. No. 66555, United States, Texas, Lamar County, Camp Maxey.
- Lampropeltis doliata polyzona* Cope: U.M.M.Z. No. 74928, Guatamala.
- Lampropeltis getulus boylii* (Baird and Girard): A.M.N.H. No. 36719, no data.
- Lampropeltis getulus holbrooki* (Stejneger): C.G. No. 2757, no data.
- Lampropeltis pyromelana* (Cope): A.M.N.H. No. 15086, United States, Arizona, Cochise County, Huachuca Mountains, Marshall Canyon.
- Lampropeltis rhombomaculata* (Holbrook): C.M. No. 24929, United States, Mississippi, Forrest County.
- Leimadophis almadensis* (Wagler): C.M. No. 2968, Bolivia, Santa Cruz, Buenavista.
- Leimadophis melanotus* (Shaw): U.M.M.Z. No. 124283, Venezuela.
- Leimadophis reginae* (Linné): U.M.M.Z. No. 92027, Ecuador.
- Leimadophis typhlus* (Linné): C.M. No. 34842, Bolivia, Santa Cruz, San José de Chiquitos.
- Leptodeira annulata* (Linné): U.M.M.Z. No. 121276, Mexico, Veracruz; West, 1895. See also *Dipsas annulata* (Linné).
- Leptodsira latifasciata* (Günther): U.M.M.Z. No. 120223, Mexico, Michoacan.
- Leptodeira rufescens* (Gmelin) = *Crotaphopeltis hotamboeia* (Laurenti), West, 1895.
- Leptodeira splendida* Günther: U.M.M.Z. No. 121547, Mexico, Michoacan.
- Leptophis diplotropis* (Günther): U.M.M.Z. No. 114585, Mexico, Oaxaca.
- Leptophis liocercus* Günther: Phisalix,² 1922.
- Leptophis nigromarginatus* Günther: Phisalix, 1922.
- Leptophis occidentalis* Günther = *Leptophis richardi occidentalis* (Günther): Phisalix, 1922.
- Leptophis richardi occidentalis* (Günther): C.M. No. 37259, Ecuador, Guayaquil, banana import. See also *Leptophis occidentalis* Günther.
- Leptotyphlops macrorhynchops* (Jan): C.G. No. 3148, Israel; C.G. No. 3149, Israel.
- Lioheterodon madagascariensis* Duméril and Bibron: Phisalix, 1922.
- Lioheterodon modestus* Günther: Phisalix, 1922.
- Liophis albiventris* Jan: Phisalix, 1922.

¹ Phisalix included this form in two groups: (1) those with maxillary teeth of equal size and (2) those with maxillary teeth not of equal size but with the posterior teeth enlarged.

² Oliver (1948) did not recognize *Leptophis liocercus* Günther but placed *Coluber liocercus* Wied in synonymy with *Thalerophis richardi liocercus* Wied.

- Liophis andreae* Reinhardt: *Lapsus* for *Liophis andreae* Reinhardt and Lutkens: Phisalix, 1922.
- Liophis cobella* (Linné): U.M.M.Z. No. 51256, Peru. See also *Rhadinaea cobella* Linné.
- Liophis merremii* (Wied) = *Liophis miliaris* (Linné): Neimann, 1892.
- Liophis miliaris* (Linné): A.M.T. No. 4, no data. See also *Liophis merremii* (Wied).
- Liopholidophis dolichocercus* Peracca; Phisalix, 1922.
- Liotyphlops albirostris* Peters: Haas, 1964.
- Lycodon aulicus* (Linné): A.M.N.H. No. 86754, Philippines, Negros Island, Cuernos de Negros, 20 miles west of Dumaguete City, Maite River, Camp Lookout; C.M. No. 2455, Philippines, La Carlota; Phisalix, 1922; Sarkar, 1923.
- **Lycophidion capense* (Smith): Phisalix, 1922.
- Lystrophis dorbignyi* (Duméril and Bibron): C.M. No. 31419, Argentina, Santa Fe, La Capital, Rio Colastine; Phisalix, 1922.
- Lytorhynchus diadema* Duméril and Bibron: Phisalix, 1922.
- Macropisthodon rudis* Boulenger: A.M.N.H. No. 34520, China, Fukien, Chungan-Hsein.
- Macropisthodon subminiatus* Schlegel = *Amphisma subminiaturum* Duméril and Bibron: Phisalix, 1922.
- Malpolon monspessulanus* (Hermann): C.G. No. 2185, no data. See also *Coelopeltis insignatus* Wagler (*sic*); *Coelopeltis lacertina* Schlegel; *Coelopeltis monspessulana* (Hermann).
- Masticophis bilineatus* Jan: U.M.M.Z. No. 69661, United States, Arizona.
- Masticophis mentovarius* (Duméril, Bibron, and Duméril): U.M.M.Z. No. 116548, Nicaragua.
- Masticophis taeniatus ornatus* Baird and Girard: U.M.M.Z. No. 123469, United States, Texas.
- Mehelya capensis* (Smith): See *Simocephalus capensis* Smith.
- Mehelya poensis* (Smith): A.M.N.H. No. 63769, Uganda, Nyenga.
- Miodon gabonensis collaris* (Peters): A.M.N.H. No. 12449, Congo, Medje.
- Myron richardsoni* Gray: C.N.H.M. No. 97649, Australia, Northern Territory.
- Natriciteres fuliginosus* (Günther): See *Tropidonotus fuliginosus* Günther.
- Natriciteres olivacea* (Peters): A.M.N.H. No. 11913, Congo, Medje.
- Natrix cyclopion floridana* Goff: C.M. No. 36936, United States, Florida, Collier County; U.M.-M.Z. No. 106289, United States, Florida.
- Natrix erythrogaster erythrogaster* Forster: U.M.-M.Z. No. 103183, United States, South Carolina.
- Natrix maura* Linné: See *Tropidonotus viperinus* Latreille.
- Natrix natrix* (Linné): Smith and Bellairs, 1947.
- See also *Tropidonotus natrix* (Linné); *Tropidonotus torquatus* Lacépède.
- Natrix rhombifera* Hallowell: U.M.M.Z. No. 77734, United States, Arkansas.
- Natrix sipedon pleuralis* Cope: U.M.M.Z. No. 84144, United States, South Carolina.
- Natrix taxispilota* Holbrook: U.M.M.Z. No. 110420, United States, Florida.
- Natrix tessellata* (Laurenti): See *Tropidonotus tessellatus* (Laurenti).
- Ninia atrata* (Hallowell): See *Streptophorus atratus* Hallowell.
- Oligodon ornatus musyi* (Roux): A.M.N.H. No. 34592, China, Fukien, Chungan-Hsein.
- Oligodon subgriseus* Duméril and Bibron: Phisalix, 1922.
- Opheodrys vernalis* (Harlan): C.G. No. 2378, United States, New York, Wyoming County.
- Ophis albocinctus* Duvernoy = *Crotaphopeltis hotamboeia* (Laurenti): Duvernoy, 1833.
- Ophis heterurus* Duvernoy = *Crotaphopeltis hotamboeia* (Laurenti): Duvernoy, 1833.
- Ophisthotropis latouchi* (Boulenger): A.M.N.H. No. 33928, China, Fukien, Yenping.
- Oxybelis fulgidus* (Daudin): C.M. No. 2027, Colombia, Cacagualito; West, 1895; Sarkar, 1923.
- Oxyrhopus petola* (Linné): A.M.N.H. No. 25185, Ecuador, Gualaquiza; U.M.M.Z. No. 80428, Guyana (former British Guiana).
- Pareas stanleyi* (Boulenger): A.M.N.H. No. 34606, China, Fukien, Chungan-Hsein.
- Philodryas schotti* (Schlegel): A.M.N.H. No. 75314, Paraguay, vicinity of Asuncion; West, 1895.
- Philothamnus dorsalis* (Bocage) = *Philothamnus semivariiegatus* (Smith): Phisalix, 1922.
- Philothamnus heterodermus* (Hallowell): See *Chlorophis heterodermus* Hallowell.
- Philothamnus irregularis* (Leach): See *Chlorophis emini* Günther.
- Philothamnus semivariiegatus* (Smith): See *Philothamnus dorsalis* (Bocage).
- Pituophis catenifer deserticola* Stejneger: U.M.-M.Z. No. 124606, United States, Nevada.
- Pituophis deppei* (Duméril and Bibron): See *Coluber deppei* (Duméril and Bibron).
- Phiocercus elapoides* Cope: U.M.M.Z. No. 124765, Mexico, Chiapas.
- Polyodontophis collaris* (Gray) = *Sibynophis collaris* (Gray): Phisalix, 1922.
- Polyodontophis subpunctatus* Duméril and Bibron: Phisalix, 1922.
- **Prosymna meleagris* (Reinhardt): Phisalix, 1922.
- Psammodynastes pulverulentus* (Boie): A.M.N.H. No. 86769, Philippines, Negros Island, Cuernos de Negros, Maite River, Camp Lookout; Neimann, 1892; West, 1895; Opper, 1898 (after Neimann).

- Psammophis schokari* (Förskal): A.M.N.H. No. 81998, Pakistan, Tatta District.
- Psammophis sibilans sibilans* (Linné): C.M. No. 37529, "Africa"; West, 1895 (teeth only were examined); Sarkar, 1923.
- Psammophylax tritaeniatus multisquamis* (Love-ridge): C.G. No. 2522, no data.
- **Pseudaspis cana* (Bocage): A.M.N.H. unnumbered, no data; Phisalix, 1922.
- Pseudoeryx plicatilis* Bocourt: A.M.N.H. No. 74781, "Colombia."
- Pseudoxenodon bambusicola* Vogt: A.M.N.H. No. 27753, China, Hainan, Nodoo.
- Pseudoxenodon macrops* Blyth: Phisalix, 1922.
- Pseudoxenodon sinensis* Boulenger: A.M.N.H. No. 12791, China, Yunnan, Yunnanfu; Phisalix, 1922.
- Seustes sulphureus* (Wagler): A.M.N.H. No. 78990, Trinidad, Arima Valley, St. Patis Estate.
- Ptyas korros* (Schlegel): See *Coryphodon korros* (Schlegel); *Zamenis korros* Schlegel.
- Ptyas mucosus* (Linné): C.G. No. 2786, Thailand, 800 kilometers south of Bangkok. See also *Zamenis mucosus* Linné.
- Rhabdophis subminiata* (Schlegel): C.G. No. 2658, Thailand, 800 kilometers south of Bangkok. See also *Tropidonotus subminiatus* Schlegel.
- Rhabdophis tigrina lateralis* (Berthold): C.M. No. 34953, Korea, Kyongii-do Province, 25 miles north-northwest of Seoul. See also *Tropidonotus lateralis* Duméril and Bibron.
- Rhadinaea cobella* Linné = *Liophis cobella* (Linné): Phisalix, 1922.
- Rhadinaea flavilata* Cope: A.M.N.H. No. 63891, United States, Florida, Okeechobee County.
- **Rhadinaea fusca* Boulenger = *Liophis miliaris* (Linné): Phisalix, 1922.
- Rhadinaea merremii* Wied = *Liophis miliaris* (Linné): Phisalix, 1922.
- Rhadinaea vittata* Peters: Phisalix, 1922. Uncertain as to whether reference is to *Conophis vittatus* Peters or to *Rhadinaea vittata* Jan.
- Rhamphiophis oxyrhynchus rostratus* Peters: A.M.N.H. No. 73833, no data.
- Rhinobothryum lentiginosum* (Scopoli): A.M.N.H. No. 55610, Peru, Loreto, Requena, Monte Carmelo.
- Rhinocheilus leonti leonti* Baird and Girard: A.M.N.H. No. 75177, United States, California, Los Angeles County, Pallet Creek.
- Salvadora grahamiae* Baird and Girard: A.M.N.H. No. 80181, United States, Arizona, Cochise County, Chiricahua Mountains, Turkey Creek; U.M.M.Z. No. 123474, United States, New Mexico.
- Salvadora mexicana* Duméril and Bibron: U.M.M.Z. No. 114427, Mexico: Michoacan.
- Scaphiodontophis annulatus* Duméril, Bibron, and Duméril: A.M.N.H. No. 70239, Honduras, Atlantida, Lancetilla.
- Scaphiophis albopunctatus* Peters: A.M.N.H. No. 12147, Congo, Niangara; Phisalix, 1922.
- Sibon nebulata nebulata* (Linné): A.M.N.H. No. 64479C, Trinidad, Tucker Valley; U.M.M.Z. No. 119749, Mexico, Oaxaca.
- Sibynomorphus mikani newwiedi* von Ihering: U.M.M.Z. No. 79678, Brazil.
- Sibynophis chinensis chinensis* (Günther): A.M.N.H. No. 34534, China, Fukien, Chungan-Hsien.
- Sibynophis collaris* (Gray): See *Polydontophis collaris* (Gray).
- Simocephalus capensis* Smith = *Mehelya capensis* (Smith): Phisalix,¹ 1922.
- Simotes arnensis* Shaw: Phisalix, 1922.
- Simotes taeniatus* Günther: Phisalix, 1922.
- Simotes violaceus* Cantor: Phisalix, 1922.
- Spalerosophis diadema* (Schlegel): A.M.N.H. No. 85458, Pakistan, Karachi (Federal) District, Malir. See also *Zamensis diadema* (Schlegel).
- **Spilotes anomalus* Boettger: *Lapsus* for *Spilotes anomalus*: Phisalix, 1922.
- Spilotes pullatus* Linné: U.M.M.Z. No. 121141, Mexico, Veracruz.
- Stegonotus modestus* (Schlegel): A.M.N.H. No. 85714, Territory of New Guinea, Morobe District, Upper Markham Valley, Umi River.
- Stenorhina freminivilli* Duméril and Bibron: A.M.N.H. No. 69968, Guatemala, El Peten, Sojio.
- Storeria occipitomaculata* (Storer): C.G. No. 2377, United States, New York, Wyoming County.
- **Streptophorus atratus* Hallowell = *Nina atrata* (Hallowell): Phisalix, 1922.
- Tachymenis chilensis* Schlegel: A.M.N.H. No. 75053, "Chile."
- Tantilla rubra* Cope: U.M.M.Z. No. 107145, Mexico, Tamaulipas.
- Tarbophis variegatus* Reinhardt = *Telescopus variegatus* (Reinhardt): Sarkar, 1923.
- Tarbophis vivax* Bonaparte = *Telescopus fallax* (Fleischmann): Radovanović, 1932.
- Telescopus fallax* (Fleischmann): E.K. No. M3, Isreal. See also *Tarbophis vivax* Bonaparte.
- Telescopus semiannulatus* Smith: A.M.N.H. No. 49926, Tanganyika, Mawere-Shamba.
- Thamnodynastes nattereri* Mikan: West, 1895.
- Thamnophis cyrtopsis cyrtopsis* (Kennicott): U.M.M.Z. No. 69679, United States, Texas.
- Thamnophis elegans vagrans* Baird and Girard: U.M.M.Z. No. 122924, United States, Colorado.
- Thamnophis sirtalis* (Linné): A.M.T. No. 2,

¹ Phisalix included this form in two groups: (1) those with maxillary teeth equal in size and (2) those with posterior fangs.

- United States, New York, Erie County; Smith and Bellairs, 1947.
- Thelotornis kirtlandi* (Hallowell): U.M.M.Z. No. 61241, Natal.
- Trachischium fuscum* Günther: Phisalix, 1922.
- Trachischium tenuiceps* (Blyth): C.N.H.M. No. 109763, Nepal.
- Trachyboa boulengeri* Peracca: Smith and Bellairs, 1947.
- Tretanorhinus variabilis variabilis* Duméril and Bibron: A.M.N.H. No. 81153, Cuba, Las Villas, 1.6 kilometers east of Sierra Morena.
- Trimerorhinus rhombeatus* Seba: West, 1895.
- Trimorphodon biscutatus* (Duméril and Bibron): A.M.N.H. No. 66153, Mexico, Guerrero, Magueyes, Laguna Coyuca; U.M.M.Z. No. 123332, Costa Rica.
- Trimorphodon tau* Cope: U.M.M.Z. No. 118949, Mexico, Michoacan.
- Tropidodipsas sartorii* Cope: A.M.N.H. No. 56190, no data.
- Tropidonotus fuliginosus* Günther = *Natriciteres fuliginosus* (Günther): Phisalix, 1922.
- Tropidonotus lateralis* Duméril and Bibron = *Rhabdophis tigrina lateralis* (Berthold): Phisalix, 1922.
- Tropidonotus melanogaster* Peters = *Natrix melanogaster* (Peters): Phisalix, 1922.
- Tropidonotus natrix* (Linné) = *Natrix natrix* (Linné): Duvernoy, 1832; Leydig, 1873; Opper, 1898; Phisalix, 1922; Radovanović, 1932.
- Tropidonotus parallelus* Boulenger = *Amphiesma parallela* (Boulenger): Phisalix, 1922.
- Tropidonotus piscator* Schneider = *Xenochrophis piscator* (Schneider): Phisalix, 1922.
- Tropidonotus stolatus* Linné = *Amphiesma stolata* (Linné): Phisalix, 1922; Sarkar, 1923.
- Tropidonotus subminiatus* Schlegel = *Rhabdophis subminiata* (Schlegel): Neimann, 1892; Opper, 1898; Noguchi, 1909; Phisalix, 1922.
- Tropidonotus tessellatus* (Laurenti) = *Natrix tessellata* (Laurenti): Leydig, 1873; Opper, 1898; Noguchi, 1909.
- Tropidonotus torquatus* Fleming, *lapsus* for *Tropidonotus torquatus* Lacépède = *Natrix natrix* (Linné): Noguchi, 1909.
- Tropidonotus viperinus* Latreille, *lapsus* for *Tropidonotus viperinus* Sonnini and Latreille = *Natrix maura* (Linné): Phisalix, 1922.
- Tropidonotus vittatus* Laurenti = *Xenochrophis vittatus* (Laurenti): Phisalix, 1922.
- Trypanurgos compressus* (Daudin): A.M.N.H. No. 49090, Ecuador, Río Pastaza.
- Typhlops diardi* Schlegel: Smith and Bellairs, 1947.
- Typhlops simoni* (Boettger): C.G. No. 3145, Israel.
- Typhlops vermicularis* Merrem: C.G. No. 3146, Israel.; C.G. No. 3147, Israel.
- Uromacer catesbyi* (Schlegel): A.M.N.H. No. 40988, Dominican Republic, La Bracita.
- Xenochrophis piscator* (Schneider): A.M.N.H. No. 84528, Taipei, Yung-Foh-Lee, Yang-Ming-Shan; C.G. No. 2646, Thailand, Bangkok; C.G. No. 2708, Thailand, Bangkok; C.G. No. 2709, Thailand, Bangkok.
- Xenochrophis vittata* (Laurenti): See *Tropidonotus vittatus* Laurenti.
- Xenodermus javanicus* Reinhardt: C.N.H.M. No. 67427, Indonesia, Java, surroundings of Wonosobe.
- Xenodon merremi* (Wagler): C.M. No. 34818, Bolivia, Santa Cruz, San José de Chiquitos; U.M.M.Z. No. 62986, Brazil.
- Xenodon newwiedi* Cope: U.M.M.Z. No. 109056, Brazil.
- Xenodon severus* (Linné): Phisalix, 1922.
- Xenopeltis unicolor* Reinhardt: Smith and Bellairs, 1947.
- Xylophis perroteti* Boulenger: Phisalix, 1922.
- Zamenis diadema* Schlegel = *Spalerosophis diadema* (Schlegel): Phisalix, 1922.
- Zamenis gemonensis* (Laurenti) = *Coluber gemonensis* (Laurenti): Phisalix, 1922.
- Zamenis hippocrepis* (Linné) = *Coluber hippocrepis* (Linné): Phisalix, 1922.
- Zamenis korros* Schlegel = *Ptyas korros* (Schlegel): Phisalix, 1922.
- Zamenis mucosus* Linné = *Ptyas mucosus* (Linné): Phisalix, 1922.
- Zaocys dhumnades* (Cantor): A.M.N.H. No. 61598, no data.

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