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# The Neotropical Colubrid Snake Genus *Liophis*. The Generic Concept

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**Abstract:** The Neotropical colubrid snake genus *Liophis* is redefined and includes the currently recognized genera *Dromicus* (*Leimadophis sensu lato*) and *Lygophis*. A summary table is included that contains 275 taxa heretofore thought to belong to these genera, with their original and present nomenclatural status. Many of these names have been misapplied to the genus *Liophis* and are allocated to other genera. A brief history is presented of the use of generic characters such as maxillary teeth, maxillary diastema, scale pits, hemipenes, and color pattern as they apply to the genera *Liophis*, *Dromicus* and *Lygophis*. A new generic description, diagnosis, and statements of content and distribution are presented for *Liophis*. A summary of our knowledge of the habitat, diet, and reproduction of the species of *Liophis* is given.

A brief discussion and dendrogram of the possible relationships of the tribe Xenodontini is presented.

## INTRODUCTION

Throughout the history of the study of the species associated with the genera *Dromicus*, *Leimadophis*, *Liophis* and *Lygophis*, herpetologists have been confused and dismayed at the complexity of the variation exhibited by the majority of the species. This confusion has led to a vast number (275) of species and varietal descriptions having been applied to the above genera during the past 220 years (Table 1). Variation is so great that Linnaeus' 10th edition of *Systema Naturae* (1758) contains 11 species of which five are currently considered synonyms. By the time Wagler described *Liophis* in 1830, 32 species had been described of which 19 are synonyms. By 1899, 148 names were proposed of which 103 are currently synonyms. From 1900 to the present, 79 forms were described of which 40 are synonyms. Peters and Orejas-Miranda (1970) recorded 37 forms of *Leimadophis*, 25 of *Liophis*, and 10 of *Lygophis* from the mainland of Central and South America. Of these, 18 taxa do

not belong to the above genera and only about 24 of the remaining taxa are valid species. About 110 of the 275 proposed taxa actually belong to the following genera: *Alsophis*, *Antillophis*, *Arrhyton*, *Enulius*, *Ialtris*, *Liopholidophis*, *Masticophis*, *Mastigodryas*, *Philodryas*, *Pliocercus*, *Rhadinaea*, *Saphenophis*, *Sordellina*, *Tachymenis*, and *Umbrivaga* (see Table 1).

It is easy to understand why there are so many synonyms in this group, considering the variation in characters within samples, much less geographic variation between samples. Juveniles have been allocated to one genus whereas the adults have been placed in another. Individuals with no scale row reduction have been described as belonging to a different species from conspecific individuals with scale row reductions. In one instance in what I consider to be a wide ranging polymorphic species, five young individuals with different color patterns were described as five different species, even though the adults are similar in appearance.

The pre-1971 history of the 275 names associated with some concept of *Dromicus*, *Leimadophis*, *Liophis* and *Lygophis*, is so confusing that any reference to these genera within any general work may, in reality, represent any one of 34 genera utilized for one or more of the species during the past 155 years. For example, Underwood (1967) described in detail the osteology of *Dromicus callilaemus*, which now belongs to the genus *Arrhyton*, a member of the tribe *Alsophiini*, unrelated to *Dromicus* (*sensu stricto*) of the tribe *Xenodontini*. Jan's (1863) "Elenco," Jan and Sordelli's (1860-1881) "Iconographie," Boulenger's (1893-1896) "Catalogues," Amaral's (1929) "Neotropical Snakes," and Peters and Orejas-Miranda's (1970) "Catalogues" are important works that cannot be used with accuracy because so many species are assigned to the wrong genera.

One of the most important problems facing herpetologists today is the absence of a unifying generic concept for snakes. Herpetologists have not reached a consensus as to how this problem can be solved, even with the aid of modern mathematics and the techniques for the study of additional biological attributes (karyology, proteins) now available. We still perceive *Coluber* and *Masticophis*, *Nerodia* and *Thamnophis*, *Micruurus* and *Micruroides*, and *Crotalus* and *Sistrurus* (to mention a few) as separate genera, based primarily upon numbers of teeth, head and body scale fusions and/or divisions.

The problem of ophidian generic knots cannot be resolved by "Alexander's sword," however, for each is a problem unto itself. Most herpetologists agree that snakes have an inordinate amount of conservative characteristics. The possibilities for convergence and/or parallelism of conservative attributes tends to belie attempts at establishing sister groups. Nearly every available character in current use (i.e., skull osteology, maxillary teeth, hemipenes, vertebrae, lungs, kidneys, visual

cells, chromosomes, and squamative features) tends to unify subfamilial categories, but they overlap broadly in genera with large numbers of species. Marx and Rabb's (1972) attempt to identify derived states of 50 characters associated with advanced snakes, pointed out many intra-generic variations in osteological characters, yet also showed many intergeneric similarities without variation. Our attempts to "pigeonhole" species groups into operational taxonomic units is frequently based upon a single character (e.g., anal plate entire vs. divided) and, consequently, we overlook the myriad of other attributes that are shared between the species. Perhaps our investigative procedures teach us to look more often for differences rather than similarities, and, thus, we become "splitters" more often than "lumpers."

The study of large numbers of young, male and female specimens of most species, osteological material, and some karyological information has allowed me to accumulate information that strongly suggests that *Leimadophis* (=*Dromicus*) *Liophis* and *Lygophis* are congeneric. Therefore, I have undertaken the task of unifying three complex genera into one.

TABLE 1

The following 275 species or subspecies names in this table have been applied to the genera *Dromicus*, *Leimadophis*, *Liophis* and/or *Lygophis* during the past 148 years. There are 118 names that currently belong to other genera and are indicated by a plus sign. Six names whose status is unknown are questioned. About 80% of the remaining 163 species and subspecies names of *Liophis* are of questionable status. Eight names are homonyms, at least 14 belong to other described or undescribed genera, 14 are *nomina nuda*, and about 93 are synonyms. Subspecies are not recognized in this table, but will be discussed in a forthcoming series of papers dealing with species groups of *Liophis*.

| NAME                | ORIGINAL<br>GENERIC ALLOCATION  | AUTHOR(S)             | CURRENT STATUS                |
|---------------------|---------------------------------|-----------------------|-------------------------------|
| + <i>adspersus</i>  | <i>Dromicus</i>                 | Gunlach & Peters 1864 | <i>Alsophis cantherigerus</i> |
| + <i>affinis</i>    | <i>Dromicus</i>                 | Günther 1858          | <i>Rhadinaea affinis</i>      |
| <i>albadspersus</i> | <i>Leimadophis poecilogyrus</i> | Amaral 1944           | <i>Liophis poecilogyrus</i>   |
| + <i>albiceps</i>   | <i>Rhadinaea</i>                | Amaral 1924           | <i>Rhadinaea decipiens</i>    |
| <i>albiventris</i>  | <i>Liophis reginae</i>          | Jan 1863a             | <i>Liophis albiventris</i>    |
| <i>albiventris</i>  | <i>Dromicus</i>                 | Quijada 1916          | <i>nomina nudum</i>           |
| + <i>allenii</i>    | <i>Leimadophis</i>              | Dunn 1920             | <i>Antillophis parvifrons</i> |
| <i>almada</i>       | <i>Natrix</i>                   | Wagler 1824           | <i>Liophis almадensis</i>     |
| <i>almadensis</i>   | <i>Natrix</i>                   | Wagler 1824           | <i>Liophis almадensis</i>     |
| ? <i>alternans</i>  | <i>C. (oluber)</i>              | Lichtenstein 1823     | ?                             |
| <i>alticulus</i>    | <i>Opheomorphus</i>             | Cope 1868             | <i>Liophis reginae</i>        |
| <i>alticulus</i>    | <i>Liophis cobella</i>          | Amaral 1931           | <i>Liophis pseudocobella</i>  |
| <i>amabilis</i>     | <i>Dromicus</i>                 | Jan 1863b             | <i>Liophis flavifrenatus</i>  |
| + <i>amarali</i>    | <i>Liophis (Rhadinaea)</i>      | Wettstein 1930        | <i>insertae sedis amarali</i> |
| <i>amazonicus</i>   | <i>Dromicus</i>                 | Dunn 1922             | <i>Liophis amazonicus</i>     |

| NAME                     | ORIGINAL<br>GENERIC ALLOCATION  | AUTHOR(S)               | CURRENT STATUS                   |
|--------------------------|---------------------------------|-------------------------|----------------------------------|
| <i>amazonicus</i>        | <i>Leimadophis poecilogyrus</i> | Amaral 1944             | <i>Liophis poecilogyrus</i>      |
| + <i>amoenus</i>         | <i>Enicognathus</i>             | Jan 1863a               | <i>insertae sedis amoenus</i>    |
| + <i>andicolus</i>       | <i>Leimadophis</i>              | Barbour 1915            | <i>Tachymenis peruviana</i>      |
| + <i>andreae</i>         | <i>Liophis</i>                  | Reinhardt & Lutken 1862 | <i>Antillophis andreae</i>       |
| + <i>angulifer</i>       | <i>Dromicus</i>                 | Bibron 1843             | <i>Alsophis cantherigerus</i>    |
| + <i>angustilineatus</i> | <i>Dromicus</i>                 | Schmidt & Walker 1943a  | <i>Philodryas simonsi</i>        |
| <i>anomala</i>           | <i>Coronella</i>                | Günther 1858            | <i>Liophis anomala</i>           |
| + <i>antioquiensis</i>   | <i>Rhadinaea</i>                | Dunn 1943               | <i>Saphenophis antioquiensis</i> |
| <i>argentinus</i>        | <i>Zamensis</i>                 | Brethes 1917            | <i>Liophis sagittifer</i>        |
| + <i>atahuallpae</i>     | <i>Liophis</i>                  | Steindachner 1901       | <i>Saphenophis atahuallpae</i>   |
| <i>ater</i>              | <i>Zamensis</i>                 | Günther 1872            | <i>Liophis albiventris</i>       |
| <i>australis</i>         | <i>Coronella</i>                | Günther 1858            | <i>Liophis miliaris</i>          |
| + <i>baroni</i>          | <i>Dromicus</i>                 | Boulenger 1888          | <i>Liopholodophis lateralis</i>  |
| <i>bicolor</i>           | <i>Coluber</i>                  | Reuss 1834              | <i>Liophis miliaris</i>          |
| <i>bimaculatus</i>       | <i>Liophis</i>                  | Cope 1899               | <i>Liophis bimaculatus</i>       |
| + <i>binotata</i>        | <i>Rhadinaea</i>                | Werner 1909             | <i>insertae sedis undulatus</i>  |
| <i>bipraocularis</i>     | <i>Liophis</i>                  | Boulenger 1903          | <i>Liophis bimaculatus</i>       |
| + <i>biserialis</i>      | <i>Herpetodryas</i>             | Günther 1860            | <i>Alsophis biserialis</i>       |
| + <i>bolivianus</i>      | <i>Liophis</i>                  | Werner 1909             | <i>Philodryas psammophideus</i>  |
| <i>boulengeri</i>        | <i>Leimadophis</i>              | Barbour 1914            | <i>Liophis ornatus</i>           |

| NAME  | ORIGINAL<br>GENERIC ALLOCATION   | AUTHOR(S)   | CURRENT STATUS   |
|---|--|---|--|
| + <i>boursieri</i><br><i>brachyurus</i><br><i>brazili</i><br><i>breviceps</i><br>+ <i>brevirostris</i>        | <i>Dromicus</i><br><i>Opheomorphus</i><br><i>Rhadinaea</i><br><i>Liophis</i><br><i>Dromicus</i>          | Jan & Sordelli 1867<br>Cope 1887<br>Amaral 1923<br>Cope 1860a<br>Peters 1863  | <i>Saphenophis boursieri</i><br><i>Liophis typhlus</i><br><i>Liophis frenata</i><br><i>Liophis breviceps</i><br><i>Rhadinaea brevirostris</i>      |
| <i>caesius</i><br>? <i>californica</i><br><i>canaima</i><br>+ <i>canilatus</i><br>? <i>capensis</i>           | <i>Opheomorphus doliatus</i><br><i>Liophis</i><br><i>Liophis</i><br><i>Tachymenis</i><br><i>Dromicus</i> | Cope 1862b<br>Jan 1863a<br>Roze 1957<br>Cope 1868<br>Jan 1863b                | <i>Liophis poecilogyrus</i><br>?<br><i>Liophis canaima</i><br><i>Alsophis elegans</i><br>?   |
| <i>cenchrus</i><br>+ <i>chilensis</i><br>+ <i>chitalonensis</i><br><i>chrysostoma</i><br>+ <i>cicatricosa</i> | <i>Coluber</i><br><i>Dromicus</i><br><i>Dromicus</i><br><i>Rhadinaea</i><br><i>Dromicus pleii</i>        | Daudin 1803<br>Steindachner 1867<br>Müller 1878<br>Cope 1868<br>Jan 1863b     | <i>Liophis cobella</i><br><i>Philodryas chamissonis</i><br><i>Coniophanes fissidens</i><br><i>Liophis chrysostoma</i><br><i>Mastigodryas pleei</i> |
| <i>cinereus</i><br><i>cinereus</i><br>+ <i>clavatus</i><br><i>cobella</i><br>+ <i>coeruleus</i>               | <i>Coluber</i><br><i>Dromicus</i><br><i>Dromicus</i><br><i>Coluber</i><br><i>Dromicus</i>                | Linnaeus 1758<br>Quijada 1916<br>Peters 1864<br>Linnaeus 1758<br>Fischer 1885 | <i>Liophis cobella</i> ?<br><i>nomina nudum</i><br><i>Coniophanes imperialis</i><br><i>Liophis cobella</i><br><i>Mastigodryas melanolomus</i>      |

| NAME                  | ORIGINAL<br>GENERIC ALLOCATION | AUTHOR(S)         | CURRENT STATUS                     |
|-----------------------|--------------------------------|-------------------|------------------------------------|
| <i>collaris</i>       | <i>Liophis cobella</i>         | Jan 1863a         | <i>Liophis purpurans</i>           |
| <i>concolor</i>       | <i>Dromicus</i>                | Quijada 1916      | <i>nomina nudum</i>                |
| <i>conirostris</i>    | <i>Liophis</i>                 | Günther 1858      | <i>Liophis almadensis</i>          |
| <i>copeae</i>         | <i>Dromicus juliae</i>         | Parker 1936       | <i>Liophis juliae</i>              |
| <i>corallinus</i>     | <i>Coluber</i>                 | Linnaeus 1758     | <i>Liophis triscalis</i>           |
| <i>coralliventris</i> | <i>Aporophis</i>               | Boulenger 1894    | <i>Liophis coralliventris</i>      |
| + <i>cubensis</i>     | <i>Dromicus</i>                | Garman 1887       | <i>Antillophis andreae</i>         |
| <i>cursor</i>         | <i>Coluber</i>                 | Lacépède 1789     | <i>Liophis cursor</i>              |
| + <i>cyanopleurus</i> | <i>Aporophis</i>               | Cope 1885         | <i>insertae sedis melanostigma</i> |
| + <i>diastemus</i>    | <i>Liophis elapoides</i>       | Bocourt 1886      | <i>Pliocercus elapoides</i>        |
| <i>dichroa</i>        | <i>Rhadinaea</i>               | Werner 1899       | <i>Liophis jaegeri</i>             |
| <i>dictyodes</i>      | <i>Coluber</i>                 | Wied 1824         | <i>Liophis miliaris</i>            |
| <i>dilepis</i>        | <i>Lygophis</i>                | Cope 1862a        | <i>Liophis lineatus</i>            |
| <i>doliatus</i>       | <i>Coluber</i>                 | Wied 1825         | <i>Liophis poecilogyrus</i>        |
| + <i>dolichocerus</i> | <i>Dromicus</i>                | Peracca 1892      | <i>Liopholidophis sexlineatus</i>  |
| <i>domicella</i>      | <i>Coluber</i>                 | Linnaeus 1758     | <i>Liophis poecilogyrus</i>        |
| <i>dorsalis</i>       | <i>Liophis</i>                 | Peters 1863       | <i>Liophis jaegeri</i>             |
| + <i>dorsalis</i>     | <i>Dromicus chamissonis</i>    | Steindachner 1876 | <i>Alsophis dorsalis</i>           |
| <i>ecuadorensis</i>   | <i>Leimadophis epinephalus</i> | Laurent 1949      | <i>Liophis epinephalus</i>         |
| <i>elaeoides</i>      | <i>Liophis</i>                 | Griffin 1916      | <i>Liophis typhlus</i>             |

| NAME   | ORIGINAL<br>GENERIC ALLOCATION  | AUTHOR(S)   | CURRENT STATUS  |
|--|---|---|---|
| + elegans<br>elegantissima<br>epinephalus<br>+ exiguus<br>festae   | <i>Lygophis</i><br><i>Rhadinaea</i><br><i>Liophis</i><br><i>Dromicus</i><br><i>Rhadinaea</i>                  | Tschudi 1845<br>Koslowsky 1896a<br>Cope 1862a<br>Cope 1862a<br>Peracca 1897b                  | <i>Alsophis elegans</i><br><i>Liophis anomala</i><br><i>Liophis epinephalus</i><br><i>Arrhyton exiguus</i><br><i>Liophis festae</i>                 |
| <i>flavifrenatus</i><br>+ <i>flavilatus</i><br>+ <i>flavitorques</i><br><i>flaviventris</i><br><i>forsteri</i> | <i>Lygophis</i><br><i>Dromicus</i><br><i>Liophis</i><br><i>Liophis cobella</i><br><i>Natrix G.</i>            | Cope 1862a<br>Cope 1871<br>Cope 1869<br>Jan & Sordelli 1866<br>Wagler 1824                    | <i>Liophis flavifrenatus</i><br><i>Rhadinaea flavilatus</i><br><i>Enulius flavitorques</i><br><i>Liophis poecilogyrus</i><br><i>Liophis typhlus</i> |
| <i>franciscanus</i><br><i>fraseri</i><br>+ <i>fremenvillei</i><br><i>frenata</i><br>+ <i>frenatus</i>          | <i>Leimadophis poecilogyrus</i><br><i>Liophis</i><br><i>Dryophylax</i><br><i>Rhadinaea</i><br><i>Dromicus</i> | Amaral 1944<br>Boulenger 1894<br>Dumeril, Bibron & Dumeril 1854<br>Werner 1909<br>Peters 1863 | <i>Liophis poecilogyrus</i><br><i>Liophis fraseri</i><br><i>Alsophis elegans</i><br><i>Liophis frenata</i><br><i>Rhadinaea lateristriga</i>         |
| <i>fugitivus</i><br><i>fuscus</i><br><i>gastrosticta</i><br>+ <i>genimaculata</i><br><i>giganteus</i>          | <i>Coluber</i><br><i>Opheomorphus</i><br><i>Liophis typhlus</i><br><i>Liophis</i><br><i>Liophis</i>           | Donndorf 1798<br>Cope 1885<br>Jan 1863a<br>Boettger 1885<br>Jan 1863b                         | <i>Liophis cursor</i><br><i>Liophis miliaris</i><br><i>Liophis typhlus</i><br><i>insertae sedis joberti</i><br><i>Liophis giganteus</i>             |

| NAME            | ORIGINAL<br>GENERIC ALLOCATION  | AUTHOR(S)              | CURRENT STATUS                  |
|-----------------|---------------------------------|------------------------|---------------------------------|
| + godmanni      | <i>Dromicus</i>                 | Günther 1865           | <i>Rhadinaea godmani</i>        |
| gracilis        | <i>Liophis</i>                  | Philippi 1899          | <i>nomina nudum</i>             |
| graphicus       | <i>Coluber</i>                  | Shaw 1802              | <i>Liophis reginae</i>          |
| guentheri       | <i>Liophis</i>                  | Peracca 1897a          | <i>Liophis typhlus</i>          |
| + habelli       | <i>Dromicus chamissonis</i>     | Steindachner 1876      | <i>Alsophis dorsalis</i>        |
| + helleri       | <i>Dromicus occidentalis</i>    | Van Denburgh 1912      | <i>Alsophis occidentalis</i>    |
| + hoodensis     | <i>Dromicus</i>                 | Van Denburgh 1912      | <i>Alsophis hoodensis</i>       |
| + ignitus       | <i>Dromicus</i>                 | Cope 1871              | <i>Rhadinaea decorata</i>       |
| + imerinae      | <i>Liophis</i>                  | Günther 1890           | <i>Pseudoxyrhopous imerinae</i> |
| + inca          | <i>Dromicus</i>                 | Schmidt & Walker 1943b | <i>Philodryas simonsi</i>       |
| + inconstans    | <i>Dromicus ater</i>            | Jan 1863b              | <i>Alsophis ater</i>            |
| ingeri          | <i>Liophis</i>                  | Roze 1958c             | <i>Liophis ingeri</i>           |
| + insignissimus | <i>Liophis</i>                  | Amaral 1926            | <i>Rhadinaea persimilis</i>     |
| insularis       | <i>Liophis</i>                  | Quijada 1916           | <i>nomina nudum</i>             |
| intermedius     | <i>Leimadophis poecilogyrus</i> | Amaral 1944            | <i>Liophis poecilogyrus</i>     |
| isolepis        | <i>Xenodon</i>                  | Cope 1870              | <i>Liophis typhlus</i>          |
| jaculatoria     | <i>Coluber</i>                  | Linnaeus 1758          | <i>Liophis lineatus</i>         |
| jaegeri         | <i>Coronella</i>                | Gunther 1858           | <i>Liophis jaegeri</i>          |
| + jani          | <i>Liophis</i>                  | Dugès 1865             | <i>Hypsiglena torquata</i>      |
| + joberti       | <i>Enicognathus</i>             | Sauvage 1884           | <i>insertae sedis joberti</i>   |

| NAME                  | ORIGINAL<br>GENERIC ALLOCATION | AUTHOR(S)                      | CURRENT STATUS                    |
|-----------------------|--------------------------------|--------------------------------|-----------------------------------|
| <i>juliae</i>         | <i>Aporophis</i>               | Cope 1879                      | <i>Liophis juliae</i>             |
| <i>juvenalis</i>      | <i>Leimadophis taeniurus</i>   | Dunn 1937                      | <i>Liophis epinephalus</i>        |
| + <i>lachrymans</i>   | <i>Lygophis</i>                | Cope 1870                      | <i>Rhadinaea lachrymans</i>       |
| <i>lamonae</i>        | <i>Leimadophis bimaculatus</i> | Dunn 1944a                     | <i>Liophis bimaculatus</i>        |
| + <i>lateristriga</i> | <i>Liophis</i>                 | Berthold 1859                  | <i>Rhadinaea lateristriga</i>     |
| <i>lativittatus</i>   | <i>Aporophis lineatus</i>      | Müller 1928                    | <i>Liophis lineatus</i>           |
| + <i>laureatus</i>    | <i>Dromicus</i>                | Günther 1868                   | <i>Rhadinaea laureatus</i>        |
| ? <i>leucogaster</i>  | <i>Liophis</i>                 | Jan 1863a                      | <i>Umbrivaga pygmaeus</i> ?       |
| + <i>leucomelas</i>   | <i>Dromicus</i>                | Dumeril, Bibron & Dumeril 1854 | <i>Alsophis antillensis</i>       |
| <i>lecurus</i>        | <i>Dromicus</i>                | Quijada 1916                   | <i>nomina nudum</i>               |
| + <i>lincolni</i>     | <i>Leimadophis parvifrons</i>  | Cochran 1931                   | <i>Antillophis parvifrons</i>     |
| <i>lineata</i>        | <i>Rhadinaea</i>               | Jensen 1900                    | <i>Liophis jaegeri</i>            |
| <i>lineatus</i>       | <i>Coluber</i>                 | Linnaeus 1758                  | <i>Liophis lineatus</i>           |
| <i>liquanus</i>       | <i>Dromicus</i>                | Quijada 1916                   | <i>nomina nudum</i>               |
| <i>longiventris</i>   | <i>Liophis</i>                 | Amaral 1925                    | <i>Liophis longiventris</i>       |
| <i>luctuosa</i>       | <i>Liophis</i>                 | Philippi 1899                  | <i>Philodryas chamissonis</i>     |
| <i>lutea</i>          | <i>Liophis</i>                 | Quijada 1916                   | <i>nomina nudum</i>               |
| + <i>macrocercus</i>  | <i>Dromicus</i>                | Günther 1882                   | <i>Liopholidophis sexlineatus</i> |
| <i>macrops</i>        | <i>Liophis</i>                 | Werner 1925                    | <i>Liophis typhlus</i>            |
| <i>macrostoma</i>     | <i>Leimadophis reginae</i>     | Amaral 1935                    | <i>Liophis reginae</i>            |

| NAME                      | ORIGINAL<br>GENERIC ALLOCATION | AUTHOR(S)             | CURRENT STATUS                     |
|---------------------------|--------------------------------|-----------------------|------------------------------------|
| <i>maculata</i>           | <i>Liophis reginae</i>         | Steindachner 1867     | <i>Liophis reginae</i>             |
| <i>maculatus</i>          | <i>Dromicus</i>                | Quijada 1916          | <i>nomina nudum</i>                |
| <i>maculicauda</i>        | <i>Leimadophis reginae</i>     | Hoge 1954             | <i>Liophis reginae</i>             |
| + <i>maculivittis</i>     | <i>Dromicus (Alsophis)</i>     | Peters 1877           | <i>Mastigodryas pleei</i>          |
| + <i>madagascariensis</i> | <i>Dromicus</i>                | Günther 1872          | <i>Liopholidophis lateralis</i>    |
| <i>mariae</i>             | <i>Leimadophis</i>             | Barbour 1914          | <i>Liophis juliae</i>              |
| <i>marmorata</i>          | <i>Dromicus</i>                | Quijada 1916          | <i>nomina nudum</i>                |
| <i>marmorata</i>          | <i>Liophis</i>                 | Quijada 1916          | <i>nomina nudum</i>                |
| + <i>melanauchen</i>      | <i>Enicognathus</i>            | Jan 1863a             | <i>incertae sedis melanauchen</i>  |
| + <i>melanocephalus</i>   | <i>Dromicus</i>                | Peters 1863           | <i>Rhadinaea poecilopogon</i>      |
| + <i>melanocephalus</i>   | <i>Aporophis</i>               | Griffin 1916          | <i>insertae sedis steinbachi</i>   |
| <i>melanonotus</i>        | <i>Liophis</i>                 | Cope 1860a            | <i>Liophis melanotus</i>           |
| + <i>melanostigma</i>     | <i>Natrix</i>                  | Wagler 1824           | <i>insertae sedis melanostigma</i> |
| <i>melanotus</i>          | <i>Coluber</i>                 | Shaw 1802             | <i>Liophis melanotus</i>           |
| + <i>melopyrrha</i>       | <i>Dromicus andreae</i>        | Thomas & Garrido 1967 | <i>Antillophis andreae</i>         |
| + <i>mentalis</i>         | <i>Dromicus</i>                | Günther 1862b         | <i>Ialtris dorsalis</i>            |
| <i>meridionalis</i>       | <i>Aporophis lineatus</i>      | Schenkel 1901         | <i>Liophis lineatus</i>            |
| <i>merremii</i>           | <i>Coluber</i>                 | Wied 1821             | <i>Liophis miliaris</i>            |
| ? <i>m-nigrum</i>         | <i>Coluber</i>                 | Raddi 1820            | ?                                  |
| <i>miliaris</i>           | <i>Coluber</i>                 | Linnaeus 1758         | <i>Liophis miliaris</i>            |

| NAME                  | ORIGINAL<br>GENERIC ALLOCATION  | AUTHOR(S)              | CURRENT STATUS                     |
|-----------------------|---------------------------------|------------------------|------------------------------------|
| <i>minervae</i>       | <i>Coluber</i>                  | Linnaeus 1758          | <i>Liophis lineatus</i>            |
| + <i>miolepis</i>     | <i>Dromicus</i>                 | Boettger 1891          | <i>Rhadinaea occipitalis</i>       |
| ? <i>modestus</i>     | <i>Dromicus</i>                 | Jan 1863b              | ?                                  |
| <i>modesta</i>        | <i>Rhadinaea</i>                | Koslowsky 1896b        | <i>Liophis sagittifer</i>          |
| <i>montanus</i>       | <i>Leimadophis poecilogyrus</i> | Amaral 1944            | <i>Liophis poecilogyrus</i>        |
| <i>mossoroensis</i>   | <i>Liophis</i>                  | Hoge & Lima-Verde 1972 | <i>Liophis mossoroensis</i>        |
| + <i>multilineata</i> | <i>Dromicus</i>                 | Peters 1863            | <i>Rhadinaea multilineata</i>      |
| <i>natricoides</i>    | <i>Rhadinaea merremi</i>        | Werner 1926            | <i>Liophis miliaris</i>            |
| + <i>nebulatus</i>    | <i>Leimadophis</i>              | Barbour 1916           | <i>Antillophis andreae</i>         |
| + <i>nicagus</i>      | <i>Taeniophallus</i>            | Cope 1868              | <i>insertae sedis melanostigma</i> |
| + <i>niger</i>        | <i>Leimadophis parvifrons</i>   | Dunn 1920              | <i>Antillophis parvifrons</i>      |
| + <i>nuntius</i>      | <i>Dromicus</i>                 | Jan 1863b              | <i>Rhadinaea lateristriga</i>      |
| + <i>obtusa</i>       | <i>Rhadinaea</i>                | Cope 1863              | <i>Insertae sedis obtusa</i>       |
| + <i>occidentalis</i> | <i>Dromicus</i>                 | Van Denburgh 1912      | <i>Alsophis occidentalis</i>       |
| + <i>occipitalis</i>  | <i>E. (nicognathus)</i>         | Jan 1863a              | <i>Rhadinaea occipitalis</i>       |
| <i>oligolepis</i>     | <i>Liophis</i>                  | Boulenger 1905         | <i>Liophis reginae</i>             |
| <i>olivacea</i>       | <i>Liophis typhlus</i>          | Jan 1863b              | <i>Liophis typhlus</i>             |
| + <i>omiltemanus</i>  | <i>Dromicus</i>                 | Günther 1894           | <i>Rhadinaea omiltemanus</i>       |
| <i>opisthotaenia</i>  | <i>Liophis</i>                  | Boulenger 1908         | <i>Liophis bimaculatus</i>         |
| <i>orientalis</i>     | <i>Coronella</i>                | Günther 1864           | <i>Liophis purpurans</i>           |

| NAME                   | ORIGINAL<br>GENERIC ALLOCATION  | AUTHOR(S)                      | CURRENT STATUS                  |
|------------------------|---------------------------------|--------------------------------|---------------------------------|
| + <i>orientalis</i>    | <i>Leimadophis andreae</i>      | Barbour & Ramsden 1919         | <i>Antillophis andreae</i>      |
| <i>orina</i>           | <i>Rhadinaea</i>                | Griffin 1916                   | <i>Liophis miliaris</i>         |
| <i>ornata</i>          | <i>Liophis reginae</i>          | Jan 1863a                      | <i>Liophis reginae</i>          |
| <i>ornatissima</i>     | <i>Liophis</i>                  | Jan 1863a                      | <i>Liophis poecilogyrus</i>     |
| <i>ornatus</i>         | <i>Dromicus</i>                 | Garman 1887                    | <i>Liophis ornatus</i>          |
| + <i>paraniger</i>     | <i>Dromicus parvifrons</i>      | Thomas & Schwartz 1965         | <i>Antillophis parvifrons</i>   |
| + <i>parvifrons</i>    | <i>Dromicus</i>                 | Cope 1862a                     | <i>Antillophis parvifrons</i>   |
| <i>paucidens</i>       | <i>Lygophis</i>                 | Hoge 1953                      | <i>Liophis paucidens</i>        |
| + <i>peninsulae</i>    | <i>Dromicus andreae</i>         | Schwartz & Thomas 1960         | <i>Antillophis parvifrons</i>   |
| <i>perfuscus</i>       | <i>Liophis</i>                  | Cope 1862a                     | <i>Liophis perfuscus</i>        |
| + <i>persimilis</i>    | <i>Liophis</i>                  | Cope 1869                      | <i>Rhadinaea persimilis</i>     |
| <i>pictostriatus</i>   | <i>Leimadophis poecilogyrus</i> | Amaral 1944                    | <i>Liophis poecilogyrus</i>     |
| <i>pinetincola</i>     | <i>Leimadophis poecilogyrus</i> | Amaral 1944                    | <i>Liophis poecilogyrus</i>     |
| <i>platensis</i>       | <i>Leimadophis poecilogyrus</i> | Amaral 1944                    | <i>Liophis poecilogyrus</i>     |
| + <i>pleei</i>         | <i>Dromicus</i>                 | Dumeril, Bibron & Dumeril 1854 | <i>Mastigodryas pleei</i>       |
| <i>poecilogyrus</i>    | <i>Coluber</i>                  | Wied 1825                      | <i>Liophis poecilogyrus</i>     |
| <i>poecilolaemus</i>   | <i>Coronella</i>                | Günther 1872                   | <i>Liophis purpurans</i>        |
| + <i>poecilostomus</i> | <i>Lygophis</i>                 | Cope 1875                      | <i>Alsophis elegans</i>         |
| + <i>poecilstictus</i> | <i>L. (iophis)</i>              | Jan 1863a                      | <i>Philodryas patagoniensis</i> |
| + <i>polylepis</i>     | <i>Dromicus</i>                 | Buden 1966                     | <i>Arrhyton polylepis</i>       |

| NAME   | ORIGINAL<br>GENERIC ALLOCATION  | AUTHOR(S)   | CURRENT STATUS   |
|--|---|---|--|
| ? <i>praeornata</i><br><i>prasina</i><br>+ <i>protenus</i><br><i>pseudocobella</i><br><i>pulchella</i>     | <i>Rhadinaea</i><br><i>Liophis typhlus</i><br><i>Dromicus</i><br><i>Liophis</i><br><i>Coronella</i>                   | Werner 1909<br>Jan 1863b<br>Jan 1863b<br>Peracca 1914<br>Jan 1863a                          | ?<br><i>Liophis typhlus</i><br><i>Antillophis parvifrons</i><br><i>Liophis pseudocobella</i><br><i>Liophis anomala</i>                               |
| <i>pulcher</i><br><i>purpurans</i><br><i>putnami</i><br>+ <i>putnami</i><br>+ <i>pygmaeus</i>              | <i>Liophis</i><br><i>Ablabes</i><br><i>Liophis</i><br><i>Dromicus</i><br><i>Liophis</i>                               | Steindachner 1867<br>Dumeril, Bibron & Dumeril 1854<br>Cope 1862a<br>Jan 1863b<br>Cope 1868 | <i>Liophis sagittifer</i><br><i>Liophis purpurans</i><br><i>Liophis cursor</i><br><i>Manolepis putnami</i><br><i>Umbrivaga pygmaeus</i>              |
| <i>quadrilineata</i><br>+ <i>quinquelineatus</i><br><i>raninus</i><br><i>reginae</i><br>+ <i>rehi</i>      | <i>Liophis reginae</i><br><i>Liophis</i><br><i>Coluber (Natrix)</i><br><i>Coluber</i><br><i>Liophis</i>               | Jan 1863a<br>Günther 1881<br>Merrem 1820<br>Linnaeus 1758<br>Werner 1909                    | <i>Liophis reginae</i><br><i>Pseudoxyrhopus quinque-lineatus</i><br><i>Liophis melanotus</i><br><i>Liophis reginae</i><br><i>Sordellina punctata</i> |
| <i>reticulatus</i><br>+ <i>rosamondae</i><br>+ <i>rufidorsatus</i><br>+ <i>rufiventris</i><br><i>rufus</i> | <i>Leimadophis poecilogyrus</i><br><i>Dromicus parvifrons</i><br><i>Dromicus</i><br><i>Dromicus</i><br><i>Liophis</i> | Parker 1931<br>Cochran 1934<br>Günther 1858<br>Dumeril, Bibron & Dumeril 1854<br>Jan 1863a  | <i>Liophis poecilogyrus</i><br><i>Antillophis parvifrons</i><br><i>Alsophis elegans</i><br><i>Alsophis rufiventris</i><br><i>Liophis perfuscus</i>   |

| NAME                   | ORIGINAL<br>GENERIC ALLOCATION | AUTHOR(S)              | CURRENT STATUS                    |
|------------------------|--------------------------------|------------------------|-----------------------------------|
| <i>rutilus</i>         | <i>Lygophis</i>                | Cope 1862a             | <i>Liophis anomala</i>            |
| <i>sagittifer</i>      | <i>Liopeltis</i>               | Jan 1863b              | <i>Liophis sagittifer</i>         |
| <i>sagittifera</i>     | <i>Rhadinaea</i>               | Boulenger 1894         | <i>Liophis sagittifer</i>         |
| <i>schottii</i>        | <i>X. (enodon)</i>             | Schegel 1837           | <i>Liophis poecilorynus</i>       |
| <i>scolecomorphus</i>  | <i>Trigonocephalus</i>         | Bacque 1906            | <i>Liophis almadensis</i>         |
| <i>semiaureus</i>      | <i>Opheomorphus merremi</i>    | Cope 1862b             | <i>Liophis miliaris</i>           |
| <i>semilineata</i>     | <i>Natrix</i>                  | Wagler 1824            | <i>Liophis reginae</i>            |
| <i>serpentinus</i>     | <i>Coluber</i>                 | Daudin 1803            | <i>Liophis cobella</i>            |
| + <i>sexlineatus</i>   | <i>Dromicus</i>                | Günther 1882           | <i>Liopholidophis sexlineatus</i> |
| + <i>simonsi</i>       | <i>Philodryas</i>              | Boulenger 1900         | <i>Philodryas simonsi</i>         |
| + <i>slevini</i>       | <i>Dromicus</i>                | Van Denburgh 1912      | <i>Alsophis slevini</i>           |
| + <i>splendens</i>     | <i>L. (iophis)</i>             | Jan 1863a              | <i>Pliocercus euryzonus</i>       |
| + <i>stahli</i>        | <i>Leimadophis</i>             | Stejneger 1904         | <i>Arrhyton exiguum</i>           |
| + <i>steinbachi</i>    | <i>Rhadinaea</i>               | Boulenger 1905         | <i>Incertae sedis steinbachi</i>  |
| + <i>steindachneri</i> | <i>Dromicus</i>                | Van Denburgh 1912      | <i>Alsophis steindachneri</i>     |
| + <i>stumpffi</i>      | <i>Dromicus</i>                | Boettger 1881          | <i>Liopholidophis lateralis</i>   |
| + <i>stygius</i>       | <i>Dromicus parvifrons</i>     | Thomas & Schwartz 1965 | <i>Antillophis parvifrons</i>     |
| <i>subfasciatus</i>    | <i>Liophis</i>                 | Cope 1862a             | <i>Liophis poecilorynus</i>       |
| <i>sublineatus</i>     | <i>Liophis merremii</i>        | Cope 1860a             | <i>Liophis poecilorynus</i>       |
| + <i>subocularis</i>   | <i>rhadinaea</i>               | Boulenger 1902         | <i>Rhadinaea decorata</i>         |

| NAME                                      | ORIGINAL<br>GENERIC ALLOCATION                         | AUTHOR(S)                      | CURRENT STATUS   |
|---|--|--------------------------------|--|
| + <i>subspadix</i><br><i>subtetragona</i> | <i>Dromicus exiguus</i><br><i>Dromicus chamissonis</i> | Schwartz 1967<br>Philippi 1899 | <i>Arrhyton exiguum</i><br><i>nomina nudum</i>                 |
| + <i>tachymenoides</i>                    | <i>Dromicus</i>  | Schmidt & Walker 1943a         | <i>Philodryas tachymenoides</i>                                |
| + <i>taeniatus</i><br><i>taeniogaster</i> | <i>Dromicus</i><br><i>Liophis</i>                      | Peters 1863<br>Jan 1863a       | <i>Rhadinaea taeniata</i><br><i>Liophis cobella</i>            |
| + <i>taeniolatus</i><br><i>taeniurus</i>  | <i>Enicognathus</i><br><i>Liophis</i>                  | Jan 1863a<br>Tschudi 1845      | <i>Insertae sedis melanostigma</i><br><i>Liophis taeniurus</i> |
| + <i>temminkii</i>                        | <i>Dromicus</i>  | Schlegel 1837                  | <i>Philodryas chamissonis</i>                                  |
| + <i>temporalis</i><br><i>tenuis</i>      | <i>Dromicus</i><br><i>Dromicus</i>                     | Cope 1860b<br>Quijada 1916     | <i>Rhadinaea lateristriga</i><br><i>nomina nudum</i>           |
| <i>terlinatus</i>                         | <i>Coluber</i>   | Lacépède 1826                  | <i>Liophis lineatus</i>  |
| + <i>tortuganus</i>                       | <i>Leimadophis</i>                                     | Dunn 1920                      | <i>Antillophis parvifrons</i>                                  |
| + <i>transversus</i><br><i>trebbaui</i>   | <i>Liophis</i><br><i>Liophis</i>                       | Jan 1863b<br>Roze 1958a        | <i>Alsophis ater</i><br><i>Liophis trebbaui</i>                |
| <i>trifasciatus</i>                       | <i>Liophis</i>   | Werner 1899                    | <i>Liophis sagittifer</i>                                      |
| + <i>tristriata</i>                       | <i>Rhadinaea</i>                                       | Rendahl & Vestergren 1940      | <i>Saphenophis tristriata</i>                                  |
| + <i>tristriata</i><br><i>triscalis</i>   | <i>Dromicus pleii</i><br><i>Coluber</i>                | Jan 1863b<br>Linnaeus 1758     | <i>Mastigodryas pleei</i><br><i>Liophis triscalis</i>          |
| <i>typhlus</i>                            | <i>Coluber</i>   | Linnaeus 1758                  | <i>Liophis typhlus</i>   |
| + <i>tricinctus</i>                       | <i>Liophis</i>   | Jan 1863a                      | <i>Pliocercus elapoides</i>                                    |

| NAME                | ORIGINAL<br>GENERIC ALLOCATION  | AUTHOR(S)                      | CURRENT STATUS                  |
|---------------------|---------------------------------|--------------------------------|---------------------------------|
| + <i>undulatus</i>  | <i>Coluber</i>                  | Wied 1824                      | <i>Insertae sedis undulatus</i> |
| + <i>unicolor</i>   | <i>Dromicus</i>                 | Dumeril, Bibron & Dumeril 1854 | <i>Alsophis canterigerus</i>    |
| + <i>varia</i>      | <i>Liophis wagleri</i>          | Jan 1863a                      | <i>Masticophis mentovarius</i>  |
| <i>variegatus</i>   | <i>Dromicus</i>                 | Quijada 1916                   | <i>nomina nudum</i>             |
| + <i>variegatus</i> | <i>Dromicus</i>                 | Schmidt 1926                   | <i>Alsophis portoricensis</i>   |
| <i>vereundus</i>    | <i>L. (iophis)</i>              | Jan 1863a                      | <i>Liophis almadensis</i>       |
| <i>violaceus</i>    | <i>Coluber</i>                  | Lacépède 1789                  | <i>Liophis reginae</i>          |
| + <i>viperinus</i>  | <i>Dromicus</i>                 | Günther 1868                   | <i>Rhadinaea brevirostris</i>   |
| <i>viridicyanea</i> | <i>Liophis reginae</i>          | Jan & Sordelli 1866            | <i>Liophis poecilogyrus</i>     |
| <i>viridis</i>      | <i>Liophis</i>                  | Günther 1862a                  | <i>Liophis viridis</i>          |
| + <i>vitellinus</i> | <i>Dryophylax</i>               | Cope 1878                      | <i>Alsophis elegans</i>         |
| <i>vittatus</i>     | <i>Coluber</i>                  | Hallowell 1845                 | <i>Liophis melanotus</i>        |
| <i>wagleri</i>      | <i>Liophis</i>                  | Jan 1863a                      | <i>Liophis almadensis</i>       |
| + <i>whymperi</i>   | <i>Coronella</i>                | Boulenger 1882                 | <i>Saphenophis whymperi</i>     |
| <i>williamsi</i>    | <i>Urotheca</i>                 | Roze 1958b                     | <i>Liophis williamsi</i>        |
| + <i>w-nigrum</i>   | <i>Dromicus</i>                 | Werner 1909                    | <i>Ialtris dorsalis</i>         |
| + <i>wuchereri</i>  | <i>Dromicus (Lygophis)</i>      | Günther 1863                   | <i>Rhadinaea occipitalis</i>    |
| <i>xerophilus</i>   | <i>Leimadophis poecilogyrus</i> | Amaral 1944                    | <i>Liophis poecilogyrus</i>     |
| <i>y-graecum</i>    | <i>Liophis (Lygophis)</i>       | Peters 1882                    | <i>Liophis almadensis</i>       |
| <i>zweifeli</i>     | <i>Leimadophis</i>              | Roze 1959                      | <i>Liophis zweifeli</i>         |

## HISTORICAL RESUME

Prior to 1932, little was done to clarify the generic relationships of *Dromicus*, *Leimadophis*, *Liophis* and *Lygophis*. Dunn (1932a) was perhaps the first to attempt to understand the nature of *Dromicus*. His discussion of the generic relationships dealt primarily with the Greater Antillean colubrid genera *Dromicus* (*sensu lato*), *Alsophis*, *Arrhyton*, *Hypsirhynchus*, *Uromacer* and *Ialtris*. Dunn's definition of *Dromicus* included species that are now in the genera *Arrhyton*, *Hypsirhynchus*, *Philodryas* and *Antillophis*. However, he indicated that the type species of *Dromicus* was *Coluber cursor* and although he had not examined the hemipenis of *cursor*, he thought that *C. cursor* was representative of a different genus than *Leimadophis*, the type species of which is *Coronella almadensis* (Wagler). Dunn indicated that *almadensis* has smooth apical discs on the hemipenes, whereas the hemipenes of species of *Dromicus* he had examined possess spines to the bifurcation of the lobes which are then replaced by calyces to the tip. Therefore, Dunn's (1932a) concept of *Dromicus* included all species that contain definitive zones of spines and calyces on the hemipenes. It was unfortunate that Dunn did not examine the hemipenis of the type species of the genus, which was shown by Maglio (1970) to have smooth apical discs and no calyces.

Later Dunn (1932b, 1944a) discussed the relationships of *Rhadinaea*, *Alsophis*, *Leimadophis* (which he did not consider to be congeneric with *Dromicus*), *Liophis*, and *Lygophis*. Dunn separated *Leimadophis* and *Liophis* by the presence of a posterior maxillary diastema in the former and its absence in the latter. He placed *Lygophis* close to *Leimadophis* because of the similarity of their maxillary dentition, but retained *Lygophis* as a separate genus because it does not have scale pits and is striped from snout to tail.

Peters (1963) discussed the complex situation and unsatisfactory nature of the generic definitions and species content of the genera *Leimadophis*, *Liophis*, and *Lygophis* (*Dromicus* was believed to be confined to the Galapagos Archipelago and the Antilles at that time). Peters believed Dunn (1932b) had based his data solely on Colombian material of the three genera, and whereas Dunn's arrangement might separate Colombian species of these genera, the same criteria did not separate species occurring outside of Colombia. Peters found that the maxillary diastema was present in *Coluber cobella*, the type species of the genus *Liophis*; therefore, the absence of the diastema could not be used as a definitive generic character. Shreve (1934) assigned specimens of *Dromicus boursieri* to *Lygophis* (based upon E. R. Dunn's recommendation), believing they had dentition similar to *Leimadophis* and *Lygophis* and that they were fully striped. However, Peters (1963) showed that the maxillary dentition of *boursieri* and specimens he had examined of *Coronella whymperi* (=*Saphenophis boursieri*, *fide* Myers, 1969) were similar to *Liophis cobella*. Peters suggested that the position of the

prediastemal teeth of the maxilla in relation to the ectopterygoid process of the maxilla may prove to be of value. Peters found that the ultimate prediastemal tooth and half of the penultimate tooth lie posterior to the anterior edge of the ectopterygoid process in *Liophis cobella*. In *Leimadophis almadensis* the ultimate prediastemal tooth lies anterior to the anterior edge of the ectopterygoid process. Peters found the latter condition also typical of other *Leimadophis* (*pygmaeus*, *reginae*, *pseudocobella*, *typhlus*), but that in *Liophis miliaris* the position of the ultimate prediastemal tooth is also anterior to the anterior edge of the ectopterygoid process. I have examined this character in over 300 specimens of *bimaculatus*, *cobella*, *festae*, *miliaris*, *pseudocobella*, *reginae*, and *taeniurus* and find it to be variable within any given species sample. The position of the ultimate prediastemal tooth in relation to the anterior edge of the ectopterygoid process seems to be dependent upon the total number of teeth anterior to the diastema. In one species where samples have 22-27 prediastemal teeth, those with 22 and 24 teeth tend to have the ultimate tooth in front of the anterior edge of the ectopterygoid process, those with 25 teeth vary in either direction, whereas those with 26 to 27 teeth definitely have the ultimate tooth posterior to the anterior edge of the ectopterygoid process.

Dunn (1944a) [probably following Boulenger, 1894] also utilized color pattern, presence or absence of scale pits, and number of scale rows to further define the genera *Leimadophis*, *Liophis* and *Lygophis*. Those species fully striped from nose to tail with 17 to 19 midbody scale rows and no scale pits were placed in *Lygophis*; those with dark posterior lateral stripes, some trace of anterior bars or spots, with a single scale pit, and 17-15 or 19-17 scale row reduction patterns were placed in *Leimadophis*; those with variable dorsal markings but no body stripes, with 17-15 scale row reduction pattern, and no scale pits were placed in *Liophis*. Peters (1963) suggested that *Lygophis* should contain all species striped throughout their body length whether head stripes were present or not, and *Liophis* should contain those species not striped on the body, pending an analysis of the characters in all of the species. This arrangement has been followed by most recent authors. However, the Peters' (1963) arrangement is poor because one species, *Leimadophis sagittifer*, has two races, one spotted and one lined, which would place each subspecies in a different genus.

Maglio (1970) reviewed the osteology, external squamative features, and hemipenial morphology of West Indian xenodontine colubrid snakes. He pointed out that many of the island species were not associated with their correct genera, proposed several species assemblages, and described an additional genus, *Antillophis*, for two former *Dromicus* species, *andreae* of Cuba and *parvifrons* of Hispaniola. He also suggested that *Dromicus* Bibron 1843 predated *Leimadophis* Fitzinger 1843 (*fide* Smith and Grant, 1958) and should be recognized as the

proper genus for his *melanotus* species assemblage. Maglio's *melanotus* assemblage included *cursor*, the type species of *Dromicus*, *melanotus* (mainland and islands), and the island forms *ornatus*, *perfuscus* and *juliae*. He pointed out the similarity of the characters of *almadensis*, the type species of *Leimadophis*, to members of his *melanotus* assemblage. Maglio suggested that *cobella*, the type species of *Liophis*, was closely related to his *melanotus* species assemblage, differing only in the presence of basal hooks on the hemipenis (*fide* Roze, 1964) and the absence of a maxillary diastema (already shown to be variable by Peters, 1963). Maglio suggested that *Dromicus* and *Liophis* may be congeneric but maintained them as separate genera.

Myers (1974) compared *Rhadinaea* to several Neotropical colubrid snake genera, including *Liophis*, *Leimadophis*, *Lygophis* and *Umbrivaga* and found them to differ from *Rhadinaea* as a result of possessing acalculcate hemipenes with apical discs and, in general, having moderately different color patterns. Myers stated that there is no relationship between *Rhadinaea* and members of the *Leimadophis* (=*Dromicus*) - *Liophis*-*Lygophis* complex, although they have been often confused in the past. Myers (1974, footnote p. 236) indicated that there are several species erroneously assigned to *Liophis*, and that some may be related to *Rhadinaea*, but that his knowledge of these groups was sketchy and that further discussion must wait until these species are better known. Myers (1973) removed the species *atahuallpae* from *Leimadophis* and *antioquiensis*, *boursieri* and *tristriatus* from *Lygophis* and placed them in a new genus, *Saphenophis*. Later Myers (1974) removed several species from *Liophis* (*sensu lato*, Peters and Orejas-Miranda, 1970) and placed them in the genus *Rhadinaea*. In addition to Myers' findings, my examination of type specimens of species assigned to the *Dromicus*-*Liophis*-*Lygophis* complex reveals that *Liophis subocularis* is a junior synonym of *Rhadinaea decorata*, *Liophis amarali* is a *Rhadinaea* (its species relationship has not been determined at this time) and that *Lygophis amoenus* and *Liophis leucogaster* cannot be assigned to existing genera at this time. I concur with Myers (1974:22) that there are species referred to *Rhadinaea* that are not assignable to any genus as presently defined. For the sake of convenience, some of these were placed in *Liophis* by Myers, but he indicated that they do not belong there. Species that cannot be assigned to presently defined genera are *genimaculata* Boettger (=*joberti* Sauvage), *obtusus* Cope, *steinbachi* Boulenger, *melanauchen* Jan, *undulata* Wied and *melanostigma* Wagler. The latter six species may form a natural group and perhaps a separate genus. Dr. Charles Myers (pers. comm.) is presently examining the morphology of these species. For further details of the confusion that has existed between *Rhadinaea* and *Liophis* see Myers (1973:17-20).

The various "generic" characters mentioned above will not distinguish *Dromicus* (*Leimadophis sensu lato*), *Liophis* or *Lygophis*. Inasmuch as I

have been unable to find a single character that will separate the three genera even 80 percent of the time, it seems advisable to consider them congeneric. *Liophis* Wagler 1830 is the earliest available name for the three genera.

With the removal of those species that do not have a smooth apical disc on the hemipenes, there are approximately 40 species remaining in the genus *Liophis*. Of the 40 species, about 15 are probably conspecific, leaving about 25 valid species in the genus.

The following synonymy of *Liophis* includes strict synonyms and several other names that have been misapplied to nominal species. There are five genera (*Dryophylax*, *Enicognathus*, *Herpetodryas*, *Taeniophallus*, *Tachymenis*) that do not appear in the synonymy, but are frequently seen in early literature for species that have recently been transferred to other genera (see Table 1).

### *Liophis* Wagler

*Coluber* (nec Linnaeus 1758) Shaw 1802: (part); Daudin 1803: (part); Lichenstein, 1823: (part); Wied 1824: 1825: (part). [*L. cobella*, *L. cursor*, *L. lineatus*, *L. melanotus*, *L. miliaris*, *L. poecilogyrus*, *L. reginae*, *L. triscalis*, *L. typhlus*].

*Natrix* (nec Boie 1820) Wagler 1824: (part). [*L. almadensis*, *L. typhlus*].

*Liophis* Wagler 1830 Nat. Syst. Amphib.: 187 Type species: *Coluber cobella* Linnaeus.

*Xenodon* (nec Boie 1820) Schlegel 1837: (part); Cope 1870: (part). [*L. poecilogyrus*, *L. typhlus*].

*Dromicus* Bibron in de la Sagra 1843. Hist. Fis. Pol. Nat. Cuba, Spanish Ed., 4:133. Type-species: *Coluber cursor* Lacépède.

*Pariopeltis* Fitzinger 1843 Syst. Rept.:25. Type-species; *Coluber triscalis* Linnaeus.

*Opheomorphus* Fitzinger 1843 Syst. Rept.:25. Type-species: *Coluber miliaris* Linnaeus.

*Leimadophis* Fitzinger 1843 Syst. Rept.:26. Type-species: *Coronella almadensis* Wagler.

*Pseudophis* Fitzinger 1843 Syst. Rept.:26. Type-species: *Xenodon schotti* Schlegel.

*Lygophis* Fitzinger 1843 Syst. Rept.:26. Type-species: *Herpetodryas lineatus* Schlegel (=*Coluber lineatus* Linnaeus).

*Calophis* Fitzinger 1843 Syst. Rept.:26. Type-species: *Herpetodryas cursor* Schlegel (=*Coluber cursor* Lacépède).

*Limadophis* Agassiz 1846 (emendation of *Leimadophis* Fitzinger) Nomencl. Zool. Index Universalis:210.

*Ablabes* (nec Dumeril 1852) Dumeril, Bibron and Dumeril 1854: (part). [*L. purpurans*].

*Coronella* (nec Laurenti 1768) Günther, 1858: (part). [*L. anomala*, *L. jaegeri*, *L. miliaris*, *L. purpurans*].

*Ophiomorphus* Cope 1862b (emendation of *Opheomorphus* Fitzinger) Proc. Acad. Nat. Sci. Philadelphia, 1862:75.

*Liopeltis* (nec Fitzinger 1843) Jan, 1863: (part). [*L. sagittifer*].

*Rhadinaea* (nec Cope 1863) Cope, 1868: (part); Koslowsky 1895; 1896a: (part); Peracca, 1897: (part); Jensen, 1900: (part); Werner, 1909: (part); Amaral, 1923: (part); Dunn, 1943: (part). [*L. anomalus*, *L. brazili*, *L. chrysostoma*, *L. festae*, *L. frenata*, *L. sagittifer*].

*Zamensis* (nec Wagler 1830) Günther, 1872: (part). [*L. bimaculatus*].

*Aporophis* Cope 1878, Proc. Amer. Philos. Soc., 17:34. Type-species: *Coluber lineatus* Linnaeus.

*Trigonocephalus* (nec Oppel 1811) Bacque, 1906: (part). [*L. almadensis*].

### GENERIC DESCRIPTION

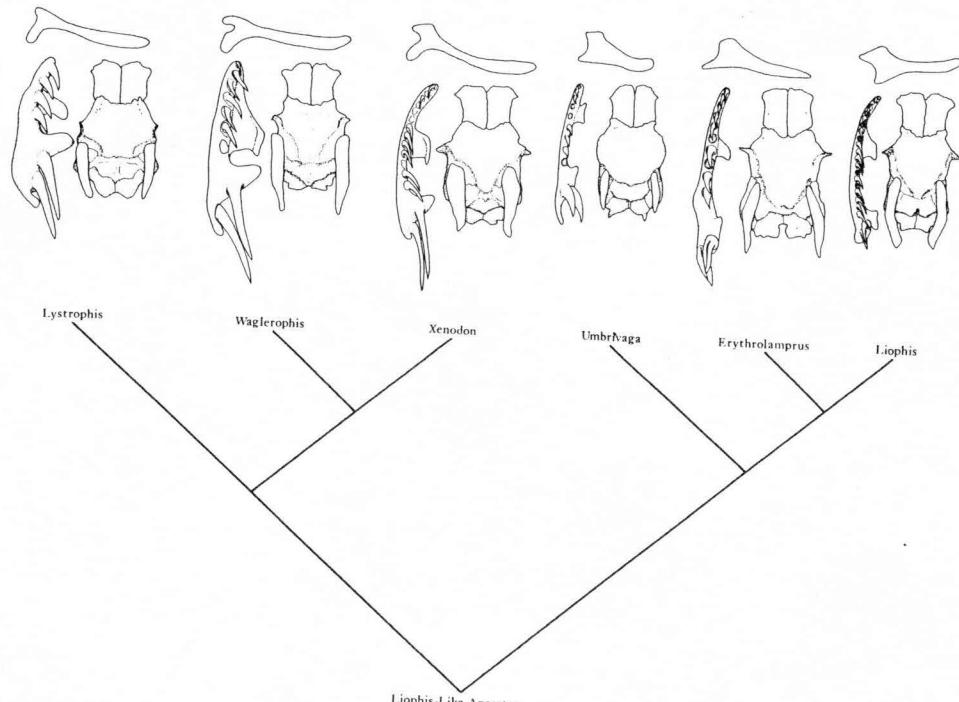
*Liophis* currently contains about 40 species (Table 2) that are characterized by having slightly to moderately bilobed, spinose hemipenes with a smooth apical disc, no calyces, and a *sulcus spermaticus* that divides from one-fourth to one-half the distance from the base. The hemipenes may be long or short, usually with a naked basal pocket and with or without a large row of spines near the base. The maxillary bone is long and relatively immobile with 10 to 30 teeth, the last two are ungrooved and may be slightly to moderately enlarged, usually separated from the others by a slight to moderate diastema, and usually offset. The palatine teeth vary from 10-23, the pterygoid teeth from 20-35, and the dentary teeth from 16-35. *Liophis* has a rather typical colubrid skull with a medial dorsal process of the prefrontal bone present and an anteroventral medial wing of prefrontal bone present or absent, and, if present, usually reduced in size. The anterolateral process of the parietal bone is present but does not form part of the orbital ridge.

*Liophis* attains a maximum total length of 1631 mm with a tail/total length ratio of 13.5 to 31.0 percent. The number of scale rows varies from 15 with no reduction to 19 with one or two reductions. Scale pits are present or absent; in the former case, one and occasionally two are present. The number of ventrals varies from 129 to 212 and subcaudals from 38 to 106. A typical complement of nine colubrid head scales is present (loreal rarely reduced or absent); temporals are always present and usually are 1+2; preoculars are usually single, postoculars are usually two; infralabials are usually 10, supralabials are usually 8; parietals, nasals and prefrontals are always paired; and there are always two pair of chin shields. color is highly variable, ranging from unicolor to as many as four vivid colors on one individual. Color pattern is highly variable, ranging from no pattern to a pattern of stripes, spots, blotches, bands, or any combination thereof on any part of the body.

*Diagnosis.* — *Liophis* is distinguished from other Neotropical snake genera with similar hemipenes as follows: 1) from *Umbrivaga* by having 10 or more palatine teeth rather than 8 or less and by having the maxilla and associated teeth orientated vertically rather than in a medial direction. 2) from *Lystrophis* by the presence of a normal premaxilla loosely connected to the septomaxilla and nasals rather than premaxilla enlarged, wedge-shaped, and firmly associated with the septomaxilla and nasals; also by having more than 10 teeth on the maxilla rather than 8 or less. 3) from *Lystrophis*, *Xenodon* and *Waglerophis* by having a long and relatively immobile maxilla rather than a short and partly rotating maxilla; by having the maxillary process of the ectopterygoid without a deep central emargination or by being boot-shaped and having the supratemporal equal in width throughout its length or slightly rounded anteriorly rather than by having the anterior end almost twice as wide as posterior end; in addition, by never having more than 19 scale rows at midbody nor an entire anal plate. 4) from *Erythrolamprus* by having well developed anterolateral projections of frontal immediately followed by an almost waist-like restriction of the frontals at the level of the anterior third of the orbit rather than by having the anterolateral projections absent or poorly developed and little waist-like restriction of the frontals; the maxillary process of the ectopterygoid is usually without a relatively long anterior projection passing dorsally and to the inside of the maxilla, rather than the anterior end of ectopterygoid having a well-developed and lengthy anterior projection (see figure 1 for illustrations of osteological characters); never with complete color rings of equal width about the body or tail rather than with complete color rings on the body and tail; tail length 13.5 to 31 percent of total length rather than 10 to 13 percent; posterior grooved teeth never present rather than usually present (occasionally absent in *E. mimus*).

*Distribution.* — *Liophis* is widely distributed in cis-Andean South America, reaching 43° south latitude in Argentina (Figure 2). Several species are found in the northern Andes, reaching an elevation of 3500 m and three species range down the western Andes to 20° south latitude. Three species are found in trans-Andean South America, ranging as far north as northeastern Costa Rica and south to the southwestern lowlands in the region of Guayaquil, Ecuador. Five species are confined to the Caribbean Islands, one species each to Curacao, Barbados, Martinique, St. Lucia, Dominica, and Guadalupe. At least four mainland species reach Trinidad and two reach Tobago.

*Ecology.* — Members of the genus *Liophis* are primarily terrestrial but some are semifossorial or semiaquatic. They are nearly always found associated with moist environments. *Liophis* are generally found around bogs, swamps, marshes, ponds, and streams that are associated with rain forests, montane forests, deciduous forests, thorn forests, grassland, and paramo (personal field observations).



**Figure 1.** — The upper illustration is a dorsal view of the right ectopterygoid (anterior end to left), followed below (left) by ventral view of right maxilla and (right) dorsal view of skull (premaxilla, nasal, prefrontal, and postorbital not illustrated). The illustrations were made by use of a Wild Heerburg M-7 binocularscope with camera lucida and at various magnifications and are not directly comparable. From left to right, the upper illustrations are represented by *Lystrophis dorbignyi*, *Waglerophis merremi*, *Xenodon rhabdocephalus*, tribe Xenodontini.

Stomach contents of several species reveal that arthropods, millipedes, earthworms, fish (*Synbranchus*), salamanders, anurans (*Bufo*, *Eleutherodactylus*, *Hyla*, *Leptodactylus*, *Phyllobates*, and *Colostethus*) and their larvae, lizards (*Ameiva* and *Gymnophthalmus*) and birds are principal prey items (Abalos *et al.*, 1965; Beebe 1946; Dixon and Soini, 1977; Duellman 1978; Dunn 1944b; Freiberg 1957; Myers, Daly and Malkin, 1978; Sexton and Heatwole, 1965; Test *et al.*, 1966; Vaz-Ferreira *et al.*, 1973; Wehekind 1955).

Reproductive information is sparse. One species (*viridis*) was shown to have sperm storage capabilities by Fox (1956). Coping (1957) indicated the *L. albiventris* lays its eggs in heaps of rotting vegetation. Vaz-Ferreira *et al.*, (1970) showed that several unrelated species of colubrid snakes utilize communal nest sites, such as the nests of the leaf-cutting ant, *Acromyrmex*. They recorded clutches of 4 and 7 *L. jaegeri* eggs laid between 4 and 10 December. Fitch (1970) examined 40 females of *L. reginae* from Peru that contained between 1 and 8 ( $\bar{x}=4.53$ ) eggs. Oviducal eggs were present in females of *L. reginae* in every month except May and July. Dunn (1944b) recorded the laying of 16 eggs by one female of *L. bimaculatus* from Bogota, Colombia, that hatched 11 months later. Sexton and Heatwole (1965) found three gravid female *L. epinephalus* in Panama with 5, 7 and 10 eggs on 22 June, 23 June, and 29 July, respectively. Beebe (1946) recorded one Guyanan *L. breviceps* with 8 eggs on 9 October and one *L. typhlus* from Guyana with 5 eggs on 17 June. Test *et al.* (1966) found a specimen of *L. zweifeli* from Rancho Grande, Venezuela, containing 3 shelled oviducal eggs on 8 April and another with 5 large ova on 4 July.

#### TABLE 2

The generic content of *Liophis* currently consists of 40 species (20 subspecies not included), of which about 25 are valid. I have listed the 40 species as they are currently recognized. However, in a forthcoming series of papers, several species (those marked with a plus sign) will be shown to be conspecific with other species.

|                      |                         |                        |                    |
|----------------------|-------------------------|------------------------|--------------------|
| + <i>albiventris</i> | + <i>coralliventris</i> | <i>lineatus</i>        | + <i>purpurans</i> |
| <i>almadensis</i>    | <i>cursor</i>           | <i>longiventris</i>    | <i>reginae</i>     |
| + <i>amazonicus</i>  | <i>epinephalus</i>      | <i>melanotus</i>       | <i>sagittifer</i>  |
| <i>anomala</i>       | <i>festae</i>           | <i>miliaris</i>        | <i>taeniurus</i>   |
| + <i>bimaculatus</i> | + <i>flavifrenatus</i>  | + <i>mossoroensis</i>  | + <i>trebbau</i>   |
| + <i>brazili</i>     | + <i>fraseri</i>        | <i>ornatus</i>         | <i>triscalis</i>   |
| <i>breviceps</i>     | <i>frenata</i>          | <i>paucidens</i>       | <i>typhlus</i>     |
| + <i>canaima</i>     | + <i>ingeri</i>         | <i>perfuscus</i>       | <i>viridis</i>     |
| + <i>chrysostoma</i> | <i>jaegeri</i>          | <i>poecilogyrus</i>    | <i>williamsi</i>   |
| <i>cobella</i>       | <i>juliae</i>           | + <i>pseudocobella</i> | + <i>zweifeli</i>  |

## RELATIONSHIPS

*Liophis* belongs to the subfamily Xenodontinae, tribe Xenodontini, along with *Xenodon*, *Lystrophis*, *Waglerophis*, *Erythrolamprus*, and *Umbrivaga*. These were proposed as a single group by Dowling (1975) because of similar hemipenial morphology and the absence of posterior vertebral hypapophyses. For illustrations of hemipenial morphology, see Cope (1900), Dowling (1975), Emsley (1963), Gans (1964), Maglio (1970), Orejas-Miranda (1966), and Romano and Hoge (1972).

In the absence of a fossil record, any discussion of relationships within the group and its history must be based on inferred affinities of its living members. There are approximately 40 species of *Liophis*, six of *Xenodon*, six of *Erythrolampus*, three of *Umbrivaga*, three of *Lystrophis*, and one of *Waglerophis*. *Liophis*, *Erythrolampus*, and *Xenodon* are widespread in cis-Andean South America and their range extends northward to Costa Rica, Nicaragua and Mexico, respectively. *Waglerophis* is confined to the open plant formations of the caatinga, cerrado, and chaco of Brazil, Paraguay, and northern Argentina. *Lystrophis* appears to have a distribution similar to *Waglerophis* but is more restricted to southeastern South America between 15° and 40° south latitude. *Umbrivaga* has the most restricted distribution, occurring in the Amazon basin from Iquitos to Manaus, the western edge of the Colombian Llanos near Loma Linda, and in the cloud forests of Rancho Grande, Venezuela.

The species of the Xenodontini are about evenly distributed in South America with five being Andean, 11 being Amazonian, 11 occurring north of the Amazon, and 17 south of it; with five other species on Caribbean islands.

Five of the six genera in the tribe Xenodontini show some degree of specialization for foraging and feeding strategies. The specializations involve part or all of the anterior part of the skull, maxilla (and teeth), palatine, pterygoid, ectopterygoid, quadrate, supratemporal, gape, eye size, and external scale modifications. My interpretation of the affinities of the six genera is based on the gross examination of the preceding characters (see Table 3) and is highly speculative at best.

*Liophis* appears to be the most generalized genus of the group in its osteology, external morphology, habitat, and food preferences. *Erythrolamprus* is the sister genus to *Liophis*. It has a generalized external morphology, but with a broader skull, grooved post-diastemal maxillary teeth and less generalized food preferences (ophiophagous). *Umbrivaga* is more specialized than the former two genera, showing a general reduction in body size, scale rows, numbers of ventrals, caudals, labials, and teeth, a rounded skull, a maxilla with enlarged sword-like, post-diastemal teeth that point medially and it specializes on reptile eggs as a food resource (personal observation). *Xenodon*, *Waglerophis*, and

*Lystrophis* have a common denominator in a relatively short, rotating maxilla with very large post-diastemal teeth that aid in swallowing frogs and/or toads (Kardong, 1979). *Xenodon* and *Waglerophis* are closely related but can be separated from one another by characters of cranial morphology, number of maxillary teeth, and gross hemipenital morphology. Both genera feed principally on *Leptodactylus*, *Bufo*, and other anurans. *Lystrophis* is the most specialized member of the group, with a highly modified snout and associated bones, a very short maxilla, with few teeth, and it principally forages for toads (*Odontophrynus*, *Melanophryniscus*) and lizards (*Teius*) in the same manner as does the North American hognose snake, *Heterodon*.

Since four of the genera have modified maxillary bones and teeth for specific feeding strategies they likely evolved early from a *Liophis*-like ancestor. However, one of the four genera (*Umbrivaga*) does not have a rotating maxillary and probably evolved later and from another branch (see Figure 1).

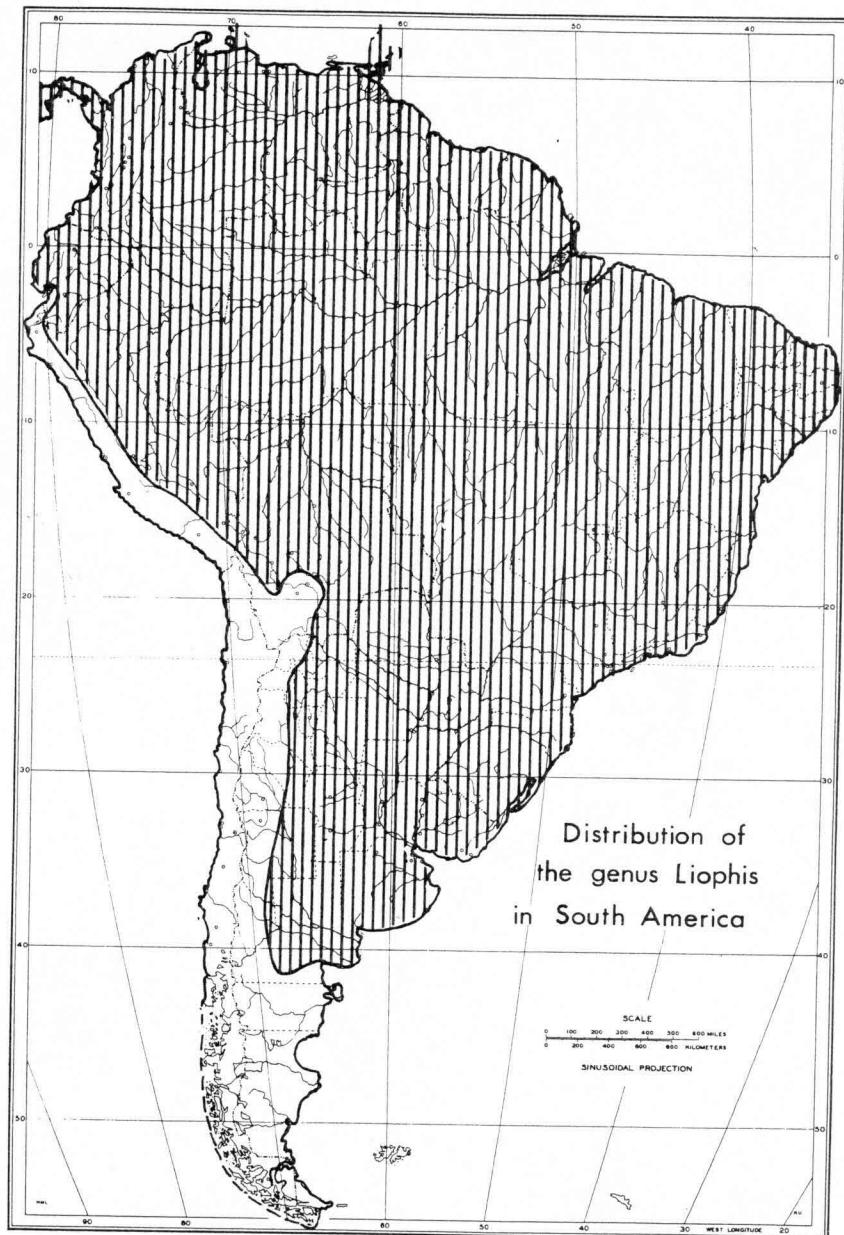


Figure 2. — Distribution of the colubrid snake genus *Liophis* in South America.

**TABLE 3**

List of genera and species of snakes whose skull and individual tooth bearing bones were examined during the course of the study.

| SPECIES               |                       | NO. OF SKULLS<br>+ DENTIGEROUS BONES | MUSEUM NOS.<br>FOR SKULLS |
|-----------------------|-----------------------|--------------------------------------|---------------------------|
| <i>Erythrolamprus</i> | <i>aesculapii</i>     | 2+8                                  | FMNH 2621, TCWC 44610     |
|                       | <i>bizona</i>         | 1                                    | MCZ 56082                 |
|                       | <i>mimus</i>          | 1                                    | MCZ 50225                 |
|                       | <i>venustissimus</i>  | 1                                    | MCZ 3487                  |
| <i>Liophis</i>        | <i>almadensis</i>     | 2+4                                  | MCZ 17950, TCWC 53409     |
|                       | <i>amazonicus</i>     | 1+5                                  | MCZ 2820                  |
|                       | <i>anomala</i>        | 1+24                                 | MCZ 853                   |
|                       | <i>bimaculatus</i>    | 1+21                                 | MCZ 17133                 |
|                       | <i>breviceps</i>      | 0+58                                 |                           |
|                       | <i>chrysostoma</i>    | 0+28                                 |                           |
|                       | <i>cobella</i>        | 3+153                                | MCZ 19210, 16385, 838     |
|                       | <i>coralliventris</i> | 0+2                                  |                           |
|                       | <i>cursor</i>         | 1+17                                 | MCZ 6011B                 |
|                       | <i>epinephalus</i>    | 3+326                                | CRE 1160, 1763, MCZ 15299 |
|                       | <i>flavifrenatus</i>  | 1+22                                 | MCZ 17912                 |
|                       | <i>festae</i>         | 0+14                                 |                           |
|                       | <i>fraseri</i>        | 0+34                                 |                           |
|                       | <i>jaegeri</i>        | 1+41                                 | MCZ 5633                  |
|                       | <i>juliae</i>         | 2+35                                 | MCZ 32055, 57819          |
|                       | <i>lineatus</i>       | 1+97                                 | MCZ 32758                 |

TABLE 3 (cont.)

| SPECIES                       | NO. of SKULLS<br>+ DENTIGEROUS BONES | MUSEUM NOS.<br>for SKULLS       |
|-------------------------------|--------------------------------------|---------------------------------|
| <i>Liophis mariae</i>         | 2                                    | MCZ 6138A, B                    |
| <i>melanotus</i>              | 5+1                                  | MCZ 48756, 83049, TCWC 3 uncat. |
| <i>miliaris</i>               | 1+54                                 | MCZ 2829                        |
| <i>opisthotaenia</i>          | 0+20                                 |                                 |
| <i>ornatus</i>                | 1+14                                 | MCZ 6137                        |
| <i>perfuscus</i>              | 1+8                                  | MCZ 78621                       |
| <i>poecilogyrus</i>           | 2+77                                 | MCZ 2665, 140378                |
| <i>pseudocobella</i>          | 1+26                                 | MCZ 65382                       |
| <i>reginae</i>                | 2+343                                | MCZ 49068, TCWC 42112           |
| <i>rufus</i>                  | 0+1                                  |                                 |
| <i>taeniurus</i>              | 1+40                                 | MCZ 11297                       |
| <i>triscalis</i>              | 0+23                                 |                                 |
| <i>typhlus</i>                | 1+57                                 |                                 |
| <i>williamsi</i>              | 0+6                                  | TCWC 38049                      |
| <i>Lystrophis dorbignyi</i>   | 2+2                                  | MCZ 20745, TCWC 53499           |
| <i>Umbrivaga mertensi</i>     | 1+2                                  | UMMZ 124216                     |
| <i>pyburni</i>                | 1+7                                  | UTA 3421                        |
| <i>pygmaeus</i>               | 1+15                                 | TCWC 40545                      |
| <i>Waglerophis merremi</i>    | 1+1                                  | TCWC 518                        |
| <i>Xenodon rhabdocephalus</i> | 3+8                                  | MCZ 32448, 38717, TCWC 517      |
| <i>severus</i>                | 1+4                                  | TCWC 516                        |
| TOTAL                         | 50+1598                              |                                 |

## SUMMARY

In summary, a large and difficult group of South American snakes is redefined and the intrageneric affinities are reassessed in order to reflect a more natural relationship.

A detailed table is presented that includes all taxa formerly thought to belong to the genera *Dromicus*, *Leimadophis*, *Liophis*, and *Lygophis* and their current disposition.

A historical resume is presented indicating how and/or why early authors used certain species and/or generic combinations. The species content of those early generic concepts were extremely confusing and most are herein placed with their proper genera. Morphological characters, such as hemipenial ornamentation, posterior maxillary diastemal width, scale pit numbers, scale row reduction patterns, and color patterns once used to diagnose the genera *Dromicus*, *Leimadophis*, *Liophis*, and *Lygophis*, are shown to vary or to be frequently shared among the four genera. Hence, the genera have been combined under the oldest available name, *Liophis* Wagler, 1830. A complete synonymy is presented for the latter genus in addition to a redefinition and diagnosis.

A brief summary is presented of diet, habitat, and reproduction for some of the species of the genus *Liophis*.

The distribution and intergeneric relationships of *Liophis* are discussed in light of the morphological similarities with other members of the tribe Xenodontini.

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## LITERATURE CITED

- Abalos, J. W., C. Baez and R. Nader. 1965. Serpientes de Santiago del Estero (Republic Argentina). *Act. Zool. Lilloana* 20:211-283.
- Agassiz, L. 1846. *Nomenclatoris Zoologici Index Universalis, continens nomina systematica classium, ordinum, familiarum et generum omnium, tam viventium quam fossilium, secundum ordinem alphabeticum unicum disposita, adjectis homonymiis plantarum, nec non variis adnotationibus et emendationibus.* viii + 393 pp. Solodurum: Jent et Gassmann.
- Amaral, A. do. 1923. New genera and species of snakes. *Proc. New England Zool. Club* 8:85-105.
- \_\_\_\_\_. 1924. New genus and species of South American snakes contained in the United States National Museum. *J. Washington Acad. Sci.* 14:200-202.
- \_\_\_\_\_. 1925. *Historia natural Zoologia. Ofidios de Mato Grosso. Comm. Linhas Telegraf.* Mato Grosso ao Amazonas 5(84):1-29.
- \_\_\_\_\_. 1926. Novos generos e especies de ophidios brasileiros. *Arch. Mus. Nac., Rio de Janeiro* 26:96-121.
- \_\_\_\_\_. 1929. Estudos sobre ophidios Neotropicos XVII. Valor systematico de varias formas de ophidios neotropicos. *Mem. Inst. Butantan* 4:1-68.
- \_\_\_\_\_. 1931. Studies of neotropical ophidia XXIII. Additional notes on Colombian snakes. *Bull. Antivenin Inst. America* 4(4):85-89.
- \_\_\_\_\_. 1935. Collecta herpetologica no centro do Brasil. *Mem. Inst. Butantan* 9:235-246.
- \_\_\_\_\_. 1944. Notas sobre a ofiologia neotropica e brasilica. X. Distribucao geografica e racial de *Leimadophis poecilogyrus* (Wied). *Pap. Avul. Zool., Sao Paulo* 5:75-82.
- Bacqué, A. 1906. Trois trigonocéphales du Paraguay. *Rev. Mus. La Plata* 12:111-119.
- Barbour, T. 1914. A contribution to the zoogeography of the West Indies with special reference to amphibians and reptiles. *Mem. Mus. Comp. Zool.* 44:205-359.
- \_\_\_\_\_. 1915. A new snake from southern Peru. *Proc. Biol. Soc. Wash.* 28:149-150.
- \_\_\_\_\_. 1916. The reptiles and amphibians of the Isle of Pines. *Ann. Carnegie Mus.* 10:297-308.
- Barbour, T., and C. T. Ramsden. 1919. The herpetology of Cuba. *Mem. Mus. Comp. Zool.* 47(2):71-213.
- Beebe, W. 1946. Field notes on the snakes of Kartabo, British Guiana, and Caripito, Venezuela. *Zoologica* 31(4):11-52.
- Berthold, A. A. 1859. Einige neue reptilien des Akad. zoolog. Museums in Gottingen. *Nachr. Georg-Augustus Univ. U.K. Ges. Wiss. Gottingen* 1859(17):179-181.
- Bibron, G. 1843 *in cocteau*, J. T., and G. Bibron, Reptiles. *In Ramon de la Sagra, D., Historia fisica, politica y natural de la Isla de Cuba. part 2, Historia Natural* 4:130-132. Paris, Libreria de Arthus Beetrand.
- Bocourt, M. F. 1886. Mission scientifique au Mexique et dans l' Amerique

- Centrale . . . Recherches zoologiques, Livr. 10:593-656. Paris: Imprimerie Nationale (1870-1909).
- Boettger, O. 1881. Diagnoses reptilium et batrachiorum novorum ab ill. Antonio Stumpff in insula Nossi-Be Madagascariensi lectorum. Zool. Anz. 4:358-362.
- \_\_\_\_\_. 1885. Berichtigung der liste von reptilien und amphibien am Paraguay. Zeitschr. Naturw. 58:436-437.
- \_\_\_\_\_. 1891. Reptilien und batrachier aus Bolivia. Zool. Anz. 14:343-347.
- Boulenger, G. A. 1882. Account of the reptiles and batrachians collected by Mr. Edward Whymper in Ecuador in 1879-1880. Ann. Mag. Nat. Hist. 9(5):457-467.
- \_\_\_\_\_. 1888. Descriptions of new reptiles and batrachians from Madagascar. Ann. Mag. Nat. Hist. (6)1:101-107.
- \_\_\_\_\_. 1893. Catalogue of the snakes in the British Museum (Natural History). Vol. 1, xiii + 448 pp., London: Trustees of the Museum.
- \_\_\_\_\_. 1894. Catalogue of the snakes in the British Museum (Natural History). Vol. 2., 382 pp., London: Trustees of the Museum.
- \_\_\_\_\_. 1896. Catalogue of the snakes in the British Museum (Natural History). Vol. 3, xiv + 727 pp., London: Trustees of Museum.
- \_\_\_\_\_. 1900. Descriptions of new batrachians and reptiles collected by Mr. P. O. Simons in Peru. Ann. Mag. Nat. Hist. (7)7:181-186.
- \_\_\_\_\_. 1902. Descriptions of new batrachians and reptiles from northwestern Ecuador. Ann. Mag. Nat. Hist. (7)9:51-57.
- \_\_\_\_\_. 1903. Descriptions of new snakes in the collection of the British Museum. Ann. Mag. Nat. Hist. (7)12:350-354.
- \_\_\_\_\_. 1905. Descriptions of new snakes in the collection of the British Museum. Ann. Mag. Nat. Hist. (7)15:453-456.
- \_\_\_\_\_. 1908. Descriptions of new South American reptiles. Ann. Mag. Nat. Hist. (8)1:111-115.
- Brèthes, J. 1917. Description d'un nouveau Colubridae aglypha de la République Argentine: "Zamenis argentinus" Brèthes, sp. n. Physis 3(13):92-94.
- Buden, D. W. 1966. An evaluation of Jamaican *Dromicus* (Serpentes, Colubridae) with the description of a new species. Breviora 238:1-10.
- Cochran, D. M. 1931. New reptiles from Beata Island, Dominican Republic. Proc. Biol. Soc. Washington 44:89-92.
- \_\_\_\_\_. 1934. Herpetological collections made in Hispanola by the Utowana Expedition, 1934. Occ. Pap. Boston Soc. Nat. Hist. 8:163-188.
- Cope, E. D. 1860a. Catalogue of the Colubridae in the museum of the Academy of Natural Sciences of Philadelphia, with notes and descriptions of new species. Part 2. Proc. Acad. Nat. Sci. Philadelphia 12:241-266.
- \_\_\_\_\_. 1860b. Descriptions of reptiles from tropical America and Asia. Proc. Acad. Nat. Sci. Philadelphia 12:368-374.
- \_\_\_\_\_. 1862a. Synopsis of the species of *Holcosus* and *Ameiva*, with diagnosis of new West Indian and South American Colubridae. Proc. Acad. Nat. Sci. Philadelphia 13:60-82.

- \_\_\_\_\_. 1862b. Catalogues of the reptiles obtained during the explorations of the Parana, Paraguay, Vermejo and Uruguay Rivers, by Capt. Thos. J. Page, U.S.N.; and of those procured by Lieut. N. Michler, U.S. Top. Eng., commander of the Expedition conducting the Survey of the Atrato river. Proc. Acad. Nat. Sci. Philadelphia 14:346-359.
- \_\_\_\_\_. 1863. Descriptions of new American Squamata, in the museum of the Smithsonian Institution, Washington. Proc. Acad. Nat. Sci. Philadelphia 15:100-106.
- \_\_\_\_\_. 1868. An examination of the Reptilia and Batrachia obtained by the Orton Expedition to Ecuador and the upper Amazon, with notes on other species. Proc. Acad. Nat. Sci. Philadelphia 20:96-140.
- \_\_\_\_\_. 1869. Sixth contribution to the herpetology of tropical America. Proc. Acad. Nat. Sci. Philadelphia 20:305-313.
- \_\_\_\_\_. 1870. Seventh contribution to the Herpetology of tropical America. Proc. Amer. Philos. Soc. 11:147-169.
- \_\_\_\_\_. 1871. Ninth contribution to the herpetology of tropical America. Proc. Acad. Nat. Sci. Philadelphia 23:200-224.
- \_\_\_\_\_. 1875. Report on the reptiles brought by Professor James Orton from the middle and upper Amazon, and western Peru. Jour. Acad. Nat. Sci. Philadelphia, Ser. 2, 8:159-183.
- \_\_\_\_\_. 1878. Synopsis of the cold blooded vertebrata, procured by James Orton during his exploration of Peru in 1876-1877. Proc. Amer. Philos. Soc. 17:33-49.
- \_\_\_\_\_. 1879. Eleventh contribution to the herpetology of tropical America. Proc. Amer. Philos. Soc. 18:261-277.
- \_\_\_\_\_. 1885. Twelfth contribution to the herpetology of tropical America. Proc. Amer. Philos. Soc. 22:167-194.
- \_\_\_\_\_. 1887. Synopsis of the batrachia and reptilia obtained by H. H. Smith, in the Province of Mato Grosso, Brazil. Proc. Amer. Philos. Soc. 24:44-60.
- \_\_\_\_\_. 1899. Contributions to the herpetology of New Granada and Argentina. Philadelphia Mus. Sci. Bull. (1):1-22.
- \_\_\_\_\_. 1900. The crocodilians, lizards, and snakes of North America. Annual Rept. U.S. Natl. Mus. pp. 155-1294.
- Copping, R. 1957. Reptiles and amphibians of the highlands of Ecuador. Brit. J. Herp. 2(3):54-56.
- Daudin, F. M. 1803. Histoire naturelle generale et particuliere des reptiles. 7:436 pp., Paris: F. Dufart.
- Dixon, J. R. and P. Soini. 1977. The reptiles of the upper Amazon basin, Iquitos region, Peru. II. Crocodilians, turtles and snakes. Milwaukee Publ. Mus., Contr.Biol. & Geol. 12:1-91.
- Donndorff, J. A. 1798. Zoologische Beytrage zur XIII. Ausgabe des Linneischen Natursystems. Dritter Band. Amphibien and Fische. Leipzig: Weidmannschen Buchhandlung.
- Dowling, H. G. 1975. The nearctic snake fauna, pp 190-202 in Dowling, H. G. (ed.) 1974 HISS Yearbook of Herpetology. Herpetological Information Search Systems, New York. 256 p.

- Duellman, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. *Misc. Publ. Univ. Kansas Mus. Nat. Hist.* 65:1-352.
- Dugès, A. G. D. 1865. Du *Liophis jani*. *Mem. Acad. Sci. Lett. Montpellier* 6:32-33.
- Dumeril, A. M. C., G. Bibron and A. H. A. Dumeril. 1854. *Erpetologie generale ou histoire naturelle complete des reptiles*. 7:780 pp., Paris: Encl. de Roret.
- Dunn, E. R. 1920. On the Haitian snakes of the genera *Leimadophis* and *Uromacer*. *Proc. New England Zool. Club* 7:37-44.
- \_\_\_\_\_. 1922. Two new South American Snakes. *Proc. Biol. Soc. Washington* 35:219-220.
- \_\_\_\_\_. 1932a. The colubrid snakes of the Greater Antilles. *Copeia* 1932(2):89-92.
- \_\_\_\_\_. 1932b. The status of the snake genus *Rhadinaea* Cope. *Occ. Pap. Mus. Zool. Univ. Michigan* (251):1-2.
- \_\_\_\_\_. 1937. New or unnamed snakes from Costa Rica. *Copeia* 1937(4):213-215.
- \_\_\_\_\_. 1943. A new snake of the genus *Rhadinaea*. *Caldasia* 11(8):307-308.
- \_\_\_\_\_. 1944a. A revision of the Columbian snakes of the genera *Leimadophis*, *Liophis*, *Lygophis*, *Rhadinaea*, and *Pliocercus*, with a note on columbian *Coniophanes*. *Caldasia* 11(10):479-495.
- \_\_\_\_\_. 1944b. Herpetology of the Bogota area. *Rev. Acad. Colombiana Cienc. Exact., Fis., Nat.* 6:68-81.
- Emsley, M. G. 1963. The re-discovery of Cope's *Liophis perfuscus* in Barbados. *Copeia* 1963:577-579.
- Fischer, J. G. 1885. Ichthyologische und herpetologische Bemerkungen. V. *Herpetologische Bemerkungen. Jahrb. Hamburg. Wiss. Anst.* 2:82-121.
- Fitch, H. S. 1970. Reproductive cycles in lizards and snakes. *Misc. Pub. Univ. Kansas Mus. Nat. Hist.* 52:1-247.
- Fitzinger, L. 1843. *Systema Reptilium. Fasciculus primus, Amblyglossae*. 106 pp., Vienna: Braumuller et Seidel.
- Fox, W. 1956. Seminal receptacles of snakes. *Anat. Rec.* 124:519-540.
- Freiberg, M. A. 1957. *Vida de Batracios y Reptiles Sudamericanos*. 192 pp., Buenos Aires: Cesarini Hnos.
- Gans, C. 1964. A redescription of, and geographic variation in, *Liophis miliaris Linne'*, the common water snake of southeastern South America. *Amer. Mus. Novitates* (2178):1-58.
- Garman, S. 1887. On West Indian reptiles in the Museum of Comparative Zoology, at Cambridge, Mass. *Proc. American Philos. Soc.* 24:278-286.
- Griffin, L. E. 1916. A catalog of the Ophidia from South America at present (June, 1916) contained in the Carnegie Museum with descriptions of some new species. *Mem. Carnegie Mus.* 7:163-228.
- Gunlach, J. and W. Peters. 1864. *in Peters, W., Ueber einige neue Saugethiere (...), Amphibien (...), und Fische (...). Monatasber. Akad. Wiss. Berlin* 1864:381-399.

- Günther, A. 1858. Catalogue of colubrine snakes in the collection of the British Museum. vi-281 pp., London: Trustees of the British Museum.
- \_\_\_\_\_. 1860. On a new snake from the Galapagos Islands. Proc. Zool. Soc. London, 1860:97-98.
- \_\_\_\_\_. 1862a. On new species of snakes in the collection of the British Museum. Ann. Mag. Nat. Hist. (3)9:52-59.
- \_\_\_\_\_. 1862b. On new species of snakes in the collection of the British Museum. Ann. Mag. Nat. Hist. (3)9:124-132.
- \_\_\_\_\_. 1863. Additions to Dr. Wucherer's article on the ophidians of Bahia. Ann. Mag. Nat. Hist. (3)12:325-326.
- \_\_\_\_\_. 1864. Reptiles of British India. xvii-452 pp., London: Robert Hardwicke Ray Society.
- \_\_\_\_\_. 1865. Fourth account of new species of snakes in the collection of the British Museum. Ann. Mag. Nat. Hist. (3)15:89-98.
- British Museum. Ann. Mag. Nat. Hist. (3)15:89-98.
- \_\_\_\_\_. 1868. Sixth account of new species of snakes in the collection of the British Museum. Ann. Mag. Nat. Hist. (4)1:413-429.
- \_\_\_\_\_. 1872. Seventh account of new species of snakes in the collection of the British Museum. Ann. Mag. Nat. Hist. (4)9:13-37.
- \_\_\_\_\_. 1881. Seventh contribution to the knowledge of the fauna of Madagascar. Ann. Mag. Nat. Hist. (5)7:357-360.
- \_\_\_\_\_. 1882. Ninth contribution to the knowledge of the fauna of Madagascar. Ann. Mag. Nat. Hist. (5)9:262-266.
- \_\_\_\_\_. 1890. Tenth contribution to the knowledge of the fauna of Madagascar. Ann. Mag. Nat. Hist. (6)5:69-72.
- \_\_\_\_\_. 1894 (1885-1902). In Godman, F. D., and O. Salvin, Biologia Centrali-Americana. 326 pp., London: Taylor and Francis.
- Hallowell, E. 1845. Description of reptiles from South America, supposed to be new. Proc. Acad. Nat. Sci. Philadelphia 2:241-247.
- Hoge, A. R. 1953. Notas erpetologicas. 1<sup>a</sup>. Contribucao ao conhecimento dos ofídios do Brasil central. Mem. Inst. Butantan 24:179-214.
- \_\_\_\_\_. 1954. Notas erpetologicas. Una nova subspecie de *Leimadophis reginae*. Mem. Inst. Butantan 24:241-244.
- Hoge, A. R. and J. S. Lima-Verde. 1972 (1973). *Liophis mossoroensis* nov. sp. do Brasil (Serpentes: Colubridae). Mem. Inst. Butanta 36:215-220.
- Jan, G. 1963a. Enumerazione sistematica degli ofidi appartenenti al gruppo Coronellidae. Arch. Zool. Anat. Fisiol. 2(2):213-330.
- \_\_\_\_\_. 1863b. Elenco sistematico degli Ofidi descritte e disegnati per l'Iconografia Generale. vii-143 pp., Milano: A. Lombardi.
- Jan, G. and F. Sordelli. 1866 (1860-1881). Iconographie generale des ophidiens. Premier Tome, Livr. 15-19. Milan: chez les Auteurs.
- \_\_\_\_\_. and \_\_\_\_\_. 1867 (1860-1881). Iconographie generale des ophidiens. Tome Second, Livr. 23-25. Milan: chez les Auteurs.
- Jensen, A. S. 1900. Lagoa Santa Egnens Slanger. Et Bidrag til det indre

- Brasiliens herpetologi. Vidensk. Meddel. naturh. Foren. Copenhagen 1900:99-111.
- Kardong, K. V. 1979. "Protovipers" and the evolution of snake fangs. Evolution 33:433-443.
- Koslowsky, J. 1895. Batracios y reptiles de Rioja y Catamarca (República Argentina). Rev. Mus. La Plata 6:359-370.
- \_\_\_\_\_. 1896a. Reptiles y batracios de la Sierra de la Ventana (provincia de Buenos Aires). Rev. Mus. La Plata 7:151-156.
- \_\_\_\_\_. 1896b. Sobre algunos reptiles de Patagonia y otras regiones Argentinas. Rev. Mus. La Plata 7:447-457.
- Lacépède, B. G. E. L., comte de. 1789. Histoire naturelle des quadrupedes ovipares et des serpens. Tome second, 527 pp., Paris: Imprimerie du Roi.
- \_\_\_\_\_. 1826. Histoire naturelle des quadrupedes ovipares et des serpens. (New Edition) Vol. 4:106 [Not Seen].
- Laurent, R. 1949. Notes sur quelques reptiles appartenant à la collection de l'Institut Royal des Sciences Naturelles de Belgique. Bull. Inst. Roy. Sci. Nat. Belgium 25(9):1-20.
- Lichenstein, H. 1823. Verzeichniss der Doubletten des zoologischen Museums der Kinigl. Universität zu Berlin nebst Beschreibung vieler bisher unbekannten Arten von Saugethieren, Vogeln, Amphibien und Fischen. x-118 pp., Berlin: T. Trautwein.
- Linnaeus, C. 1758. Systema Naturae per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, Tomus I. Editio Decima, reformata. 824 pp. Holimiae: Laurentii Salvii.
- Maglio, V. J. 1970. West Indian Xenodontine colubrid snakes: their probable origin, phylogeny, and zoogeography. Bull. Mus. Comp. Zool. 141(1):1-54.
- Marx, H. and G. B. Rabb. 1972. Phyletic analysis of fifty characters of advanced snakes. Fieldiana Zool. 63:1-321.
- Merrem, B. 1820. Versuch eines systems der Amphibien. 191 pp., Marburg: Johann Christian Krieger.
- Müller, F. 1878. Katalog der in museum und universitatskabinet zu Basel aufgestellten Amphibien und Reptilien. Verh. Ges. Basel 6:561-709.
- Müller, L. 1928. Herpetologische Mitteilungen. Zool. Anz. 77:61-84.
- Myers, C. W. 1969. South American snakes related to *Lygophis boursieri*: a reappraisal of *Rhadinaea antioquensis*, *Rhadinaea tristriata*, *Cornella whymperi*, and *Liophis atahualpae*. Am. Mus. Novitates 2385:1-27.
- \_\_\_\_\_. 1973. A new genus for Andean snakes related to *Lygophis boursieri* and a new species (Colubridae). Am. Mus. Novitates 2522:1-37.
- \_\_\_\_\_. 1974. The systematics of *Rhadinaea* (Colubridae), a genus of new world snakes. Bull. Am. Mus. Nat. Hist. 153(1):1-262.
- Myers, C. W., J. W. Daly and B. Malkin. 1978. A dangerously toxic new frog (*Phyllobates*) used by Embera Indians of western Colombia, with discussion of blowgun fabrication and dart poisoning. Bull. Am. Mus. Nat. Hist. 161(2):307-366.
- Orejas-Miranda, B. R. 1966. The snake genus *Lystrophis* in Uruguay. Copeia 1966(2):193-205.

- Parker, H. W. 1931. Reports of an expedition to Brazil and Paraguay in 1926-1927 supported by the trustees of the Percy Sladen Memorial Fund and the Executive Committee of the Carnegie Trust for Scotland. *Amphibia and Reptilia*. J. Linn. Soc. London 37:285-289.
- \_\_\_\_\_. 1936. Some extinct snakes of the West Indies. Ann. Mag. Nat. Hist. (10)18:227-233.
- Peracca, M. G. 1892. Descrizione de nuove specie di rettili e anfibi di Madagascar. *Boll. Mus. Torino* 7(112):1-10.
- \_\_\_\_\_. 1897a. Viaggio del Dott. Alfredo Borelli nel Chaco Boliviano e nella Repubblica Argentina. *Rettili ed anfibi*. *Boll. Mus. Torino* 12(274):1-19.
- \_\_\_\_\_. 1897b. Viaggio del Dr. Enrico Festa nell'Ecuador e regioni vicine. IV. *Rettili*. *Boll. Mus. Torino* 12(300):1-20.
- \_\_\_\_\_. 1914. Reptiles et batrachiens de Colombie. *in Fuhrmann, O. & E. Mayor 1914, Voyage d'Exploration Scientifique en Colombie. Mem. Soc. Neuchatel* 5:1-1090.
- Peters, J. A. 1963. Taxonomic notes on Ecuadorian Snakes. *Beit. Neotrop. Fauna* 3(1):57-67.
- Peters, J. A. and B. Orejas-Miranda. 1970. Catalogue of the neotropical Squamata. Part 1. Snakes. *Bull. U.S. Natl. Mus.* 297:1-347.
- Peters, W. 1863. Über einige neue oder weniger bekannte Schlangenarten des zoologischen Museums zu Berlin. *Monatsber. Akad. Wiss. Berlin* 1863:272-289.
- \_\_\_\_\_. 1864. [no title]. *Monatsber. Akad. Wiss. Berlin*, 1864:388.
- \_\_\_\_\_. 1877. Sammlung des Herrn. Dr. Carl Sachs in Venezuela. *Monatsber. Akad. Wiss. Berlin* 1877:457-460.
- \_\_\_\_\_. 1882. [...] den namen der Batrachiergattung *Hylonomus* in *Hylscirtus* zu andern und [...] zwei neue Arten von Schlangen, *Microsoma notatum* und *Liophis ygraecum*. *Sitzungsber. Ges. naturf. Fr. Berlin* 1882(8):127-129.
- Philippi, R. A. 1899. Sobre las serpientes de Chile. *Anales Univ. Chile*, 104:715-723.
- Quijada, B. 1916. Catalogo sistematico de los reptiles Chilenos y extranjeros conservados en el Museo Nacional de Historia Natural. *Bol. Mus. Nac.* (9):22-47.
- Raddi, G. 1820. Di Alcune specie nuovi de rettili e piante brasiliene. *Atti. Soc. Ital. Sci. Modena* 18:1-39.
- Reinhardt, J. and C. F. Lutken. 1862. Bidrag til det vestindiske origes og navnligen til de danskvestindiske oers herpetologie. *Vidensk. Medd. naturhist. For. Copenhagen* 1862(10-18):153-291.
- Rendahl, H. and G. Vestergren. 1940. Notes on Colombian snakes. *Arkiv Zool., Uppsala* 33A:1-16.
- Reuss, A. 1834. Zoologische Miscellen. Reptilien. Ophidier. *Mus. Senckenberg* 1:129-162.
- Romano, S. A. and A. R. Hoge. 1972. Nota sobre *Xenodon* e *Ophis* Serpentes Colubridae. *Mem. Inst. Butantan* 36:209-214.
- Roze, J. A. 1957. Ofidios coleccionados por la expedicion Franco-Venezuelana al

- alto Orinoco, 1951 a 1952. Bol. Mus. Cien. Nat. 1(3/4):179-195.
- \_\_\_\_\_. 1958a. Resultados zoologicos de la expedicion de la Universidad Central de Venezuela a la region del Auyantepui en la Guyana Venezolana, Abril de 1956. 5. Los reptiles del Auyantepui, Venezuela. Act. Biol. Venezolica 2(22):243-270.
- \_\_\_\_\_. 1958b. A new species of the genus *Urotheca* (Serpentes, Colubridae) from Venezuela. Breviora 88:1-5.
- \_\_\_\_\_. 1958c. Los reptiles de Chimanta Tepui (Estado Bolivar, Venezuela) colectados por la expedicion botanica del Chicago Natural History Museum. Act. Biol. Venezolica 2(25):299-314.
- \_\_\_\_\_. 1959. Taxonomic notes on a collection of Venezuelan reptiles in the American Museum of Natural History. American Mus. Novitates 1934:1-14.
- \_\_\_\_\_. 1964. The snakes of the *Leimadophis-Urotheca-Liophis* complex from Parque Nacional Henri Pittier (Rancho Grande), Venezuela, with a description of a new genus and species (Reptilia, Colubridae), Senck. Biol. 45(3/5):533-542.
- Sauvage, M. H.-E. 1884. Sur quelques reptiles de la collection du Museum d'histoire naturelle. Bull. Soc. Philomat., Paris (7)8:142-147.
- Schenkel, E. 1900 (1901). Acther nachtrag zum Katalog der Herpetologischen Sammlung des Basler Museums. Verh. Naturf. Ges. Basel 13:142-199.
- Schlegel, H. 1837. Essai sur la physionomie des serpens. Vol. 2, 606 pp., Amsterdam: M. H. Schonekat.
- Schmidt, K. P. 1926. The amphibians and reptiles of Mona Island, West Indies. Zool. Ser. Field Mus. Nat. Hist. 12(12):148-173.
- Schmidt, K. P. and W. F. Walker. 1943a. Snakes of the Peruvian coastal region. Zool. Ser. Field Mus. Nat. Hist. 24(27):297-324.
- \_\_\_\_\_ and \_\_\_\_\_. 1943b. Three new snakes from the Peruvian Andes. Zool. Ser. Field Mus. Nat. Hist. 24(28):325-329.
- Schwartz, A. 1967. A review of the genus *Dromicus* in Puerto Rico and the Virgin Islands. Stahlia 9:1-17.
- Schwartz, A. and R. Thomas. 1960. Four new snakes (*Tropidophis*, *Dromicus*, *Alsophis*) from the Isla de Pinos and Cuba. Herpetologica, 16:73-90.
- Sexton, O. J. and H. Heatwole. 1965. Life history notes on some Panamanian snakes. Carrib. J. Sci. 5:39-48.
- Shaw, G. 1802. General Zoology or Systematic natural history. III(2). London: Thomas Davidson.
- Shreve, B. 1934. Notes on Ecuadorian snakes. Occ. Paps. Boston Soc. Nat. Hist. 8:125-132.
- Smith, H. M. and C. Grant. 1958. The proper names for some Cuban snakes: An analysis of dates of publication of Ramon de la Sagra's Historia Natural de Cuba, and Fitzinger's Systema Reptilium. Herpetologica 14:215-222.
- Steindachner, F. 1867. Herpetologische Notizen. Sitzungsber. Akad. Wiss. Berlin 55(1):265-273.
- \_\_\_\_\_. 1876. Die Schlangen und Eideschsen der Galapagos-Inseln. Festschr. zool.-bot. Ges. Wien 1876:303-329.

- \_\_\_\_\_. 1901. Herpetologische und ichthyologische Ergebnisse einer Reise nach Sudamerika mit einer Einteilung von Therese Prinzessin von Baiern. Anz. K. Akad. Wiss., Math.-Naturwiss. Cl., Vienna 38:194-196.
- Stejneger, L. 1904. The herpetology of Porto Rico. Rept. U.S. Natl. Mus. 1902:549-724.
- Test, F. H., O. J. Sexton and H. Heatwole. 1966. Reptiles of Rancho Grande and vicinity, Estado Aragua, Venezuela. Misc. Pub. Mus. Zool. Univ. Michigan 128:1-63.
- Thomas, R. and O. H. Garrido. 1967. A new subspecies of *Dromicus andreae* (Serpentes, Colubridae). Ann. Carnegie Mus. 39:219-226.
- Thomas, R. and A. Schwartz. 1965. Hispaniolan snakes of the genus *Dromicus* (Colubridae). Rev. Biol. Trop. 13(1):59-83.
- Tschudi, J. J. von. 1845. Reptilium conspectus quae in Republica Peruana reperiuntur et pleraque observata vel collects sunt in itinere a Dr. J. D. de Tschudi. Arch. Naturg. 11(1):150-170.
- Underwood, G. 1967. A contribution to the classification of the snakes. 179 pp., London: Trustees of the British Museum (Natural History).
- Van Denburgh, John. 1912. Expedition of the California Academy of Sciences to the Galapagos Islands, 1905-1906. IV. The snakes of the Galapagos Islands. Proc. California Acad. Sci. (4)1:323-374.
- Vaz-Ferreira, R., L. C. de Zolessi and F. Achaval. 1970. Oviposicion y desarrollo de ofidios y lacertilios en hormigueros de *Acromyrmex*. Physis 29:431-459.
- \_\_\_\_\_, \_\_\_\_\_ and \_\_\_\_\_. 1973. Oviposicion y desarrollo de ofidios y lacertilios en hormigueros de *Acromyrmex*. II. Trab. V. Congr. Latinoam. Zool. 1:232-244.
- Wagler, J. 1824. Serpentum brasiliensium species novae ou histoire naturelle des especes nouvelles de serpens, recueillies et observees pendant le voyage dans l'interieur de Bresil dans les années 1817, 1818, 1819, 1820, execute par ordre de Sa Majesté le Roi de Baviere, publiee par Jean de Spix, . . . ecrite d'apres les notes du voyageur par Jean Wagler. viii-75 pp., Monachii: Franc. Seraph. Hubschmann.
- Wagler, J. G. 1830. Natürliches System der Amphibien, it vorangehender Classification der Säugthiere und Vögel. vi + 354 pp., Munchen, Stuttgart und Tubingen: J. G. Cotta.
- Wehekind, L. 1955. Notes on the foods of the Trinidad snakes. Brit. J. Herp. 2:9-13.
- Werner, F. 1899. Beschreibung einiger neuer Schlangen und batrachier. Zool. Anz. 22(581):114-117.
- \_\_\_\_\_. 1909. Über neue oder seltene reptilien des Naturhistorischen Museums in Hamburg. Mitt. Naturf. Mus. Hamburg 26:205-247.
- \_\_\_\_\_. 1925. Neue oder wenig bekannte Schlangen aus dem Wiener naturhistorischen Staatsmuseum. Sitz. Akad. Wiss. Wien 134:45-66.
- Wettstein, O. 1930. Eine neue colubride Schlange aus Brasilien. Zool. Anz. 88:93-94.
- Wied-Neuwied, Maximilian, Prinz zu. 1821. Reise nach Brasilien in den Jahren 1815 bis 1817. Vol. 2, xviii-345 pp., Frankfurt A.M.: Henrich Ludwig Bonner.
- \_\_\_\_\_. 1824. Abbildungen zur Naturgeschichte Brasiliens. Weimar (1822-1831) Lief. 8, Isis, 14(1), col. 1103.
- \_\_\_\_\_. 1825. Beiträge zur Naturgeschichte von Brasilien. Vol. I. xxii + 614 pp. Weimar: Gr. H.S. priv. Landes-Industrie-Comptoirs.

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