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RELATIONSHIPS AND TAXONOMIC STATUS OF THE NORTH
AMERICAN NATRICINE SNAKE GENERA *LIODYTES*,
REGINA, AND *CLONOPHIS*By DOUGLAS A. ROSSMAN¹

OUR present understanding of the characteristics and limits of the colubrid subfamily Natricinae is in a highly confused state, and a paper that proposes to discuss several natricine genera must first, of necessity, clearly indicate to which concept of this subfamily the author adheres. To me this subfamily is best interpreted in the sense of Cope (1893: 479, 482; 1895: 200), who defined the Natricinae as colubrid snakes with hypapophyses on all dorsal vertebrae and with noncalyculate hemipenes that are minutely spinose but bear one or more enlarged basal hooks. Of the workers who subsequently have commented on the status of the Natricinae, the opinions expressed by Dunn (1928: 19-20), Bogert (1940: 8-10), and Malnate (1960: 66-69) have had the greatest influence on students of snake systematics.

Dunn's arrangement of American colubrids (*loc. cit.*) made no reference to basal hooks but placed great emphasis on the possession of an undivided *sulcus spermaticus* by the natricines, a character that Cope considered to be diagnostic only at the generic level and one that would exclude many Old World relatives of *Natrix*. One must bear in mind, however, that Dunn was concerned only with New World colubrids and modified Cope's diagnoses accordingly. Bogert (*loc. cit.*) rejected the concept of the Natricinae as a world-wide group chiefly because Dunn's diagnostic hemipenial characteristics are not valid for many Old World forms. The rejection, however, is

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of Dunn's concept of the Natricinae, not Cope's. The latter was aware that a divided sulcus occurs in many Asiatic natricines, and he included this information in his diagnoses and keys (1893: 483; 1895: 206-207; 1900: 956). Unfortunately, most authors between 1940 and 1960 apparently were unaware of Cope's earlier work and discarded the Natricinae *sensu* Cope along with the Natricinae *sensu* Dunn.

During this period tacit agreement existed among herpetologists that the water snakes and their allies did form a natural subgroup within the Colubrinae, but it remained for Malnate (1960: 66-69) to resurrect and redefine the Natricinae as a separate subfamily. He did not, however, utilize hemipenial characters in redefining the Natricinae but distinguished this subfamily from the Colubrinae solely "by the presence of hypapophyses throughout the vertebral column" in natricines as opposed to the absence of these processes from the posterior dorsal vertebrae in colubrines. Thus defined, the subfamily Natricinae is equivalent to Smith's (1943: 10) nontaxonomic group, the Hypophysia, and as such greatly broadens the scope of this subfamily by adding nearly 50 genera to the group which Cope (1900: 956) delimited. These additions would include such seemingly diverse elements as the African "lycodontines" (Bogert, 1940: 11), virtually all of the Malagasy colubrids (Guibé, 1958), and many others (Boulenger, 1893: 177-180; Smith, 1943: 138-139).

Our present limited knowledge of the function of hypapophyses and of their distribution among the various taxa (recent and fossil) renders uncertain the phylogenetic significance of these structures. I believe, however, that the presence of posterior hypapophyses in genera which, on the basis of other characters (hemipenes, osteology, or scutellation), do not appear to have a close relationship to the Natricinae (*sensu* Cope) probably indicates that this condition evolved independently in several phyletic lines. This opinion is in accord with the conclusions of Cope (1894: 832) who commented that "Boulenger has since found this character [posterior hypapophyses] in a good many forms which I had not examined, and which have no affinity to water snakes. This character, while important, presents the same evanescent stages in certain types that the dental characters before noticed exhibit." The latter alludes to the grooved condition of the posterior maxillary teeth in the Opisthoglypha, a grouping within the Colubridae now generally believed to be polyphyletic. The subfamily Natricinae as redefined by Malnate also appears to me to be a polyphyletic assemblage of genera, requiring extensive splitting and reinterpretation by future workers. On the

other hand, the dozen or so genera comprising the Natricinae of Cope constitute a fairly compact, natural phyletic unit that merits taxonomic recognition. This subfamily needs to be more clearly defined (Malnate, 1960: 42, has shown that the hemipenes of some Asiatic species lack a basal hook), but I believe that the definition of the Natricinae provided by Cope (1895: 200) and restated in the initial paragraph of the present paper offers a sound basis for future studies.

The relationships of the non-natricine forms of the Hypophysia remain to be determined. McDowell (1961: 505) has stated that the natricines and their allies have a type of hypapophysis which is peculiar to them. The hypapophyses of a specimen of *Helicops angulatus* examined by me appear identical to those observed in various natricines, yet on other grounds (which are discussed elsewhere in this paper) the genus *Helicops* does not seem to be closely related to the Natricinae.

Malnate (1960: 68-69) expanded upon ideas put forth by Schmidt (1923: 35-36) and by Smith (1943: 138) in suggesting that the presence of posterior hypapophyses may be a more primitive condition than the absence of these processes, in which case the Natricinae (= Hypophysia) probably were ancestral to the Colubrinae (= Anhypophysia). This phyletic concept markedly differs from that envisioned by Cope (1900: 707-708) or by Clark (1944: 427-433), each of whom concluded that the finely spinose, noncalyculate hemipenis found in natricines is the most advanced type and that the subfamily Natricinae occupies an advanced position within the family Colubridae. Only much additional data and further analysis will reveal which hypothesis is correct.

The purpose of the present paper is to discuss the relationships and taxonomic status of three of the smaller North American natricine genera: the monotypic *Liodytes* Cope; the recently resurrected *Regina* Baird and Girard; and the long-neglected *Clonophis* Cope.

Specimens of all genera and a majority of the species of the Natricinae (*sensu* Cope) were examined in regard to body form and color pattern. More detailed examinations of preserved and/or skeletal material were made of the following species: *Amphiesma craspedogaster*, *A. stolata*, *Fowlea piscator*, *Liodytes alleni*, *Natrix aequifasciata*, *N. annularis*, *N. cyclopion*, *N. erythrogaster*, *N. fasciata*, *N. harteri*, *N. natrix*, *N. percarinata*, *N. rhombifera*, *N. sipedon*, *N. taxispilota*, *N. tessellata*, *N. valida*, *Regina grahamii*, *R. kirtlandii*, *R. rigida*, *R. septemvittata*, *Rhabdophis tigrina*, *Semi-*

natrix pygaea, *Storeria dekayi*, *S. occipitomaculata*, *S. storeroides*, *Thamnophis brachystoma*, *T. cyrtopsis*, *T. elegans*, *T. eques*, *T. marciannus*, *T. melanogaster*, *T. proximus*, *T. radix*, *T. rufipunctatus*, *T. sauritus*, *T. sirtalis*, *Tropidoclonion lineatum*, *Virginia striatula*, *V. valeriae*.

I. RELATIONSHIPS OF LIODYTES

The genus *Liodytes* was erected by Cope (1885: 194) to accommodate the secretive aquatic snake originally described by Garman (1874) as *Helicops alleni*. Cope indicated that *Liodytes* differed from *Helicops* only in having smooth rather than keeled dorsal scales. *Liodytes* actually does have keeled dorsal scales in the supra-anal region and on the tail; thus, if the character cited by Cope were indeed the only one distinguishing the two genera we might reasonably conclude that the two are congeneric. That other differences do exist is affirmed by the fact that most subsequent classifications, including Cope's final arrangement (1900: 733, 956), associated *Helicops* with the colubrid subfamily Xenodontinae (our present concept of this group includes Cope's Dromicinae) and placed *Liodytes* in the Natricinae. Despite the fact that the two genera have been allocated to different subfamilies, the majority of herpetologists who have had occasion to comment on the relationships of *Liodytes* have stated, but without explanation, that its nearest relative is *Helicops*. A notable exception was Dunn (1928: 22), who indicated that the two genera are not at all closely related and that their similarities are due to parallelism (Simpson, 1961: 78-79, probably would consider this to be an example of convergence rather than parallelism). Bogert (1940: 9), however, took the view that *Helicops* is "almost certainly closest to the ancestral stock of *Liodytes*." Inasmuch as this alleged relationship provided Bogert with one of his arguments against world-wide application of Dunn's (*op. cit.*: 20) subfamilial arrangement of New World colubrids (particularly the Natricinae), the possibility that *Liodytes* and *Helicops* are not closely related takes on added significance. Bogert's interpretation has been by far the more widely accepted one in recent years (to my knowledge only Smith and Huheey, 1960: 162, have specifically postulated that *Liodytes* was derived from a natricine stock), but the problem has not received the critical reappraisal that it requires.

COMPARISON OF LIODYTES WITH HELICOPS

Series of preserved and skeletal *Liodytes alleni* were compared with preserved specimens of *Helicops angulatus*, *H. carinicauda* (type-species), *H.*

leopardinus, *H. modestus*, and *H. polylepis*, and with a complete skeleton and additional skull of *H. angulatus* and a skull of *H. carinicauda*. Everted and retracted hemipenes of several *Liodytes* were compared with one everted organ each of *Helicops leopardinus* and *H. pictiventris*, and with the *in situ* hemipenes of two *H. angulatus* and one *H. modestus*.

The only character shared by the two genera which is not widespread among colubrid snakes generally is the possession of a single internasal, and even this condition occurs regularly in the natricine *Virginia striatula*. The differences between *Liodytes* and *Helicops* are numerous and striking; some of these differences are summarized below.

Form and Proportions.—The head of *Helicops* is flat and broad, being reminiscent of that seen in the Asiatic river snakes of the subfamily Homalopsinae; *Liodytes*, on the other hand, has a head which is laterally compressed. Moreover, the head is proportionally longer in *Helicops* than in *Liodytes*; it comprises 6.0% (5.8-6.1) of the body (snout-vent) length in six *Helicops* examined and 5.3% (5.0-5.6) in seven *Liodytes*.

Helicops has a small eye with a relatively large pupil, *Liodytes* a large eye with a small pupil. The diameter of the eye comprises 11.5% (10.0-14.1) of head length in seven *Helicops* and 16.4% (15.4-17.1) in seven *Liodytes*.

The anterior genials tend to be as long as or, usually, longer than the posterior ones in *Helicops* (anterior genial length/posterior genial length ratio equals 0.95-1.43, mean 1.15); in *Liodytes* the situation is reversed (AG/PG= 0.68-0.90, mean 0.75).

Hemipenis.—The hemipenis of *Helicops* is moderately bilobed and has a *sulcus spermaticus* that is divided proximal to the bifurcation of the organ. The hemipenes of two *H. angulatus* and one *H. modestus* examined *in situ* extend to the level of subcaudals 10, 12, and 11, respectively. In each case the hemipenis bifurcates two subcaudal lengths anterior to the distal end of the organ. Proximal to the bifurcation the hemipenis is ornamented with uniformly large spines; distally the lobes appear to be spinose but the everted hemipenes are, unfortunately, only partially everted and details of the apical ornamentation cannot be clearly observed.

In *Liodytes*, on the other hand, each hemipenis is single or weakly bilobed (extending to subcaudal 7 or 8 *in situ*) with a simple sulcus which terminates in the shallow depression between the lobes. There are two large

basal hooks, both situated on the same side of the sulcus, and many rows of small spines which decrease in size distally. The apical region is nude. The hemipenis of *Liodytes* is basically the same as that found in other New World natricines.

Osteology.—*Liodytes* agrees with other natricines in having hypapophyses well developed throughout the vertebral column. This condition also characterizes *Helicops angulatus*, but Rosén (1905: 170-171) has shown that there are no hypapophyses on the posterior dorsal vertebrae of *H. leopardi-*

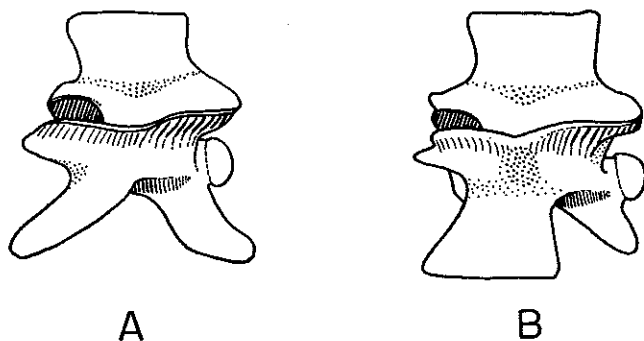


FIGURE 1. Lateral view of a caudal vertebra of (A) *Liodytes alleni* (13th post-dorsal) and of (B) *Helicops angulatus* (19th post-dorsal).

nus or *H. modestus*. The interspecific inconstancy of this character within a single genus is unusual, although not unique, and the taxonomic significance of this situation in *Helicops* requires further investigation.

Although the dorsal vertebrae of *Liodytes* and *Helicops angulatus* are similar in appearance, the caudal vertebrae of the two are strikingly different. The difference lies chiefly in the shape of the transverse processes, which are relatively narrow, rounded distally, and anteroventrally directed in *Liodytes* (Fig. 1A) but broad, truncate, and ventrolaterally directed in *H. angulatus* (Fig. 1B). The condition in *H. angulatus* is not approached in any of the natricines examined or in various species of such diverse non-natricine genera as *Abastor*, *Carpophis*, *Coluber*, *Diadophis*, *Elaphe*, *Heterodon*, *Lampropeltis*, *Masticophis*, *Opheodrys*, and *Sonora*. It remains to be seen whether or not this condition is characteristic of all species of *Helicops*.

The broadness of the head in *Helicops* results in part from a lateral expansion of the prefrontal bones. The prefrontal is about the same length pro-

portionally in *Liodytes* as in *Helicops*, but is as wide as or wider than it is high in the latter whereas in *Liodytes* it is twice as high as it is wide. The postorbital of *Helicops* is massive, while that of *Liodytes* is relatively slender.

The interorbital foramen situated beneath the frontals and above the parasphenoid is well developed in *Liodytes* but extremely small in *Helicops*.

Helicops has a quadrate which is narrow and rounded while that of *Liodytes* is, by comparison, broad and flat.

The anterior elements of the palato-maxillary arch are relatively short in *Helicops*, the maxilla comprising only 42.0% (39.3-43.6) of the total length of the arch; it comprises 51.4% (49.5-52.9) in *Liodytes* (the percentage ranges from 47 to 55 in twelve other natricine species examined). The maxillary dentition of *Helicops* is diacranterian and one of the two enlarged rear teeth is offset (Fig. 2A). *Liodytes* also possesses enlarged rear teeth but these are arranged in a linear sequence with the preceding teeth and, contrary to Cope (1886: 495) and many subsequent authors, are not preceded by a diastema (Fig. 2B).

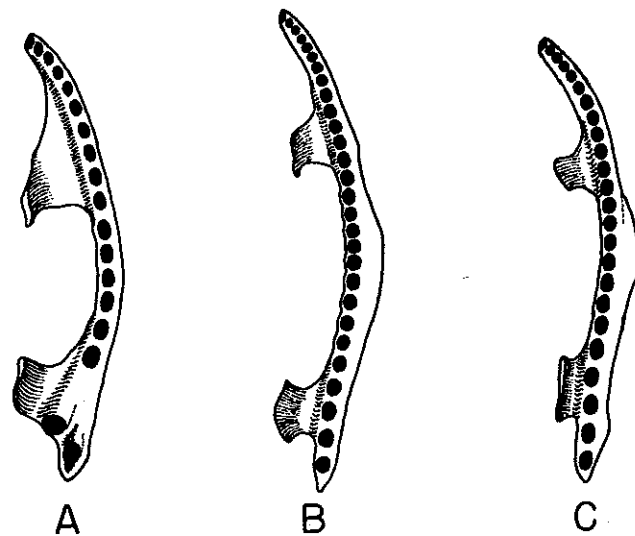


FIGURE 2. Ventral view of the left maxilla of (A) *Helicops angulatus*, (B) *Liodytes alleni*, and (C) *Regina rigida*.

Perhaps one of the most distinctive osteological features in *Helicops* is the shelflike extension of the palatine process of the maxilla, which extends almost to the anterior tip of that bone (Fig. 2A). This condition was noted in all the species of *Helicops* examined. There is nothing similar to it in *Liodytes*, in the other New World natricine genera, or in the few Old World natricines for which skeletal material was available. In *Liodytes* and these natricines the anterior edge of the process joins the shaft of the maxilla at a much more acute angle and terminates well back from the anterior tip of the bone (Fig. 2B, 2C).

In view of the marked dissimilarity of the two genera, it is doubtful that any close relationship exists between them. Conversely, *Liodytes* possesses all of the diagnostic characteristics of the Natricinae and should be associated with that subfamily.

COMPARISON OF *LIODYTES*, *REGINA*, AND *NATRIX*

The striking superficial resemblance, particularly of the head region, between *Liodytes alleni* and the glossy water snake, *Regina rigida*, led me to wonder if *Liodytes* might be related to the group of striped water snakes recently resurrected as the genus *Regina* (Smith and Huheey, 1960). I fully agree with Smith and Huheey that the species *grabamii*, *rigida*, and *septemvittata* form a natural evolutionary unit that differs in many respects from the genus *Natrix* and should be considered a distinct genus. The species *kirtlandii*, however, which Smith and Huheey would also include in *Regina*, differs from the other three species in a number of important features of color pattern, proportions, osteology, and ecology. I do not believe that it is closely allied to *Regina* and shall discuss its generic status in another section of this paper.

A detailed comparison of *Liodytes* with *Regina* and with other natricine genera (especially *Natrix*) indicates that the affinities of *Liodytes* do lie with *Regina* and that, indeed, they should be considered congeneric despite the possession of several unique features by *alleni*. The results of this character analysis are discussed below.

Color pattern.—All four species are characterized by a pattern of longitudinal striping that apparently is unique among natricines. Although there is interspecific variation in the number of stripes and their relative widths (see Fig. 3), the basic pattern consists of a series of dark brown to black stripes on a lighter brown ground color (in dark individuals this pattern

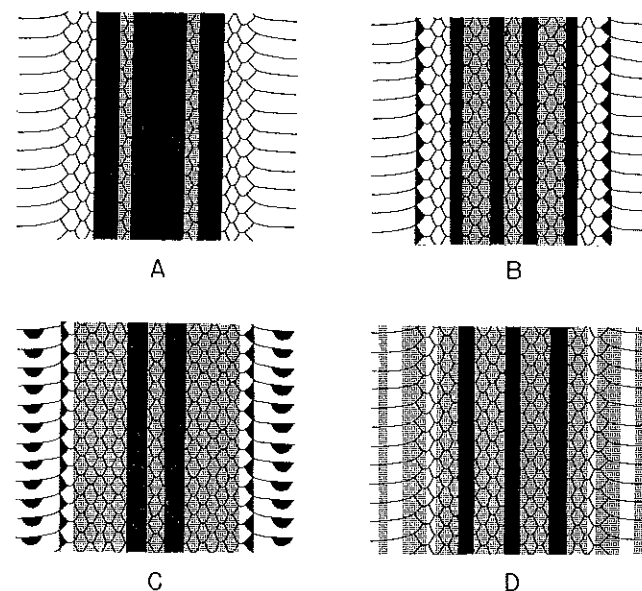


FIGURE 3. Color pattern at mid-body of (A) *Regina alleni*, (B) *R. grabamii*, (C) *R. rigida*, and (D) *R. septemvittata*.

may be difficult to discern); a light stripe occurs on one or more of the rows adjacent to the white or cream-colored venter and is approximately the same color as the venter. The species *rigida* and *septemvittata* characteristically have several well-defined rows of dark spots or stripes extending the length of the venter; the occurrence of dark ventral markings in *alleni* and *grabamii* is not consistent and the markings when present tend to form a single median row. In all forms the light-colored, unmarked labials contrast with the uniformly dark head. To my knowledge the only other species of striped natricine to have this black-brown-cream tricolor pattern of striping is *Fowlea vittata* of Southeast Asia (see van Hoesel, 1959, Figs. 38-40), and its pattern differs from that of *Regina* in having a cross-banded rather than striped venter, strongly barred rather than unmarked labials, and a pair of light parietal spots rather than a uniformly dark head.

Form and Proportions.—As stressed by numerous authors, and most recently by Nakamura and Smith (1960), the head in *Regina* is narrow and barely distinct from the neck, in marked contrast to the broad, prominent head of all *Natrix*. In this respect, too, *alleni* agrees with *Regina*. The significance of this characteristic is discussed in the section on osteology.

Not only is the head narrower in *Regina* than in *Natrix*, but Nakamura and Smith (*op. cit.*, Fig. 1) have graphically demonstrated that it is also proportionately shorter in animals of comparable lengths (proportionate head length decreases with increasing size). The authors expressed this in terms of a head length/total length index, but use of this ratio assumes that the tail is of the same proportionate length in all species (Smith, 1961: 250, 256, has shown that it averages 7 to 8% longer in *septemvittata* than in *grahamii*), hence I prefer to express head length as a per cent of body length (snout to vent). The head comprises 4.1% (3.8-4.4) of body length in eight *grahamii*, 4.3% (3.9-4.6) in nine *septemvittata*, 4.7% (4.5-4.8) in four *rigida*, and 5.3% (5.0-5.6) in seven *alleni*. In *Natrix* of a comparable size the head usually constitutes from 5.2 to 6.1% of body length; thus *alleni* is actually closer to *Natrix* in this regard than it is to the other species of *Regina*. However, it should be noted (Fig. 4) that in the latter genus as proportionate head length increases from one species to the next (lowest in *grahamii*, highest in *alleni*) the number of trunk vertebrae, as reflected by ventral number, decreases (highest in *grahamii*, lowest in *alleni*). This suggests an evolutionary shortening of the body in this phyletic line that was not accompanied by a comparable shortening of the head.

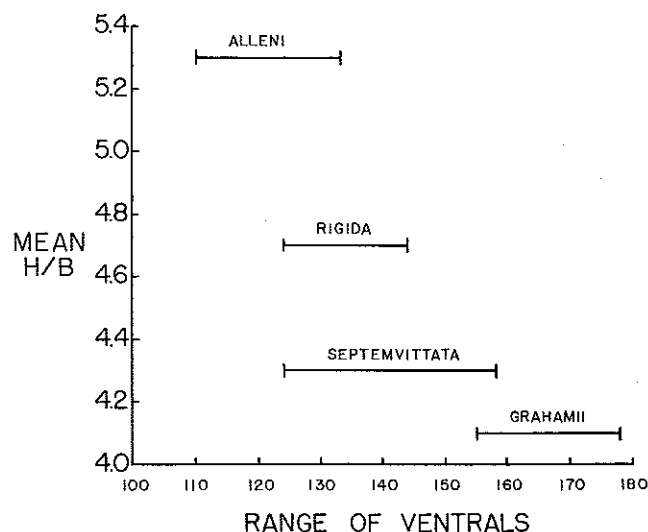


FIGURE 4. Graphic comparison of the mean head length/body length ratio (expressed as a %) with the total range of ventral number in the four species of *Regina*.

The proportional increase in head length is accompanied by an increase in the relative size of the eye. The diameter of the eye comprises 14.9% (14.2-15.9) of the head length in seven *grahamii*, 15.5% (14.4-16.2) in eight *septemvittata*, 15.6% (15.4-16.0) in three *rigida*, and 16.4% (15.4-17.1) in eight *alleni*. The values for most species of *Natrix* fall between 13 and 16%.

The pupil in all four species of *Regina* is diminutive in comparison with that of any *Natrix*. This extremely distinctive feature is difficult to express quantitatively but could scarcely fail to be noticed by anyone even casually examining a living example of *Regina*. Pupil size in a live individual may vary somewhat in response to the amount or intensity of light shining on the eye, but in a series of measurements taken on both freshly killed and preserved material the diameter of the pupil comprises 30.1% (24.6-38.0) of the eye diameter in eleven *Regina* (only one exceeds 34%), 45.4% (33.3-50.0) in nine *Natrix* (only one comprises less than 40%).

Scutellation.—The most distinctive differences between *alleni* and the other three species of *Regina* occur in the scutellation, but all these appear to me to be modifications or specializations of a basic structural "plan" common to all four species but varying in each. As previously mentioned, *alleni* has unkeeled dorsal scales except on the tail and supra-anal region; all the scales have a glossy appearance. Both *grahamii* and *rigida* show a tendency toward reduction in keeling in that the scales of the row adjacent to the venter are unkeeled (Cliburn, 1958: 199, reported a specimen of *rigida* with three unkeeled rows), and the dorsal scales in *rigida* also have a glossy appearance. The loss of keeling and the possession of glossy scales appear to be correlated with a semifossorial existence.

In *alleni* the acumination of snout with the resulting reduction and fusion of the internasals and contact between the nasal scales also appears to be related to burrowing habits. The shape of the snout in *rigida* is very similar to that of *alleni*; the nasals, although not in contact, are situated much closer to each other than in *grahamii* or *septemvittata*, and the internasals are reduced in size. The latter situation is best reflected by the internasorostral contact/nasorostral contact index² which shows the internasals to be broadest in the nine *septemvittata* examined (I/N = 1.06-1.40, mean 1.15), somewhat narrower in nine *grahamii* (0.75-1.11, mean 0.94), considerably narrower in

² Internasorostral contact as used in this study is the combined contact of both internasals with the rostral.

six *rigida* (0.57-0.71, mean 0.65), and incalculable in all *alleni* because the latter has no internasorostral contact. It is interesting to note in regard to the progressive narrowing of the snout from *septemvittata* through *grabamii* to *rigida* and finally *alleni* that the degree of proclivity for burrowing in these species apparently follows the same sequence; *septemvittata* is the least fossorial species in the genus (the summary of the literature in Wright and Wright, 1957: 491-492, 507, implies that *grabamii* is more fossorial than *septemvittata*) and *alleni* the most fossorial. On the other hand, with the narrowing of the internasals, the nares have come to be directed more dorso-laterally, a condition which Malnate (1960: 44-45) associated with aquatic habits. Several authors have called *alleni* the most aquatic Florida snake (Carr, 1940: 92; Auffenberg, 1950: 16).

The nasal in all *Regina* and *Natrix* examined by me is a single semidivided scale. It gives the appearance of being completely divided in *Natrix* because the naris is situated very close to the dorsal margin of the scale, but in no case have I been able to find a suture extending dorsally from the naris. The distance from the naris to the dorsal margin of the nasal is never greater than one-third the height of the naris in the *Natrix* examined; in all species of *Regina* the distance is usually equal to the height of the naris, rarely less and occasionally more. This reflects not only the fact that the naris is more medially situated in *Regina* but also that it is proportionally smaller than in *Natrix*. The height of the naris expressed as a per cent of the height of the nasal ranges from 38 to 50% in *Natrix*, 20 to 33% in *Regina*. Of the latter, *grabamii* and *septemvittata* have the larger nares, *alleni* and *rigida* the smaller.

The number of preoculars on each side is characteristically two in *grabamii*, *rigida*, and *septemvittata*, but only one in *alleni* (only one *alleni* among 24 examined had more than one preocular on each side). The possession of only one preocular is a frequent variation in *rigida*; 75% of the *R. r. deltae* examined by Huheey (1959: 308) had but one preocular on at least one side of the head. The number is much less variable in both *grabamii* (only 4% of those examined by Smith, 1961: 250, had an undivided preocular) and *septemvittata* (none of those recorded by Smith, 1961: 256, and only one reported by Wood and Duellman, 1950: 176, showed this condition). All 24 *alleni* examined possess three postoculars on each side of the head; 27% of the *R. rigida sinicola* reported by Huheey (*loc. cit.*) have three on at least one side; 27% of Illinois *grabamii* have three on at least one side (Smith, 1961: 250); and no Illinois (Smith, 1961: 256)

and only 3.2% of Ohio *septemvittata* (Wood and Duellman, *loc. cit.*) have three.

The supralabial number in 24 *alleni* is predominantly eight on both sides of the head (three exceptions have counts of 7+8, 8+9, and 9+9, respectively), thus differing from the other *Regina* which usually have seven. In *R. r. rigida* 18% have eight supralabials on one or both sides (Huheey, *loc. cit.*); such is also the case in 28% of Illinois *grabamii* (Smith, 1961: 250), and in 3% of Illinois and 9% of Ohio *septemvittata* (Smith, 1961: 256; Wood and Duellman, *loc. cit.*). I know of no *Regina* other than *alleni* that ever has as many as nine supralabials. This species is also peculiar in that the third (to a slight degree) and the fourth supralabials enter the orbit; when there are eight supralabials in the other *Regina*, it is the fourth and fifth that enter the orbit (this appears to be true also of most other natrixine species which have eight supralabials). In these animals the additional scute forms anterior to the orbit, whereas in *alleni* the eighth scute apparently is derived from the series posterior to the eye (the two *alleni* which have nine supralabials do add the extra scute anterior to the orbit). It may be that in the course of its evolutionary development *alleni* underwent a lengthening of the posterior part of its head to compensate (by lengthening the gape) for the extreme compression and shortening of the snout region which could conceivably reduce the functional efficiency of the feeding mechanism required to seize and ingest such bulky prey as crayfish, which constitute the chief item in the diet of the species.

The parietal scales extend ventrolaterally between the postoculars and anterior temporal to establish a very narrow contact with the supralabials in 56.5% of the *alleni* examined (Dowling, 1950:25, noted this condition in 13 of 403 *Seminatrix pygaea* that he examined; Roger Conant has informed me that it occurs as a rare anomaly in several forms of *Natrix*). There is, however, a pronounced ventrolateral extension of the parietals in *rigida*, although actual contact with the supralabials has not been observed.

Sexual dimorphism in ventral number ranges from a mean approximately eight scales greater in male *grabamii* (Smith, 1961: 249), through little more than two scales greater in male *septemvittata* (Wood and Duellman, 1950: 175), and virtually no difference in *rigida* (Huheey, 1959), to two or three scales fewer in the males of *alleni* (Duellman and Schwartz, 1958: 312). The total number of ventrals for each species (sexes combined) ranges from 155 to 178 in *grabamii*, from 124 to 158 in *septemvittata*, from 124 to 144 in *rigida*, and from 110 to 133 in *alleni* (data from Wood and

Duellman, *loc. cit.*; Carr and Goin, 1955: 293; Wright and Wright, 1957; Huheey, 1959; Neill, 1963). The very narrow overlap existing between the respective ranges of variation of *grabamii* and *septemvittata* seems rather unusual in view of the broad overlap which can be observed among the various species within other natricine genera. No explanation of its cause or significance can be offered at this time.

Reduction in the number of dorsal scale rows in *Regina* also offers some peculiar contrasts. Fifty per cent of the male, and 40 per cent of the female, *alleni* examined show no reduction on the body and have 19 rows throughout. One female has a maximum of 21 rows which reduces to 19 immediately posterior to midbody. The remaining *alleni* undergo a reduction to 17 rows near the posterior end of the body. If we follow Peters' (1960: 83) suggestion and express the point of reduction as a per cent of body length (ventral at reduction/total ventrals), we obtain a mean of 90.0% (89.0-91.8). In most other natricines that have 19-17 dorsal scale rows, the reduction index value for a species usually falls between 50 and 65%. In all these species the reduction is usually accomplished by loss of the fourth row. *R. rigida*, with its mean of 56.7% (46.4-66.4), fits the normal natricine pattern, but *septemvittata* (60.7-89.7, mean 72.7%) shows a pronounced tendency toward a more posterior reduction, and *grabamii* (76.7-94.2, mean 85.9%) is almost as extreme in this regard as *alleni* except, of course, that reduction occurs in all *grabamii* but in only about half the *alleni*. This is one of the few characters, if not the only one, in which *alleni* and *rigida* are at the opposite extremes of a morphocline.

Scale pits.—Dunn (1928: 24) indicated that *Liodytes* lacked apical pits, but I have observed what appear to be pits on some of the keeled scales in the supra-anal region and on the tail in an occasional individual of *alleni*; they are definitely present in the other three species. Conant (1961: 18-19) has shown that the presence or absence of scale pits in the natricine genus *Thamnophis* is subject to much individual and interspecific variation.

Hemipenis.—The hemipenes of all four species of *Regina* are similar and differ from the hemipenes of all North American *Natrix*. The organ in *Regina* is single or, at most, weakly bilobed in contrast to the strongly bilobed condition present in *Natrix* (Trapido, 1941, Fig. 1; Dowling and Savage, 1960, Figs. 4D, 6A). Two enlarged basal hooks are present in *alleni*, one in each of the other three species of *Regina*. The spine adjacent to the basal hook in *rigida*, however, is only slightly smaller than the hook,

thus approaching the two-hook condition of *alleni*. The *in situ* organ extends to the level of subcaudal 7 or 8 in *alleni*, 8 in *septemvittata*, 8 or 9 in *grabamii*, and 9 in the single *rigida* examined.

Osteology.—Inasmuch as the skeleton of *alleni* agrees with those of the other species of *Regina* in almost all diagnostic features, the following discussion will be concerned with the characters distinguishing this genus from *Natrix*.

Nakamura and Smith (1960: 112) called attention to the fact that the species included in *Regina* have blunter teeth than those of New World *Natrix*, and that *rigida* has the bluntest teeth of the group. The situation is somewhat more complex than they have indicated. The teeth of *grabamii* (Fig. 5B) and *septemvittata* are, indeed, relatively shorter and stouter than those of the various *Natrix* (Fig. 5A) but they are, nevertheless, pointed at the tip. The teeth of *rigida*, on the other hand, have a rounded chisel-like tip, as do the teeth of *alleni* (Fig. 5C) which are even shorter and stouter. Such a remarkable modification of the teeth probably represents an extreme

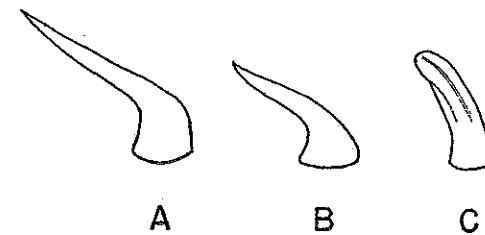


FIGURE 5. Lateral view of a maxillary tooth of (A) *Natrix cyclopion*, (B) *Regina grabamii*, and (C) *R. alleni*.

specialization for the ingestion of crayfish, inasmuch as all four species appear to be primarily crayfish eaters and are the only group of North American snakes in whose diet crustaceans occupy such a major role. Although supporting data is presently wanting, it may be that *alleni* and *rigida*, at least, are not limited to newly molted crayfish, for it seems reasonable to believe that the closely set, short, stout, chisel-like teeth could secure a firmer hold on the chitinous exoskeleton of a crayfish than could the more widely spaced, long, slender, sharply pointed teeth of most water snakes. The latter might tend to break more easily on the hard exoskeleton or, having penetrated it, have difficulty disengaging in the process of work-

ing the prey back into the esophagus. On the other hand, it may be that the teeth of *alleni* and *rigida* do not actually penetrate the exoskeleton but rather serve to gain a firm purchase on its outer surface. Anyone having the opportunity to remove ingested crayfish from the digestive tracts of *alleni* or *rigida* would do well to examine the carapace microscopically with this possibility in mind.

In redefining the genus *Regina*, Smith and Huheey (1960: 158) considered the absence of a ventral process on the basioccipital and absence of a prominent postero-median ridge on the parietal (in contrast to their presence in *Natrix*) to be important diagnostic features (see Fig. 6). Although they based their conclusions on only three of the 18 species of *Natrix*, examination of nine additional species supports their contention regarding the diagnostic significance of these characters.

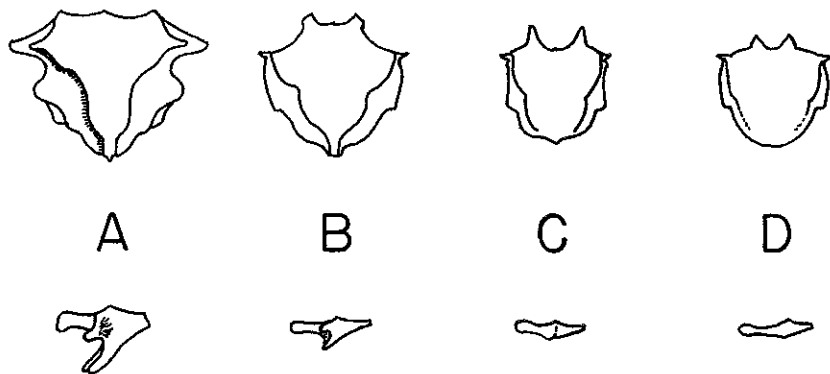


FIGURE 6. Dorsal view of the parietal and right lateral view of the basioccipital of (A) *Natrix taxispilota*, (B) *N. barteri*, (C) *Regina alleni*, and (D) *R. rigida*.

The only other osteological characters specifically mentioned in their diagnosis are the number of pterygoid teeth and the relative width of the frontals. They stated that the number of teeth on each pterygoid usually is 22 or less in *Regina*, 23 or more in *Natrix*. While this is true for *Regina* (see Table I for a summary of tooth-count variation within the genus), it is inconsistent with regard to *Natrix*; the specimens of *N. taxispilota* which I examined average about 20 teeth per pterygoid.

TABLE 1. TOOTH-COUNT VARIATION IN THE FOUR SPECIES OF *REGINA*.

Species	Maxilla			Dentary			Palatine			Pterygoid		
	N	M	R	N	M	R	N	M	R	N	M	R
<i>alleni</i>	27	27.3	26-29	27	29.5	28-32	23	16.5	14-18	23	18.2	17-20
<i>grahamii</i>	14	26.2	24-28	12	31.9	29-35	12	14.2	13-16	12	21.2	18-25
<i>rigida</i>	20	21.5	20-24	18	26.2	24-28	18	15.6	14-17	20	18.4	16-21
<i>septemvittata</i>	12	24.3	23-27	12	27.7	26-31	12	12.4	11-14	11	19.7	17-23

N = number of individual counts, not animals; M = mean; R = range of variation.

Data for *grahamii* derived from Nakamura and Smith (1960: 111) as well as from personal observation.

The smaller frontal width/skull width values obtained for *Natrix* by Nakamura and Smith (1960: 106) do not reflect a relatively narrower frontal in the water snakes (frontal width/frontal length values are similar in both genera) but rather a broader braincase. Even this is more apparent than real, however, for the greater width in *Natrix* appears to be due primarily to an expanded shelf on the prootics for articulation with the supratemporal. The shelf is greatly reduced or absent in all *Regina*.

The previously mentioned difference in relative head width between the two genera intrigued Nakamura and Smith (*op. cit.*), who attempted to account for it on the basis of differences in: relative lengths of the squamosal (= supratemporal), quadrate, and mandible; jaw musculature as correlated with diet; and temperament. My observations indicate that the width of the head at the posterior angle of the jaws (where the degree of distinctness from the neck is most noticeable) is determined by the angle of the quadrate relative to the long axis of the skull, and this in turn is dependent upon the degree of divergence of the posterior end of the pterygoid. There is relatively little divergence in *Regina* but a large amount in *Natrix* (the acute angle formed between the quadrate and the long axis of the skull ranges from 25° to 30° in *Regina*, 39° to 50° in *Natrix*), hence the marked difference in relative head width. While discussing this relationship it may be of interest to note that the point of quadrate-supratemporal articulation in most, but not all, *Natrix* lies almost entirely behind the skull; in *Regina* it occurs almost entirely in a line with the exoccipitals, since the supratemporal does not extend beyond the end of the skull in *rigida* or *septemvittata*, and extends only a short distance beyond it in *alleni* and *grahamii*.

Two osteological characters not mentioned by Smith and Huheey (1960) but which appear to be of diagnostic value are the relative length of the

prefrontal and the presence or absence of a ventral keel on the parasphenoid. The prefrontal in *Natrix* is approximately twice as high as it is long (length/height values for ten species range from 41 to 58%), whereas in *Regina* it is from three to four times as high as it is long (25 to 33%). The ventral surface of the parasphenoid bears a prominent median keel in *Natrix* which is lacking in *Regina*.

EVOLUTIONARY CONSIDERATIONS

In view of the number and nature of the characters involved, it seems unlikely that the many similarities of *alleni* to the other three species could be due to convergence; they appear to reflect instead an actual relationship, and one which is expressed most clearly by including *alleni* in the same taxon with *grabamii*, *rigida*, and *septemvittata*. Although a number of its peculiarities may appear at first glance to exclude *alleni* from this group, upon closer inspection it is apparent that in each of those characters *alleni* represents the specialized extreme of a morphocline in which all four species participate and through which all are seen to be phyletically linked.

Relationships within the group are not entirely clear. The most highly specialized form is *alleni* (*rigida*, with the exception of dorsal scale row reduction, approaches *alleni* in most characters and consequently is also advanced); *grabamii* usually occupies the opposite, primitive, extreme of the morphoclines and in accordance with Maslin's (1952: 65) principle of multiprotoformity, may be considered the most primitive species in the genus. The primitive extremes not occupied by *grabamii* are, with but one aforementioned exception, held by *septemvittata*, which may also be considered a relatively primitive form. Proportional tail length is the only character in which the latter appears at the specialized extreme of a morphocline. The relatively long tail of this species may be correlated to some degree with the semi-arboreal habits it occasionally exhibits (Wright and Wright, 1957: 507).

Present distribution and certain aspects of morphology suggest that two populations of an early *Regina* stock became separated (perhaps due to climatic changes associated with glaciation or physical factors such as a broad embayment) and, being isolated, differentiated into two species (see Blair, 1958, for numerous examples of this phenomenon). The western population apparently underwent little change and became what we now know as *grabamii*; the eastern populations, however, differentiated into two species,

septemvittata in the piedmont and uplands and *rigida*, or a proto-*rigida*, on the coastal plain (the isolating mechanism involved here is not readily apparent). The derivation of *alleni* probably came about as the result of the isolation of a proto-*rigida* stock on the Florida peninsula when it became an island, or a series of islands, during Pleistocene interglacial inundations. The fact that *rigida* does not presently penetrate the peninsula very far to the south of the "Suwanee Straits" could be interpreted to support this viewpoint (see Neill, 1957, for a discussion of the effects of this insular isolation on vertebrate speciation). On the other hand, *alleni* more closely resembles *grabamii* in color pattern and dorsal scale row reduction, and the possibility exists that *alleni* may have arisen on the Florida Pleistocene islands from proto-*grabamii* stock that migrated eastward along the very broad coastal marshes presumably exposed during the glacial periods, when sea level dropped, and became isolated with a rise in sea level. Competition from this stock might also account for the absence of *rigida* from most of peninsular Florida. Of the alternate hypotheses, I favor the former, for it relieves the necessity of attributing the numerous close similarities between *alleni* and *rigida* (particularly the peculiar teeth) to parallelism, although this possibility persists.

Concerning the rank of the taxon to which these species belong, I see no reason for considering it to be anything other than a genus. Here we have a compact, natural phyletic unit which, through its morphological adaptations toward crayfish eating and a semi-fossorial existence, has shifted into a new adaptive zone and reached a level of differentiation fully as distinct as that of any other genus in the subfamily. The genus *Regina* (for whose members the common name Crayfish Snakes would be appropriate) appears to occupy an isolated position within the subfamily Natricinae, and speculation about intergeneric relationships would be unprofitable until such time as considerably more data are available on the other natricine genera.

REDEFINITION OF *REGINA*

Genus *REGINA* Baird and Girard, 1853

Type-Species: *Coluber septemvittatus* Say, 1825 (designated by the International Commission on Zoological Nomenclature, 1962: 145).

A genus of natricine snakes characterized by having: a tricolor dorsal pattern of black, brown, and cream stripes; the dark ventral markings, when

present, forming regular rows or stripes; unmarked labials; no light parietal spots; a relatively short head, scarcely distinct from the neck; a very small pupil (usually comprising less than $\frac{1}{3}$ the eye diameter); the internasals narrowed anteriorly (less so in *septemvittata*), the nares dorsolateral (more lateral in *septemvittata*); each naris small (comprising $\frac{1}{3}$ or less the height of the nasal) and situated medially in the nasal scale; usually 7 or 8 supralabials; 19 scale rows at midbody; the anal plate divided; the relatively short hemipenes single or weakly bilobed, each with a simple *sulcus spermaticus*; all teeth ranging from relatively short and stout (*grahamii* and *septemvittata*) to chisel-like (*alleni* and *rigida*); the posterior ends of the pterygoids weakly divergent; no ventral process on the basioccipital; no postero-median ridge on the parietal bone; the prefrontal 3 to 4 times as high as it is long; no ventral keel on the parasphenoid; a moderately well-developed interorbital foramen; the quadrate not greatly expanded dorsally; the supratemporal not reduced; the nasal bones not expanded; a diet consisting largely of crayfish.

Included species.—*Coluber rigidus* Say, 1825; *Coluber septemvittatus* Say, 1825; *Regina grahamii* Baird and Girard, 1853; *Helicops alleni* Garman, 1874.

Range.—Eastern North America, from the eastern edge of the Great Plains east to the Atlantic Ocean, and from central Michigan and southern Ontario south to the Gulf of Mexico.

II. GENERIC STATUS OF *CLONOPHIS*

The natricine species *kirtlandii*, which has been variously allocated to *Natrix* or *Regina* in recent years, occupies a unique position within the sub-family and, to my mind, deserves to be placed in a separate genus for which the name *Clonophis* Cope, 1889, is available (Dunn, 1928: 24, apparently was the most recent author to utilize this name). Like the species of *Regina*, *Clonophis kirtlandii* has also entered a new adaptive zone, its adaptive trends reflecting semi-fossorial terrestrialism and earthworm eating (Conant, 1943: 334). Although its color pattern bears a superficial similarity to that of *Natrix barteri*, its skeleton is distinct from that of any *Natrix*. The relationships of *Clonophis kirtlandii* are obscure and may actually lie more closely with the species of *Storeria* (in which group it was placed by Jan, 1863: 74, and later by Boulenger, 1893: 286) than with either *Natrix* or *Regina*; the following summary of the diagnostic features of *Clonophis* may serve not only to demonstrate the distinctness of this genus but at the same time provide some clue to its affinities.

DIAGNOSTIC CHARACTERISTICS OF *CLONOPHIS*

Conant (1943) has given a very detailed description of *Clonophis kirtlandii*, hence this summary is limited to features not discussed by Conant or to those that are of particular diagnostic importance. The osteological data presented below are, in many cases, incomplete; the conclusions based on these data must be considered tentative pending completion of more detailed studies of natricine osteology now in progress.

Color pattern.—Of other North American natricines, only *Natrix barteri* and a few of the more primitive species of *Thamnophis* (i.e., *nigronuchalis*, *rufipunctatus*) have a dorsal pattern that consists of several rows of large, dark, rounded blotches and thus could be considered even remotely similar to that of *Clonophis*. There are four such rows in *Clonophis* and *N. barteri*, usually more in the aforementioned *Thamnophis*.

Form and Proportions.—*Clonophis kirtlandii* agrees with the other semi-fossorial natricines in having a relatively short head, barely distinct from the neck, and thus is unlike the various species of *Natrix*, which have a relatively long, prominent head. The head comprises 4.7% (4.4-5.0) of body length in six *kirtlandii* examined.

The pupil in *kirtlandii* is moderately large, comprising 42.5% and 44.0% of the eye diameter in the two specimens checked for this character.

Scutellation.—Unlike other North American natricines, *Clonophis kirtlandii* has broad contact between the internasals and the rostral (I/N for seven individuals = 1.41-1.75, mean 1.59). This feature, associated with the lateral position of the nares, apparently reflects the adaptation of the species to a more terrestrial environment (Malnate, 1960: 44-45). The naris, like that in *Regina*, is relatively small in relation to the nasal scale and is situated near the center of that scale.

In its reduced number of supralabials (usually 6 to a side, frequently 5) *Clonophis* is similar to *Storeria*, *Tropidoclonion*, and *Virginia*, and differs from the other four genera, which normally have seven or more.

Clonophis agrees with *Natrix valida*, all *Regina*, many *Thamnophis*, and *Tropidoclonion* in having 19 rows of scales at midbody. All other *Natrix* and a number of *Thamnophis* have more rows; *Seminatrix*, *Storeria*, a few *Thamnophis*, and *Virginia* have fewer rows. The mean dorsal scale row reduction value for four specimens of *Clonophis* is 61.0% (52.7-68.0),

which is in accord with the general pattern for natricines having 19 rows at mid-body but differs from that of all *Regina* except *R. rigida*.

Hemipenis.—Adequate data on the everted hemipenes of many species of North American natricines are not yet available, but the organ in *Clonophis* appears to be generally similar to that of *Regina* in being single or very weakly bilobed with the sulcus terminating apically between the lobes. This is in contrast to the strongly bilobed condition in *Natrix* previously cited. One enlarged basal hook is present. The organ is fairly short, usually extending *in situ* to the level of subcaudal 7 (6 to 8). A detailed description of the everted hemipenis was given by Conant (*op. cit.*: 318).

Osteology.—The maxillary teeth of *Clonophis* are subequal in length; in most other North American natricines they become progressively larger posteriorly. All teeth are relatively short, stout, and weakly curved, a combination of characteristics most similar to that observed in *Regina grabamii* or *R. septemvittata*. The teeth are much less stout than in the more specialized species of *Regina*, and they are not nearly as long and slender as the teeth of the other six genera.

Although tooth-count data are lacking for many species, the numbers on the various bones in *Clonophis kirtlandii* appear to be comparable to those recorded for *Regina* (the number of palatine teeth may be slightly less in *Clonophis*). There are approximately half again as many teeth on the maxilla and on the dentary of *Clonophis* as there are in *Storeria*. Maxillary, palatine, and pterygoid counts tend to be lower in *Clonophis* than in *Natrix* (Nakamura and Smith, 1960: 111).

The posterior ends of the pterygoids are almost nondivergent in *Clonophis*, a condition also noted in *Storeria* and *Virginia*. They are weakly divergent in *Regina*, strongly divergent in *Natrix*.

As in *Regina*, *Storeria*, and *Virginia*, *Clonophis* has no ventral process on the basioccipital nor a median ventral keel on the parasphenoid; these processes are present in *Natrix*, *Seminatrix*, and some species of *Thamnophis*.

The parietal bone in *Clonophis* is rounded and not only lacks a postero-medial ridge but bears little or no evidence of the elevated, triangular parietal shield; in this the genus agrees with *Storeria* and *Virginia*. *Regina*, *Seminatrix*, and some *Thamnophis* lack the postero-medial ridge but usually have at least some trace of the parietal shield; the shield and ridge are well developed in all *Natrix*.

In *Clonophis* the interorbital foramen is well developed. By comparison the foramen is slightly larger in *Storeria* and *Virginia*, somewhat smaller in *Regina*, and much smaller in *Natrix* and *Seminatrix*.

The quadrate of *Clonophis* is relatively small in relation to the skull and is greatly expanded dorsally; this condition has also been observed in *Storeria* and *Virginia*. The supratemporal, with which the quadrate articulates, is also somewhat reduced in *Clonophis* but extends to and overlaps the parietal-prototic suture. The bone is much more reduced in *Storeria* and does not closely approach the suture.

In most natricines the nasal bones are relatively unexpanded and have little if any dorsal contact with the premaxilla or with the frontal bones. The nasals of *Clonophis kirtlandii* and *Storeria dekayi* (but not *S. storeroides*) are markedly expanded and are in contact with the premaxilla and the frontals dorsally; the condition is most pronounced in *Clonophis*.

RELATIONSHIPS

In view of the many similarities between *Clonophis* and *Storeria*, these two genera may well be closely related although, with the exception of the expanded nasal bones (and the related broad internasal scales), *Clonophis* is much less specialized than any species of *Storeria*, including the primitive *S. storeroides*. Many of the characteristics shared by *Clonophis* and *Storeria*, however, appear to be adaptations for a semifossorial terrestrial existence, hence these similarities may be the result of convergence or parallelism rather than a reflection of close affinities. The possibility that the nearest relative of *Clonophis* resides in the Eastern Hemisphere also remains to be investigated.

REDEFINITION OF CLONOPHIS

Genus *CLONOPHIS* Cope, 1889

Type-Species: *Regina kirtlandii* Kennicott, 1856 (type by monotypy).

A genus of natricine snakes characterized by having: a dorsal pattern of four longitudinal rows of relatively large, dark, rounded blotches on a brown or grey-brown ground color; a red venter bearing a row of black spots along each lateral margin; the labials largely unmarked; a relatively short head, scarcely distinct from the neck; a moderately large pupil; the internasals broad anteriorly, the nares lateral; each naris relatively small and situated

medially in the nasal scale; 5 or 6 supralabials; 19 scale rows at midbody; the anal plate divided; the short hemipenes single or weakly bilobed, each with a simple *sulcus spermaticus*; the maxillary teeth subequal, with all teeth relatively short, stout, and weakly curved; the posterior ends of the pterygoids practically nondivergent; no ventral process on the basioccipital; the parietal bone almost smooth, with no trace of a postero-median ridge; the prefrontal a little more than twice as high as it is long; no ventral keel on the parasphenoid; a well-developed interorbital foramen; the quadrate greatly expanded dorsally; the supratemporal somewhat reduced; the nasal bones greatly expanded, in relatively broad contact with the premaxilla and the frontal bones; a diet consisting largely, if not exclusively, of earthworms and slugs.

Included species: Regina kirtlandii Kennicott, 1856.

Range: The north-central United States from western Illinois east to western Pennsylvania, and from southern Michigan south to northern Kentucky. Two isolated records for the lower Delaware River Valley are highly questionable.

SUMMARY

The various definitions and phyletic concepts of the colubrid subfamily Natricinae are discussed, and Cope's definition is adopted. He conceived of the natricines as colubrid snakes with hypapophyses on all dorsal vertebrae and with noncalyculate hemipenes that are minutely spinose but bear one or more enlarged basal hooks.

The monotypic genus *Liodytes* is compared with five species of the South American genus *Helicops*, alleged by many to be its closest living relative. The two genera are shown to be similar only in possession of a single internasal and various widespread colubrid traits. The marked differences in head shape and size, eye size, genial length, hemipenis form and length, caudal vertebra form, shape and proportions of many skull elements, shape and relative length of the maxilla, and arrangement of maxillary teeth suggest that the two genera are not closely related. The various characteristics of *Liodytes* confirm its assignment to the subfamily Natricinae.

The affinities of *Liodytes alleni* within the Natricinae are investigated and shown to lie with the crayfish-eating snakes of the genus *Regina* (excluding the species *kirtlandii*), with which *alleni* should be considered congeneric.

The validity of *Regina* is re-established and the genus redefined. An examination of the morphoclines discernable within the genus reveals that *alleni* almost invariably represents the specialized extreme, *grahamii* the primitive one. Of the two intermediate species *septemvittata* usually approaches the primitive extreme, *rigida* the specialized extreme. The possible interspecific phylogeny of the group is discussed.

The natricine species *kirtlandii*, which in recent years has shuttled between *Natrix* and *Regina*, is shown to be distinct from both of these and from all other natricine genera. To accommodate it the Copeian genus *Clonophis* is resurrected and redefined, and speculation is made concerning its possible affinities.

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