Dentitional Phenomena in Cobras and Other Elapids with Notes on Adaptive Modifications of Fangs
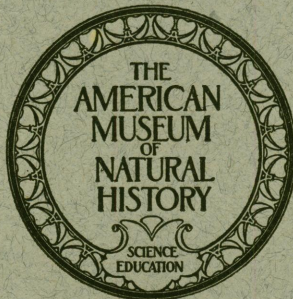
By Charles Mitchill Bogert

Article III.—DENTITIONAL PHENOMENA IN COBRAS AND OTHER ELAPIDS WITH NOTES ON ADAPTIVE MODIFICATIONS OF FANGS

By CHARLES MITCHILL BOGERT

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CONTENTS

INTRODUCTION

It has long been known that certain cobras were capable of ejecting or "spitting" their venom. The accounts of travelers and explorers in Africa contain numerous descriptions of the phenomenon, while the specific name *sputatrix* given by Boie to a Malayan cobra implies that some knowledge of this remarkable habit was known as long ago as 1827. The extensive literature dealing with spitting cobras has been partly summarized by Pitman (1938, pp. 21–22, 205–229), by Koch and Sachs (1927, p. 155), by Lankes (1940, p. 1) and by Klingelhöffer (1942, pp. 33–36), but no comparative study of the fangs or dentition of cobras has ever appeared. It can now be demonstrated that fang characters hitherto unnoticed serve to identify "spitters," although the presence of two "spitters" in Africa, and the existence of geographical gradients in fang and tooth characters in Asiatic cobras require explanatory interpretation.

This work was not undertaken with any intention of investigating taxonomic problems concerned with cobras, but the removal of maxillae to examine fangs brings to light several useful dentitional characters not previously used. Of necessity, therefore, the scope of the paper has been extended to include taxonomic conclusions, which are presented first in order to establish the nomenclatorial status of the species considered in the discussions which follow. These include considerations of the phylogenetic implications of dentitional similarities and differences, and descriptions of the venom apparatus of cobras, the method of fang replacement and the modifications of the fangs that are correlated with the habits of cobras. A detailed study of interspecific differences in fangs has not

been attempted. Although differences between species in relative fang length are indicated, satisfactory conclusions concerning these differences would involve additional problems of relative growth and ontogenetical trends. The material available is not sufficiently extensive for individual species and does not permit the necessary statistical treatment of such problems.

The classification of cobras devised by Boulenger (1896, p. 372) has been that most widely followed despite the fact that it was set up nearly half a century ago. Boulenger, however, made little use of osteological data and no use of penial characters in his classification. Subsequent emendations usually have been concerned with individual species, and nothing approaching monographic treatment has ever

been attempted. The literature dealing with the species includes many erroneous identifications, while the widespread commercial traffic in cobras has brought many specimens into collections with incorrect or incomplete data. An inadequate number of satisfactorily labeled specimens, however, is only one obstacle. The vast range of the genus *Naja* over two continents and the apparent plasticity of penial, osteological, pattern and scale characters will require that hundreds of specimens be assembled before any real understanding of infraspecific relationships can be attained. Monographic treatment is impossible at present, although the data presented herein should be of value in this connection when such treatment is feasible.

MATERIALS AND METHODS

This study is based principally on osteological data derived from 231 snakes of the family Elapidae. As particular attention is given to cobras of the genus *Naja*, the majority of the specimens examined belong to this group, 133 being referable to the genus. Some of these consist of complete skeletons or of skulls only and, with two exceptions, one or more skulls of each of seven species of the genus believed to be valid have been available. The total number of individuals is distributed by species as follows:

Naja naja	61
Naja haje	9
Naja melanoleuca	34
Naja nigricollis	24
Naja nivea	5

Other genera examined include the following, with the number of specimens indicated:

Hemachatus	11	Pseudelaps	1
Hamadryas	7	Bungarus	1
Pseudohaje	17	Hemibungarus	1
Boulengerina	4	Maticora	1
Aspidelaps	2	Micropechis	2
Elapsoidea	12	Pseudechis	2
Dendroaspis	9	Acanthophis	2
Elaps	3	Demansia	2
Micruroides	8	Denisonia	2
Leptomicrurus	2	Apistocalamus	1
Micrurus	3	Ultrocalamus	2
Glyphodon	2	Toxicocalamus	1

In addition a few representatives of the families Colubridae, Hydrophiidae, Viperidae and Crotalidae have been examined for comparative purposes, and in some cases data have been drawn from other reptilian groups. Because this study is primarily concerned with fangs and maxillary dentition, only the maxillary teeth in most specimens have been examined, although data concerning teeth in other bones which appeared to be of taxonomic or of phylogenetic significance have been tabulated.

In many instances maxillae were removed from preserved specimens for scrutiny, at least one specimen of each species being so prepared. Where extensive series were concerned, however, teeth have been counted on the bones more or less *in situ*. To insure accurate counts soft tissue was removed from tooth-bearing bones with a scalpel, after which the bone was dried by means of a jet of compressed air. Without such precautions it is possible to overlook vacant sockets, particularly in smaller specimens. It should be understood that all counts herein reported refer to the number of sockets, rather than to the actual number of teeth present, because teeth are constantly being replaced, and very few bones have all teeth present in their respective sockets. Skulls and tooth-

bearing bones, however, usually have been drawn as though all teeth were present. This has been done to simplify comparisons, as it is difficult to indicate the presence of vacant sockets in lateral views. In herpetological work no standardized methods of expressing dental formulas are in use. To avoid the necessity of longer descriptions, therefore, I have proposed the use of Roman numerals to indicate fangs, Arabic numerals for ordinary teeth, and a plus sign for gaps or diastemas. All specimen numbers, unless otherwise designated, refer to material in the collections of The American Museum of Natural History.

The term cobra, as introduced into the English language from the Portuguese, was used originally to denote the Asiatic species, *Naja naja*, or cobra de capello. The original usage, however, has been extended in the course of time, and the connotations of the term include any of several large elapids. Several proteroglyphs which erect the anterior portion of the body, flatten the neck and raise the ribs of the thoracic region to spread the so-called hood, are commonly called cobras. As used by some authors the word cobra has reference to all members of the family Elapidae, an unfortunate extension of the original meaning. Somewhat arbitrarily, in this paper I have used the term in a restricted sense to include only snakes of the genera *Naja, Hamadryas, Hemachatus, Boulengerina* and *Pseudohaje*. English equivalents for these names in popular usage are, respectively: "typical cobras"; "king cobra"; "ringhals or South African spitting cobra"; "water cobras" and "arboreal cobras." Many other elapids have no well-established common names.

ACKNOWLEDGMENTS

THE TAXONOMIC STATUS OF COBRAS

THE VALIDITY OF *Naja*

Although Boulenger (1896, p. 372) used the name *Naia* for the genus and his usage has been widely followed, Stejneger (1936b, p. 140) has most recently pointed out that *Naja* Laurenti (1768) is the correct designation for the genus. Furthermore, Stejneger points out that the Asiatic species, *Naja naja*, may be considered the "Genotype by tautonomy and practically also by monotypy, as all 6 nominal species included by Laurenti are synonyms of *Coluber naja* Linnaeus (1758:221)." Whether any type specimen is actually in existence or not is problematical. Linnaeus (1758) based his name on the plate and description of his 1754 work (Mus. Adolphi Friderici, p. 30, Pl. xxi, fig. 1) and listed as well all thirteen cobras depicted by Seba in 1734. Laurenti contented himself with a list of six species under his name *Naja*, basing his specific names on seven of the forms depicted by Seba. All but two of thirteen cobras depicted by Seba are the spectacled or binocellate cobra commonly known in ancient as well as in modern literature as the cobra de capello. The other two are of the yellowish, nearly unicolored form. All such pattern forms occur in India and some of them elsewhere as well. Whether more than one species was included in the designation of Linnaeus or in that of Laurenti cannot be stated with certainty as will be noted below. Stejneger's interpretation (monotypy) is, however, probably correct.

THE VALID SPECIES OF *Naja*

Since the only comprehensive original treatment of cobras is that of Boulenger (*supra cit.*) his work provides a starting point from which to embark on a summary of changes that are indicated. Boulenger recognized ten species within the genus *Naja* and placed an additional form (*haemachates*) in a separate genus. These may be considered in the order and orthography in which Boulenger listed them, with critical comments on their current status, as determined from search of the literature and from data presented in other sections of this paper.

1. "*Naia haje*" (p. 374). As currently understood this form includes four races:

A. *Naja haje haje* (Linnaeus). The typical forms with 19 midbody scale-rows known from the countries bordering the Sahara Desert, southward to the Belgian Congo on the west, and to southern Portuguese East Africa on the east, but absent from the western Rain Forests.

B. *Naja haje arabica* Scortecci. The race occurring in the southwestern portion of the Arabian Peninsula, with 19 midbody scale-rows, but with no increase in the number of scale-rows on the neck, and with more ventrals (210–226) than the typical form.

C. *Naja haje anchietae* Bocage. A race of *haje* characterized by 17 scale-rows at midbody. Apparently confined to the southern portion of Angola and the adjacent Kalihari Desert in Southwest Africa.

D. *Naja haje barotseensis* Angel. This race may or may not prove to be valid. It is based on a single juvenile specimen, possibly abnormal, with 15 midbody scale-rows taken in northern Rhodesia, "district de Lealiu." (For approximate distribution of *N. haje* see Map 1.)

2. "*Naia flava*" (Merrem) (p. 376). *Naja nivea* (Linnaeus) antedates Merrem's *flava*, as noted by Mertens (1937), and is the valid name for this species which inhabits a poorly defined range in Cape Province and southern Southwest Africa. (For approximate distribution see Map 2.)

3. "*Naia melanoleuca*" (p. 376). There are no recognized races of *Naja melanoleuca* Hallowell, a form authentically reported from only the Forest Province and restricted forest islands around the periphery of the continuous forest, covering most of central Africa. (For approximate distribution see Map 2.)

4. "*Naia nigricollis*" (p. 378). Primarily a savannah species, this form has a range extending from Senegambia through the Sudan to central Egypt along the Nile, and to Italian Somaliland on the north, and from Natal to Southwest Africa on the south, excluding the Cape region. Boulen-
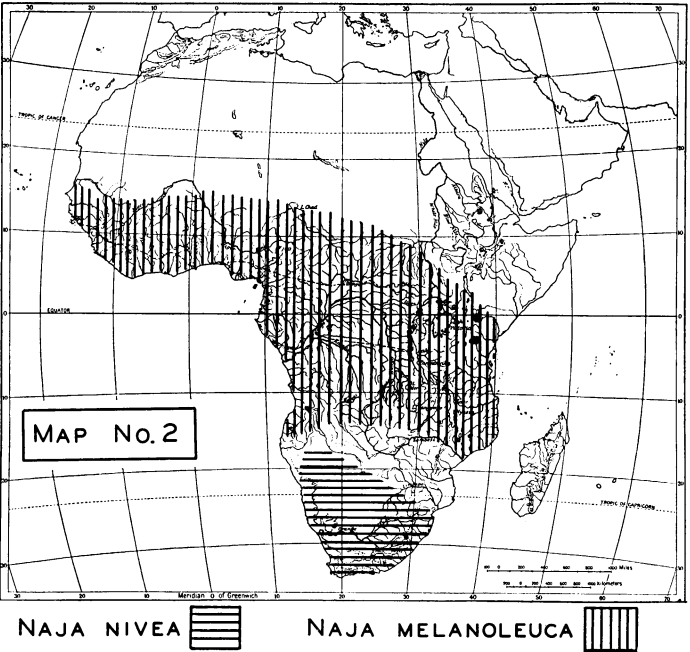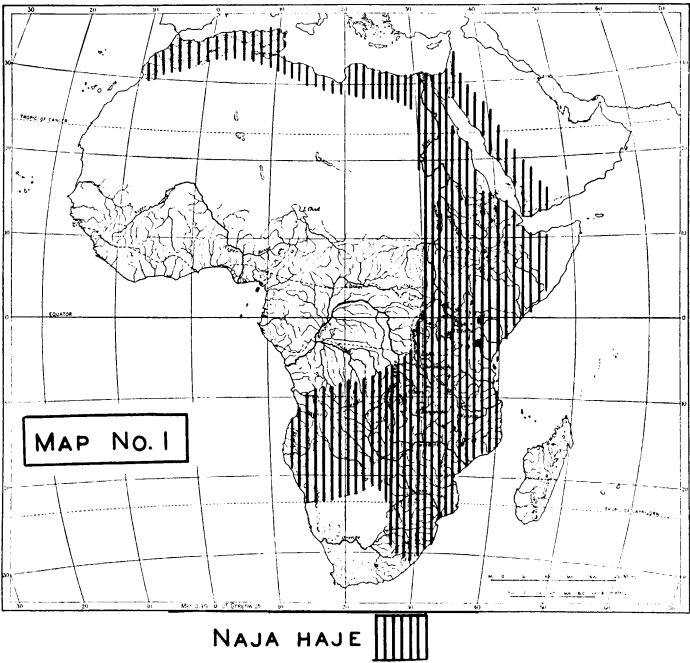
Maps 1 and 2. Approximate ranges of non-spitting cobras in Africa.

ger recognized several varieties, some of
which may be retained as subspecies,
whereas others seem to represent nothing
more than color variants. The races ten-
tatively believed to be valid, but all of
them having ill-defined ranges, include the
following:

A. *Naja nigricollis nigricollis* Rein-
hardt. As the type came from "Guinea,
West Africa" the range of the race bearing
the name would appear to include the
northern and eastern edges of the Forest
Province to the Belgian Congo, Uganda
and Tanganyika Territory and southward
to Southwest Africa, exclusive of central
Angola. Such an anomalous range indubit-
ably will require revision.

B. *Naja nigricollis katiensis* Angel.
A race from the French Sudan character-
ized by its describer as having fewer ven-
trals (165–174).

C. *Naja nigricollis pallida* Boulenger.
This race, characterized by nearly uniform
brown coloration (reddish in live speci-
mens), with a single black band on the
neck, and by higher ventral and scale-row
counts is confined to the northeast portion
of Africa from central Kenya Colony north-
ward to British Somaliland and Assouan
in Egypt and part of the Anglo-Egyptian
Sudan. (See Bogert, 1942b, p. 4.)

D. *Naja nigricollis mossambica* Peters.
The validity of this race is questionable,
but currently the name is applied to the
form inhabiting Portuguese East Africa
southward to Natal.

E. *Naja nigricollis nigricinctus* Bogert.
This race, from central and southern An-
gola, is characterized by pattern characters
which consist of 60 to 70 black bands on a
ground color of reddish brown. The speci-
mens described as [*N. nigricollis*] var.
asciata by Bocage (1895, p. 136) are refer-
able to this subspecies. This reference
was overlooked when *nigricinctus* was de-
scribed in 1940, but the name will stand
since Bocage's *fasciata* is antedated by two
names, *Naja fasciata* Laurenti, 1768, for a
cobra, and *Naja fasciata* Peters, 1861, a
synonym of *Hamadryas hannah* Cantor.
(For distribution of the species, with races
not shown, see Map 3.)

5. "*Naia tripudians*" (p. 380). As

noted in the discussion of the type species,
the proper name for cobras from south-
eastern Asia and adjacent islands is *Naja
naja* (Linnaeus). Several "varieties" as
well as races and even "species" have been
recognized, but until more adequate bases
can be established for these it seems best to
refrain from using subspecific names. In
many localities nearly 100 per cent of the
cobras conform very closely to one pattern,
whereas other regions, including some of
the islands in the Malay Archipelago, sup-
port two or more color varieties. So far
no one seems to have discovered any scale
characters that lend much support to con-
clusions derived from pattern differences.
Boulenger recognized several "varieties,"
but these are not subspecies in the sense
that this term is used in the modern con-
cept of infraspecific categories, because
the specimens he lists under each name
usually do not fall into recognized geo-
graphic or ecological areas. Bannerman
and Pocha (1905, p. 638) have attempted
to map the distribution of the "varieties"
in India, presenting data indicating that
only in southeastern India is the "*Forma
Typica*" represented in 100 per cent of
the population. Elsewhere the "*Forma
Typica*" is represented in varying percent-
ages, in some parts of India constituting
only 26 per cent of the population. There
is no evidence of any single gradient direc-
tion in the distribution. Rather the areas
as mapped by Bannerman and Pocha show
a mosaic in the frequency distribution of
the "*Forma Typica*." Others have com-
mented on the questionably useful diag-
noses for Boulenger's "varieties," notably
Stejneger (1907, p. 394), Thompson (1913,
p. 509), Wall (1913, p. 243) and more re-
cently Dunn (1927, p. 4). Pope (1935, p.
354) points out that "the problem of the
separation and definition of the forms of
Naja naja is a most complex one still await-
ing final solution," although he found the
form in China to be very constant in scale
counts.

It is altogether probable that recogniz-
able subspecies of *N. naja* can eventually
be established, but in diagnoses of new
races comparisons of specimens from only
two contiguous areas or islands will not

materially clarify the situation. Examination of several Philippine specimens of *Naja* with diverse coloration and patterns fails to disclose any difference that might be regarded as being of specific value. *Naja samarensis*, listed as a distinct species by Boulenger, appears to be no more distinct than the "varieties" of *Naja naja* he lists, and doubtless should be placed as a synonym, perhaps eventually warranting subspecific recognition. (For the distribution of *Naja naja*, as understood in this paper, see Map 4.)

On the other hand characters in the dentition point to the validity of two Asiatic forms placed by Boulenger in the synonymy of *Naja naja*. An examination of more than fifty cobras from the Asiatic mainland east of Afghanistan and Baluchistan and from the islands of the East Indies has shown that, with the exception of northern India, all *Naja* (as defined herein) inhabiting this region have a single tooth behind the paired fangs (or sockets) on the posterior end of the maxilla. The only exceptions among the material examined were six specimens: A.M.N.H. Nos. 39296–7, from near Chakwal in the Siwalik Hills, Punjab Province, India; A.M.N.H. No. 2851 from the Sutlej Valley in the same general region; M.C.Z. No. 5268, from seventy miles southwest of Ambala, India; M.C.Z. No. 3229, from Kula Valley, India; and a specimen from Basim in the private collection of Mr. George Hawkes. Four of these specimens are nearly uniform yellowish brown or darker posteriorly, while two, the specimens from Sutlej Valley and Basim, bear distinct spectacles on their hoods. The few Indian specimens examined do not disclose any overlap in territory inhabited by the form with one tooth behind the fangs and the form, represented by specimens from Basim (in central India) north ward to the Himalayas, having no teeth behind the fangs. Thus the latter may represent a distinct species, although accurately labeled specimens in sufficient quantity from eastern or southern India may disclose an intermediate region occupied by individuals both with and without the tooth behind the fangs. No scale or pattern character serves to diag-

1

2

3

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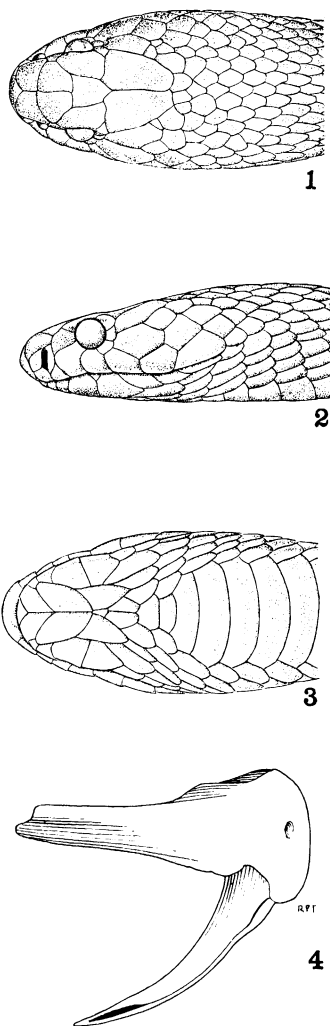
NAJA NAJA
(PUNJAB PROV., IND.)

Figs. 1–4. Dorsal, lateral and ventral views of the head (× 1), and lateral view of the maxilla (× 5) of the cobra inhabiting northern India (based on M.C.Z. No. 5268, 70 miles southwest of Ambala, India). This form, without solid teeth on the maxilla, is referred to *Naja naja* in this paper, but may represent an undescribed species or subspecies.

nose the Punjab population, despite the consistent dentitional difference in the six specimens available. The head appears

to be relatively narrower than that of other *Naja naja*, but tentatively it seems best to regard it as a probable subspecies of *Naja naja*, at least until it can be determined whether or not any published names are applicable to it. The head and maxilla are depicted in Figs. 1–4, to facilitate comparisons by workers who may have more adequate material from the critical region.

West of the southern extension of the Himalaya Mountains which includes the Sulaiman Range and the Bugti Hills (for a map of this region see Colbert, 1935), a third type of maxillary dentition occurs. Despite the fact that Boulenger included *Tomyris oxiana* in the synonymy of *tripudians*, Eichwald (1841, p. 104, and Figs. 1 and 2 opposite p. 104), in his description and diagnosis of *Tomyris*, specifically mentions that the single species inhabiting the territory from the Oxus River to the eastern shore of the Caspian Sea has two fangs followed by two teeth ("tela 2 utrinque distincta dentesque 2 imperforati breviores"). Thus, on the basis of the maxillary dentition, *Naja oxiana* profitably can be separated from *Naja naja* which almost uniformly possesses fewer solid teeth on the maxilla.

Naja morgani described (actually the "description" is little more than a diagnosis) from Persian specimens by Mocquard (1905, p. 76) some years ago is poorly known. Flower (1933, p. 829) suggests the possibility that this species may prove to be a synonym of *Walterinnesia aegyptica*, first described from Egypt (Cairo) and recently authenticated by Mertens (1929, p. 41) and by Flower (*supra cit.*) as belonging to the Egyptian fauna. Flower apparently had overlooked Thompson's paper (*supra cit.*) wherein a similar view was upheld. If Boulenger's description of the maxillary dentition of *Walterinnesia* is correct, however, Thompson presents sufficient additional information concerning Mocquard's types to disprove exactly the conclusions which he seeks to draw. He describes one of the cotypes of *Naja morgani* as having two fangs followed by two teeth on the maxilla, thus diagnosing it as a cobra belonging to the African assemblage (see discussion of dentitional char-
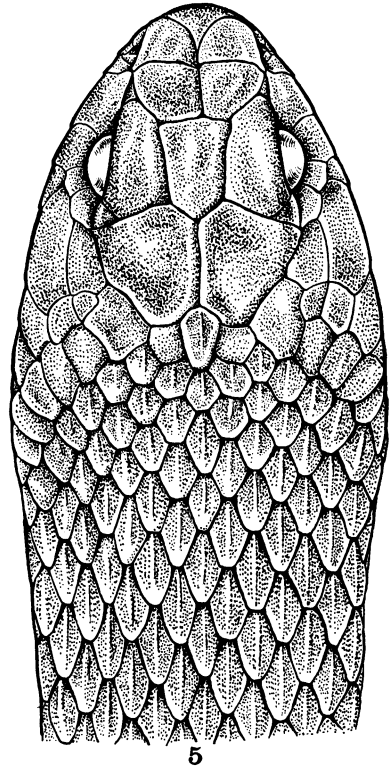
HEMACHATUS HAEMACHATUS

Fig. 5. Dorsal view of the head (× 5) of the ringhals, to show strongly keeled scales of dorsum.

acters below), and in contrast to *Walterinnesia* which possesses no teeth behind the fangs. Thompson fails to mention the fact that *Walterinnesia* is further distinct from *Naja* in having strongly keeled scales on the posterior of the body and on the tail, whereas all true *Naja* are smooth-scaled. *N. morgani*, while possessing smooth scales, has the anal scute divided, unlike any other *Naja*. Corkhill (1932a, p. 567) mentions it as being common in Irak, and thus *morgani* occupies an indefinite range, approximately indicated on Map 4.

6. "*Naia samarensis*" (p. 385). This form, without better ground for retaining it as a subspecies of *Naja naja*, had best be referred to the synonymy of the latter, as noted in the discussion above.

7. *"Naia bungarus"* (p. 386). The king cobra, often placed by various authors in genera other than *Naja*, differs from snakes of the latter genus in having fewer pterygoid teeth, three teeth behind the fangs on the maxilla, a relatively narrower brain case and a proportionately longer, more deeply bifurcate hemipenis (see Cope, 1895, Pl. xxxii, Fig. 2) than that for any elapid for which this organ has been de-

real cobra belongs in the genus *Pseudohaje* (type species *nigra*) erected by Günther in 1858 as I (1942a) have pointed out elsewhere. The correct name is *Pseudohaje goldii* (Boulenger).

10. *"Naia guentheri"* (p. 388). The original name (*nigra*) was suppressed by Boulenger (*loc. cit.*) as a homonym when the form was erroneously placed in *Naia*, and I (1942a) drew the equally erroneous

MAP No. 3

HEMACHATUS HAEMACHATUS ≡   NAJA NIGRICOLLIS ‖‖‖
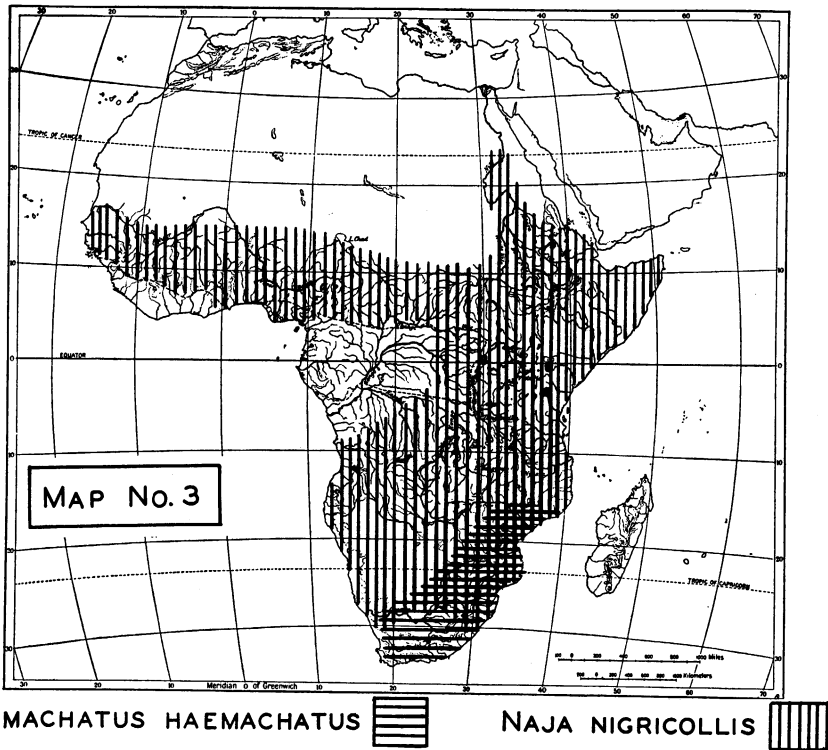
Map 3.   Approximate ranges of spitting cobras, *Naja* and *Hemachatus*, in Africa.

scribed. It is properly placed as *Hamadryas hannah*, as Pope (1935, p. 347) suggests. The known range of the species closely parallels that of *Naja naja*, but records indicate it to be slightly more limited.

8. *"Naia anchietae"* (p. 387). Placed by Mertens (1937, p. 15) as a race of *N. haje*, as noted above under the latter name.

9. *"Naia goldii"* (p. 387). This arbo-

conclusion that the form should be known as *"Pseudohaje guentheri* (Boulenger)." However, Boulenger's suppression of *nigra* does not preclude use of the name in *Pseudohaje*, and the snake can be known as *Pseudohaje nigra* Günther.

The species designated as *Sepedon haemachates* by Boulenger (p. 389) is properly retained as *Hemachatus haemachatus* (Lacépède) according to Stejneger (1936a, p.

114). This monotypic genus differs from all African *Naja* in having no solid teeth on the maxilla, fewer palatine teeth, keeled dorsal scales (see Fig. 5) and a longer, more deeply bifurcate hemipenis. It differs from all *Naja*, so far as known, in being ovoviviparous but resembles *N. nigricollis* and Malayan *N. naja* in spitting proclivities and fang adaptations. Cott's (1934, p. 970) records from Portuguese East Africa indicate that *Hemachatus* occurs within the ranges of *nigricollis, haje, melanoleuca* and doubtless *nivea*, all but the last mentioned having been taken at one locality (Charre). (For approximate range of *Hemachatus* see Map 3.)

Naja multifasciata Werner (1902) and *Naja anomala* Sternfeld (1922) are related to *Pseudohaje* and were not correctly assigned generically. They belong to a new genus, a description of which will be published shortly by my colleague, Mr. Arthur Loveridge.

This paper is primarily concerned with recent cobras, since fossil elapids are still known from so few adequate specimens that they provide little assistance in connection with studies of recent forms. However, one fossil elapid lately described is of much interest in that it is sufficiently complete to be studied in some detail, and furthermore it seems to me to be referable to the genus *Naja*. Hoffstetter (1939, p. 57, Pls. I, II) provides, together with an extremely useful summary of osteological characters in serpents with particular reference to the Elapidae, a description and excellent plates of a Middle Miocene (Vindobonian) elapid from the Grive-St. Alban fauna which he refers to a new genus and species, *Paleonaja romani*. Hoffstetter had available all or parts of thirteen cranial elements including a nearly complete maxilla and a dentary, as well as numerous vertebrae and fragments of costae. He describes in detail each of these and compares them with similar bones from *Naja haje, Naja naja* and "*Naja hannah.*" Comparisons with the latter are particularly unfortunate since by reference to Figs. 13–23 of this paper it may be observed that *hannah* differs from true *Naja* in numerous cranial characters, and on the

basis of these and other differences I have referred the species to *Hamadryas* with no question concerning the advisability of this change. The most serious error on the part of Hoffstetter, however, is his failure to examine a sufficient number of species in the genus *Naja* to determine the extent of variation within the genus. The differences between species of *Naja* and *Paleonaja* which he describes (but which are not apparent in his plates) are not greater as a whole than those existing between *Naja nigricollis* and *Naja melanoleuca* or other species, and apparently he had no cognizance of the differences between true *Naja* and the snake properly assigned to *Hamadryas* beyond those implied in his statement that "*N. hannah* appears to be the most archaic of recent species."

I am unable to observe the several differences between the fossils (as depicted in his excellent plates) and recent *Naja* which he points out in the text. More often than otherwise he compares his fossils with *Hamadryas hannah,* whereas such comparisons as I can make indicate that with little doubt they more closely approach *Naja haje.* Comparisons of *haje* with other species of living *Naja* (except *oxiana* and *morgani* which are not available) show that it is comparatively more massive than other species of the genus, although in any series of cobra skulls there is a fair amount of intraspecific variation. As nearly as can be determined *Paleonaja romani* is no more closely related to Asiatic *Naja naja* than recent African species in the genus, whereas it seems to be especially close to *haje.* Moreover, the species *romani,* granting that differences described by Hoffstetter are of specific value, can be assigned to the section of the genus that includes African *Naja.* This is clearly indicated by the presence of two teeth on the posterior extremity of the maxilla, characteristic of *nivea, haje, melanoleuca* and *nigricollis* and unlike Asiatic *N. naja* which has but one solid maxillary tooth, or no teeth behind the fangs. (Maxillary dentitional differences are discussed in more detail in an ensuing section of this paper.) Because of the size of the vertebrae, Hoffstetter attributes a length of 1800 mm. to the type

specimen, other remains presumed to be conspecific being smaller. *Naja haje* attains approximately similar dimensions, being reported (Pitman, 1938, p. 210) as large as 2300 mm.

The conclusion cannot be avoided that *Paleonaja* should be assigned to the synonymy of *Naja* Laurenti, because it possesses no character that might be considered of equal rank with those used in separating recent elapid genera. It is not especially amazing that Miocene fossil serpents can be assigned to modern genera, particularly when many mammals from the Grive-St. Alban deposits are placed without question in such well-known genera as *Vespertilio* among the bats, *Lutra* and *Martes* among mustelids, not to mention several other genera containing living representatives (*vide* Colbert, 1942, p. 1463 for a list of those known).

I am unable to comment on the other species, *depereti* and *crassus*, which Hoffstetter places in *Paleonaja*, owing to the fragmentary nature of the material, but if they are similar to *romani*, as implied, they too should be referred to *Naja*.

Snakes of the genus *Boulengerina* were at one time confused with true cobras, and in many aspects of their anatomy they are indeed closer to *Naja* than is *Hamadryas hannah*, which has been accepted in *Naja* by many authors. *Boulengerina* differs from *Naja* in possessing three teeth on the maxilla (in this one respect resembling *Hamadryas*), but comparative study of dentitional differences leads to some question concerning the validity of *Limnonaja*, the genotype of which is *christyi*, originally described by Boulenger as a species of *Boulengerina*. Schmidt (1923, p. 124) describes a specimen of this aquatic elapid, which is rare in collections, and considers it sufficiently distinct from *Boulengerina a. annulata* to warrant erection of the genus *Limnonaja* which he diagnoses as follows: "It is distinguished by the widened head, distinct from the neck, the compressed instead of cylindrical body and tail, and the transversely widened dorsal scales. In addition, its coloration is wholly distinct from that of *Boulengerina*." The specimen described by Schmidt, as well as his
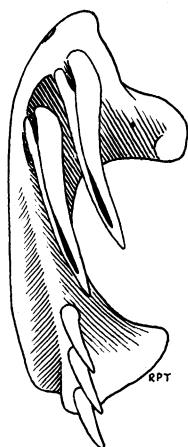
BOULENGERINA CHRISTYI
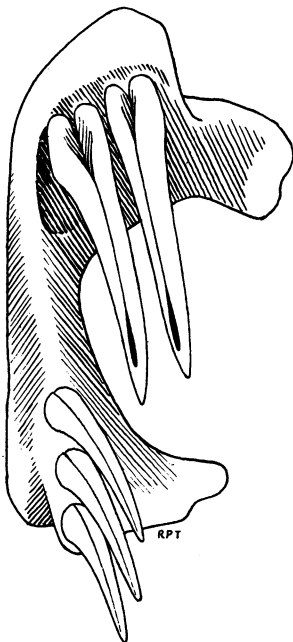
BOULENGERINA ANNULATA

Figs. 6, 7. Ventral views of the maxilla of the two species of African "water cobras," *Boulengerina*, to show similarities in shape and maxillary dentition. (*B. christyi* drawn from A.M.N.H. No. 11902, taken at Boma, Belgian Congo, maxilla, × 16, distal portion of fang, × 32. Maxilla of *B. a. annulata* depicted was removed from A.M.N.H. No. 12331, obtained at Avakubi, Belgian Congo, maxilla, × 8, distal portion of fang, × 16.)

comparative material, is in the collection of the American Museum, but comparison of the forms fails to disclose any noteworthy differences between the two in cephalic proportions, and the other differences in habitus can well be ascribed to the methods of preservation and juvenile size of the specimen of *christyi*. I am unable to discover any basis for calling the tail of *christyi* "compressed," and only a few of the dorsal scales are perceptibly widened. Differences in coloration do exist, as shown by the material available, but as five specimens of *annulata* at hand are large adult males and the specimen of *christyi* is a juvenile male, I cannot evaluate this difference, pattern characters often being subject to considerable modification during the ontogeny of elapids. In any case, I would not consider the pattern, nor the other very minor differences of habitus, to be of generic value. The maxillary dentitions of *christyi* and *annulata* are nearly identical (see Figs. 6 and 7), although reference to Table I will show that slight differences exist in the numbers of teeth on the pterygoid and dentary. Although *christyi* has 19 midbody scale-rows, *annulata* has 21 or 23, and its single subspecies has 23 or 25, and this character provides no basis for generic separation.

These differences, on the whole or singly, are not greater than, and often not so great as, the differences between species in *Naja*, for example, and while there is no rule-of-thumb for generic criteria, it is considered good practice in modern taxonomy to erect or to reinstate genera only when differences are in inverse proportion to the number of species in the group. The erection of *Limnonaja* as a monotypic genus leaves *Boulengerina* with a single species (two subspecies), although I do not believe that there is any question but that *christyi* is more closely related to *annulata* than either is to species in other elapid groups. Accordingly I propose placing *Limnonaja* Schmidt in the synonymy of *Boulengerina* Dollo.

SUMMARY OF TAXONOMIC CONCLUSIONS

With the information obtained from the literature and from preserved material,

not adequate in many cases, several conclusions presented must be considered tentative. As I interpret the information at hand, however, the genus *Naja* is comprised of but seven valid recent species. The type species, *Naja naja*, is the only one inhabiting southeastern Asia and the East Indian islands, although it is evident that it is polymorphic in pattern and penial characters, and more extended studies will undoubtedly require recognition of subspecies. Omitting any reference to subspecies, the status of which are beyond the scope of this paper except for incidental discussions, the decisions reached may be summarized as follows:

1. The valid species of *Naja* in Africa, each of which is sympatric with two or more other species, may be listed as follows:

> *Naja haje* (Linnaeus)
> *Naja melanoleuca* Hallowell
> *Naja nigricollis* Reinhardt
> *Naja nivea* (Linnaeus)

2. Apparently Asia is inhabited by four species of *Naja* also, if *Naja haje*, which ranges from Africa into Asia Minor, be included. Since they all appear to be allopatric, they may be listed from east to west in the order in which their known ranges occur:

> *Naja naja* (Linnaeus)
> *Naja oxiana* (Eichwald)
> *Naja morgani* Mocquard
> *Naja haje* (Linnaeus)

3. *Paleonaja romani* Hoffstetter of the European Middle Miocene (Vindobonian) is referable to *Naja* Laurenti, and the species should be known as *Naja romani* (Hoffstetter).

4. *Pseudohaje* Günther is a valid genus comprising two valid species, *nigra* and *goldii* as previously concluded in part (Bogert, 1942a), but amended herein to reinstate *P. nigra*.

5. *Hamadryas* Cantor is a valid genus containing a single known species, *hannah*, which Boulenger erroneously referred to *Naja*. Despite the fact that the genus is monotypic it differs sufficiently from other genera to warrant its retention.

6. *Hemachatus* Fleming may likewise be retained as a monotypic genus, with

pronounced anatomical differences that serve to distinguish it from *Naja*. I follow Stejneger (*supra cit.*) in using the name *Hemachatus haemachatus* (Lacépède) for the single species.

7. *Limnonaja* Schmidt is referred to the synonymy of *Boulengerina* Dollo (type species, *annulata*), and the type species of *Limnonaja* should be known as *Boulen-gerina christyi* Boulenger, in accordance with the views of the original describer of the species. This name provides suitable implications of relationships and avoids unnecessary splitting.

8. The genus *Walterinnesia* (specimens not examined) differs from *Naja morgani* in at least two characters, and appears to represent a valid, if monotypic, genus.

TAXONOMIC AND PHYLOGENETIC IMPLICATIONS OF DENTITIONAL CHARACTERS

In the discussion above reference has been made to the small solid teeth behind the fangs on the maxilla, and some use was made of them as taxonomic characters. Boulenger (*op. cit.*, p. 373) diagnosed the genus "*Naia*," as he understood it in 1896, as having the "maxillary extending beyond the palatine, with a pair of large grooved poison-fangs, and one to three small, faintly grooved teeth near its posterior extremity." The conclusion drawn from data herein presented requires revision of this diagnosis: *Naja* has either no solid maxillary teeth, one, or two (three occurring only as an abnormality), and there is a correlation of maxillary dentitional characters with distributional patterns.

The solid teeth on the maxillae of other elapids are not always separated from the fangs by a diastema as they are in many cobras. Several elapid genera, including *Apistocalamus*, *Toxicocalamus* and *Ultrocalamus* of New Guinea, possess six or seven teeth on the maxillary bone, the two in front being tubular fangs, followed closely by solid teeth which gradually diminish in size toward the posterior end of the bone. (The skull of *Ultrocalamus* is depicted by de Rooij, 1917, p. 258, Fig. 100, and specimens in the American Museum have been examined.) The maxillary dentition in this genus may represent a more or less primitive condition for the family Elapidae, although *Ultrocalamus* and closely related genera would appear to be specialized in some other respects. Be that as it may, the solid teeth on the maxilla of most elapids, including cobras and what appear to be their closest allies, are relatively small and separated by a wide diastema from the fangs at the front of the bone. It is extremely doubtful whether these solid teeth, when present at all in cobras, are of any functional importance. Commonly they are strongly recurved, sometimes almost hook-shaped, and they are deeply buried in the dense tissue investing the alveolar ridge. In larger cobras, and in most other elapids, these solid teeth are faintly, or often distinctly grooved, but since similar grooves are often apparent on the palatine and dentary teeth and, more rarely, on the pterygoid teeth as well, it is difficult to interpret the significance of such modifications. However, the nature of the recurved teeth (similar to questionably useful teeth behind the fangs of certain opisthoglyphs, Bogert, 1940, pp. 60–66) and the very fact that they have been lost in certain cobras suggest that, when present, they are vestigial.

It would seem to be a reasonable postulation that primitive elapids, like *Ultrocalamus* among living forms, possessed several solid teeth on the maxilla, and not greatly enlarged fangs. The few fossils sufficiently complete to be definitely assigned to the family Elapidae, however, indicate that considerable reduction in the maxillary dentition of certain branches of the family had already occurred at least as early as the Middle Miocene period (Hoffstetter, 1939), and to judge from living elapids loss of teeth has frequently recurred in widely removed branches of the family. Paired fangs (or fang sockets) are present throughout the family Elapidae, but the number of solid maxillary teeth or, indeed, their presence or absence, varies from genus to genus, intragenerically, or even intraspecifically if
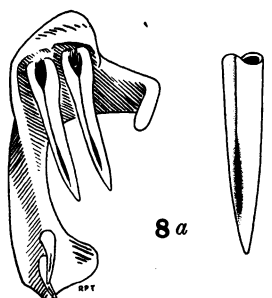
PSEUDOHAJE NIGRA
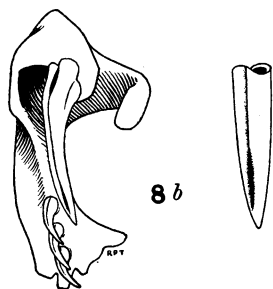
PSEUDOHAJE GOLDII
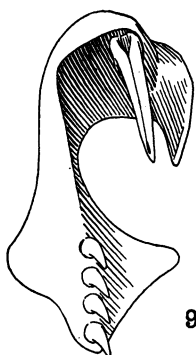
ELAPSOIDEA SUNDEVALLII

Figs. 8 (a and b). Ventral views of the maxilla of the two species of African "arboreal cobras," *Pseudohaje:* (a) A.M.N.H. No. 31556, "West Africa," (b) A.M.N.H. No. 61758 from Lukolela, Belgian Congo, illustrating the differences between species. The first reserve fang is not shown in Fig. 8b (enlargements of maxillae, × 5, distal portions of fangs, × 10).

Fig. 9. Ventral view of maxilla (× 5) of *Elapsoidea* (A.M.N.H. No. 51837, from Angola), to show presence of four solid teeth on posterior extremity of the bone. East African specimens examined all possess but three solid maxillary teeth. (First reserve fang not shown in figure.)

the inferences drawn from a study of cobras are correct. Thus *Hemachatus, Aspidelaps* and *Walterinnesia*, to cite examples, lack solid maxillary teeth; snakes of species referred to *Naja* normally have none, one or two such teeth; *Pseudohaje* may possess from two to four, whereas *Boulengerina* and *Hamadryas* both normally possess three, and *Elapsoidea* normally has three or rarely four. (See maxillae depicted in Figs. 6–12.)

In taxonomic work, modifications of dentitional characters in elapids must be interpreted with considerable caution. There is no reason to believe, for example, that similar dental formulas in different species or genera necessarily indicate either adaptive convergence or close phylogenetic relationship. Rather, these similarities between elapid genera, when considered in conjunction with other characters, sometimes suggest that parallel modifications have fortuitously evolved. Granting the vestigial nature of the solid teeth on the maxilla, mutant genes may be involved in the inheritance of one dentitional condition or another, and have gained local ascendency through the vicissitudes of chance operating in smaller, hypothetical populations comprising the ancestral stocks of various branches of elapid groups—supragenera, genera or species. Differences in maxillary dentition are to a large extent correlated with other osteological characters as may be seen by reference to Tables I and II and to Figs. 13–23; thus the statement above should not be construed to mean that mutant genes might have affected only the solid maxillary teeth. Indeed, selection, not implied in the statement above, may have been operating through other characters. It acted upon the individuals comprising the hypothetical populations as whole organisms, however, rather than upon individual characters, and it was perhaps fortuitous, whether teeth were involved or not.

Whatever factors were concerned in evolutionary trends, dentitional differences in elapids are of greater taxonomic value than most other osteological characters in the sense that they are more readily used. Teeth or sockets may be counted
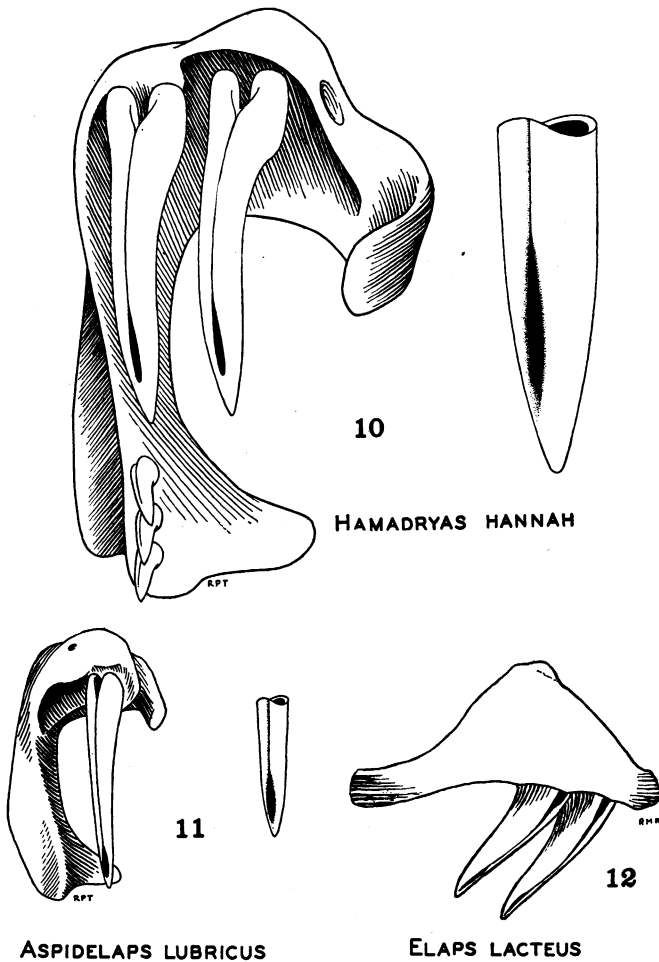
Figs. 10–12. Ventral views of the maxilla (× 5) of *Aspidelaps lubricus cowlesi* (A.M.N.H. No. 32801, from Munhino, Angola) and *Hamadryas hannah* (A.M.N.H. No. 67814, from "Asia") and lateral view of maxilla (× 10) of *Elaps lacteus* (A.M.N.H. No. 18226, from Grahamstown, South Africa), illustrating maxillary dentition of three elapids. The anterior process of the maxilla of *Elaps* articulates with a latero-posterior process of the premaxilla, a distinctive feature characterizing the genus.

and reported in terms of numerical quantities, and all evidence available indicates that the number of teeth in any tooth-bearing bone of a snake remains constant throughout the postembryonic life of the individual (barring accidents of disease or injury, of course). Furthermore, teeth or sockets may be counted with accuracy in preserved specimens merely by prying away the investing tissue of the alveolar surfaces. Many other osteological differ-

ences, on the other hand, are qualitative, or may be expressed in usable quantitative terms only as ratios, and relative proportions of bones are often subject to ontogenetical changes, as Klauber (1939) has shown for certain characters in rattlesnakes.

Before dentitional characters can be used with reliability in taxonomic work, however, the extent of variation must be determined. Moreover, it must be determined

TABLE I.—MAXILLARY DENTITION OF COBRAS AND RELATED ELAPIDS

Species	Maxillae Examined	Number Having Dental Formula:				
		II + 0	II + 1	II + 2	II + 3	II + 4
Naja naja (China, Siam, Burma)	58	—	57	1	—	—
Naja naja (Malay region)	46	—	46	—	—	—
Naja naja (southern India)	4	—	4	—	—	—
Naja naja (northern India)	16	16	—	—	—	—
Naja oxiana	1*	—	—	1	—	—
Naja morgani	1*	—	—	1	—	—
Naja haje	18	—	—	16	2	—
Naja nigricollis	48	—	—	43	5	—
Naja melanoleuca	68	—	—	63	5	—
Naja nivea	10	—	—	10	—	—
Hamadryas hannah	14	—	—	—	14	—
Hemachatus haemachatus	22	22	—	—	—	—
Pseudohaje nigra	9	—	—	8	1	—
Pseudohaje goldii	23	—	—	1	17	5
Boulengerina annulata	8	—	—	—	8	—
Boulengerina christyi	2	—	—	—	3	—
Elapsoidea sundevallii	24	—	—	—	22	2
Aspidelaps lubricus	4	4	—	—	—	—
Walterinnesia aegyptia	1*	1	—	—	—	—

* Data from literature (see text); specimens not examined by author.

for each taxonomic group; only when the nature of the variation is known can it be stated whether any given character is of subspecific, specific or of generic value, or for that matter whether it is of any taxonomic value whatever. In the work reported herein, the size of individual samples has been dependent upon the availability of material and, while samples have been relatively small, consisting of two to 108 maxillae, even in the larger series comparatively little variation has been discovered. For example, of fifty-four cobras (with 108

maxillae) available from eastern Asia and the adjacent islands, all but one possess the identical number of sockets in the maxillae, and these cobras seem to be referable to one species, *Naja naja*, possibly with races or subspecies that might be based upon external characters. Another population, tentatively referred to the same species as a possible race inhabiting northern India, is represented by a sample composed of but six specimens, all uniformly lacking solid teeth on the maxilla. (Two additional skulls lacking locality data can be referred

TABLE II.—MEAN NUMBER OF TEETH IN DENTAL ELEMENTS EXCEPT MAXILLAE
OF COBRAS AND RELATED ELAPIDS
(EXTREMES IN PARENTHESES)

Species	Number Examined	Palatine	Pterygoid	Dentary
Naja naja	46	(6) 7.2 (10)	(13) 15.7 (19)	(13) 14.0 (16)
Naja haje	8	(6) 6.5 (8)	(14) 15.9 (20)	(13) 14.0 (15)
Naja melanoleuca	12	(7) 7.1 (8)	(14) 16.1 (21)	(14) 15.8 (19)
Naja nigricollis	12	(5) 7.5 (8)	(16) 17.4 (18)	(13) 13.7 (14)
Naja nivea	6	(7) 7.3 (8)	(17) 19.2 (22)	(14) 14.5 (15)
Boulengerina annulata	6	(7) 7.3 (8)	(14) 16.2 (18)	(14) 15.7 (17)
Boulengerina christyi	2	(7) 7.0 (7)	(13) 13.0 (13)	(13) 12.0 (11)
Hemachatus haemachatus	6	(5) 5.2 (6)	(15) 16.8 (18)	(12) 13.7 (16)
Hamadryas hannah	10	(8) 8.3 (10)	(10) 10.5 (12)	(14) 14.5 (15)
Pseudohaje nigra	6	(10) 10.8 (12)	(23) 26.2 (29)	(21) 21.5 (22)
Pseudohaje goldii	10	(14) 15.3 (17)	(37) 39.0 (41)	(24) 25.2 (27)
Elapsoidea sundevallii	16	(7)* 9.5 (11)	(7) 9.4 (14)	(13) 14.9 (16)
Aspidelaps lubricus	4	(6) 6.0 (6)	(12) 12.5 (13)	(11) 13.3 (14)

* One specimen had the anterior portion of the palatine missing on one side, apparently as an abnormal congenital condition. Only two teeth present are not included in figures for mean.

to this form. Both lack solid teeth on the maxilla and have identical fang characters.) Of thirty-four *Naja melanoleuca* examined, only four had abnormal maxillary dentition, an extra tooth on one side only, in three cases, while a fourth had three solid teeth in each maxilla. Of seventy-two African snakes referable to *Naja* all but eight had two solid maxillary teeth on each side. The variation in twenty-three maxillae of *Pseudohaje goldii* is not great, sixteen having three solid teeth, five containing four teeth and but one containing two teeth, whereas in *P. nigra*, two solid teeth on the maxilla represent the usual condition. These distributions do not exhibit enough variation to warrant tests for normality.

Whenever it has been possible, at least two specimens of each taxonomic group dealt with have been examined, but a few species whose dentitional characters are pertinent to the discussion have not been available, and I have had to rely upon descriptions in the literature. More attention has been devoted to the cobras of the genus *Naja* than to related groups, but brief discussions of other genera have been included in evaluations of generic characters, if for no other reason than because some of them have been confused with *Naja* in the past. The results of a survey of the maxillary dentition in elapids mentioned are summarized in Table I.

Among snakes in general, dentitional characters of the maxilla seem to be more commonly of taxonomic or of phylogenetic significance than those of other tooth-bearing bones. Dental modifications are more frequently found in the maxilla, and in most cases where specialized teeth occur they are maxillary teeth. Other teeth are sometimes involved in specializations or in phylogenetic trends, however, and consequently it is pertinent to give some consideration to the teeth in other bones in any study of dentitional characters. Therefore, data concerning the number of teeth in the palatine, pterygoid and dentary are summarized in Table II. The samples upon which this table is based are too small to be of much value in establishing interspecific differences in most cases, but some

of these data are of value in establishing generic differences, particularly when used conjointly with other characters. It will be noted in this connection that the mean number of palatine teeth in *Hemachatus* is less than that in related forms, and that *Hamadryas*, aside from the great differences in penial characters and internal anatomy, can be distinguished from all *Naja* examined in having fewer pterygoid teeth, despite the fact that the number of teeth in this bone is somewhat variable in other cobras.

On the whole, it may be noted that differences between species in different genera are greater than those between species of the same genus. Possibly as a corollary, the snakes which differ most in qualitative skull differences likewise tend to differ more in tooth counts. There are exceptions, nevertheless, although *Boulengerina*, with skull characters not differing greatly from those of *Naja*, closely approximates this genus in number of teeth. *Hemachatus*, which possesses rather striking premaxillary differences, along with characters of the occipital region, which distinguish it from *Naja*, tends to have fewer palatine teeth than any *Naja*. *Hamadryas*, with numerous, very obvious skull differences (see Pl. xlviii and Figs. 13–27), seems to be readily separated from *Naja* in having fewer pterygoid teeth, aside from differences in maxillary dentition. In the case of *Pseudohaje*, however, the differences between the two species of the genus in dentitional characters are out of proportion to any differences in qualitative skull characters, the crania of the two being almost identical except for teeth. But in skull characters they are easily distinguished from all *Naja*.

Variation in maxillary dentition of elapids is so limited that for practical purposes differences between species, when they exist, can be treated as though they were dichotomous. However, the numbers of teeth in other bones vary to such an extent that data concerning them usually must be treated statistically in order to be readily interpreted. Tooth counts in the pterygoid series are, in general, more vari-

NAJA MELANOLEUCA

PSEUDOHAJE NIGRA

HAMADRYAS HANNAH

HEMACHATUS HAEMACHATUS
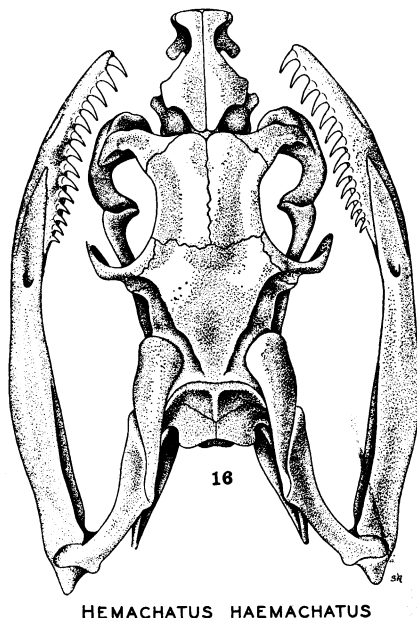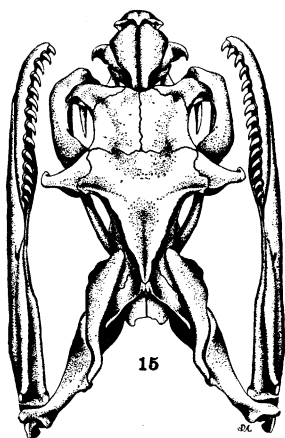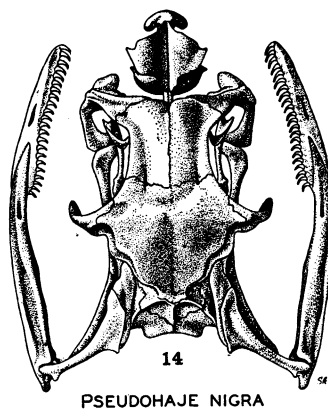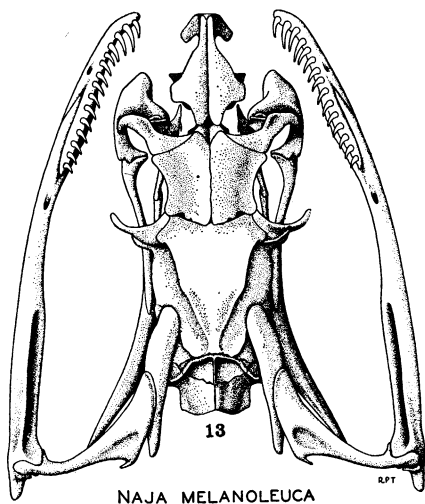
Figs. 13-16.   Dorsal views of skulls representing four related elapid genera, to show qualitative differences in cranial characters.   (Not all drawn to same scale.)

able than those in the palatine and dentary, a condition characteristic of colubrids as well as elapids.   For example, in twenty-three specimens of *Naja naja* (having forty-six bones in each tooth-bearing series) drawn from several parts of the range, the distribution of teeth in the palatine, pterygoid and dentary is as follows:

Fig. 17. Dorsal view of skull (greatly enlarged) of African "spitting cobra," showing location of cranial elements. (A.M.N.H. No. 57812, from Capelongo, Angola.)

No. of Teeth	6	7	8	9	10	13	14	15	16	17	18	19
Palatine	5	30	8	2	1							
Pterygoid						7	6	9	10	5	4	5
Dentary						11	26	6	3			

In both the palatine and dentary series the distribution is clearly not a normal one, being strongly skewed to the left. In contrast, the distribution of teeth in the pterygoid exhibits only slight negative skewness. Presumably these distributions might result from spatial factors, the alveolar surfaces of the palatine and dentary being normally filled with teeth, whereas in *Naja* the posterior portion of the pterygoid is edentulous in varying degrees, and there is always room, so to speak, for additional teeth (Fig. 25). In fact, *Pseudohaje goldii*, which probably exhibits less variation in pterygoid teeth (from 39–41 in ten bones) than most *Naja*, normally has teeth present on the posterior end of the bone. On the other hand, genetic factors must be in-

volved in many cases, since in ten pterygoid bones of *Hamadryas hannah*, the variation in pterygoid teeth is only from 10–12 and, of the ten bones, seven contain 10 sockets despite the presence of additional space on the posterior of the bone (Fig. 27).

This sample, unfortunately, is not homogeneous, the specimens from which data

species of *Hamadryas* on the basis of dentitional characters.

Unfortunately, adequate series of cobras from single localities or restricted areas are not available at present to determine whether there are significant differences between subspecies (*Naja nigricollis nigricollis* and *N. n. pallida*, for example), or

Fig. 18.   Ventral view of skull (greatly enlarged) of African "spitting cobra," showing position of cranial elements.   (A.M.N.H. No. 57812, from Capelongo, Angola.)

were drawn having no locality data except in two instances; had all specimens been taken from a single population it is probable that even less variation would have occurred.   The single *Hamadryas* having 12 pterygoid teeth on each side is from Johore, India, near the western periphery of the range of the genus.   Adequate series from several localities might well provide some basis for segregating species or sub-

differences between the sexes in dentitional characters, although this seems less probable. Such preliminary studies should be made before species or genera are compared, and it is only of small theoretical interest to compare inadequate tooth counts for two forms, *Naja naja*, with a sample drawn from many parts of the range of the species, and *Naja nigricollis*, represented by a sample of only twelve counts

FRONTAL
POSTORBITAL
PARASPHENOID
PARIETAL
SUPRAOCCIPITAL
TABULAR
PRO-OTIC
OPISTHOTIC
EXOCCIPITAL
STAPES
BASIOCCIPITAL
PTERYGOID
QUADRATE
ARTICULAR
POSTARTICULAR
SURANGULAR

NASAL
PREFRONTAL
PREMAXILLA
SEPTOMAXILLA
PALATINE
MAXILLA
ECTOPTERYGOID
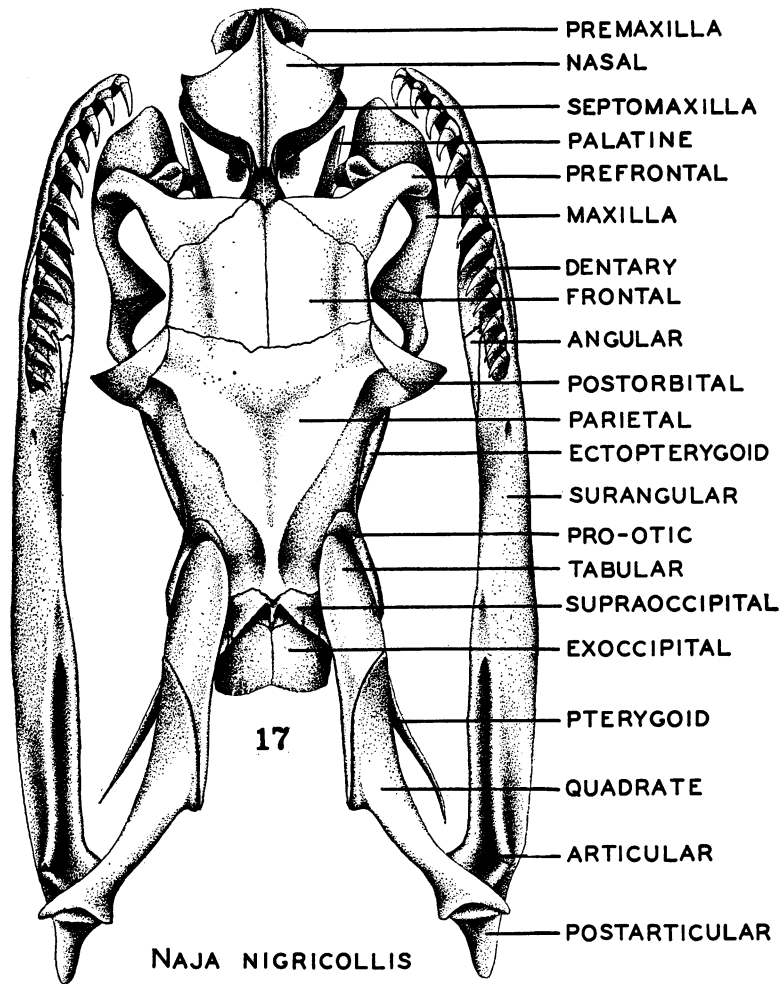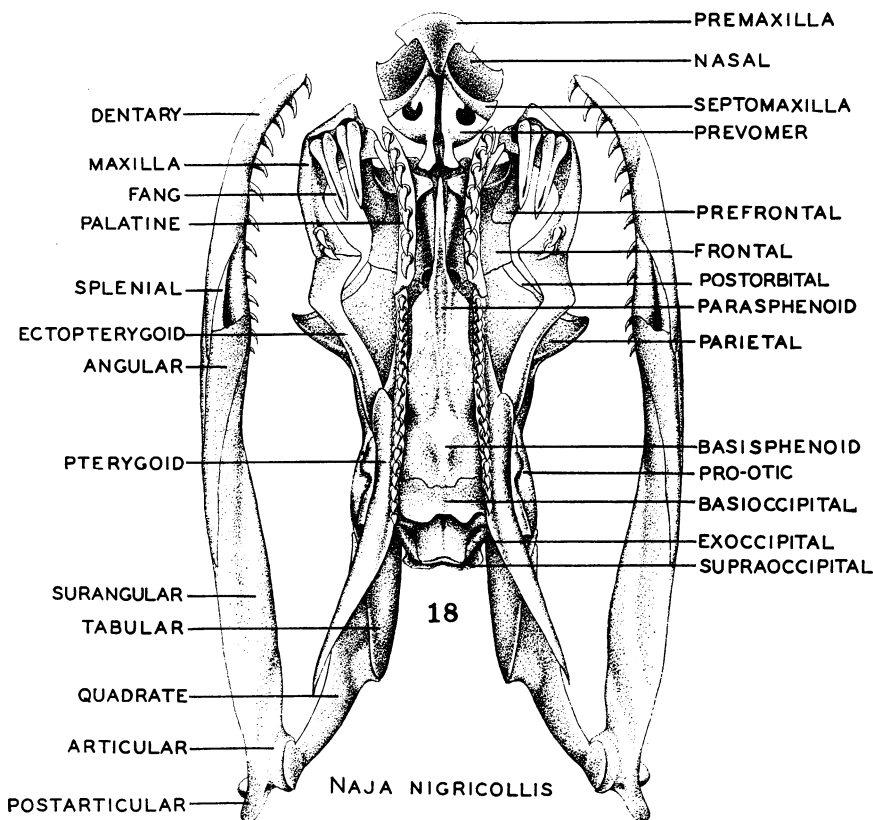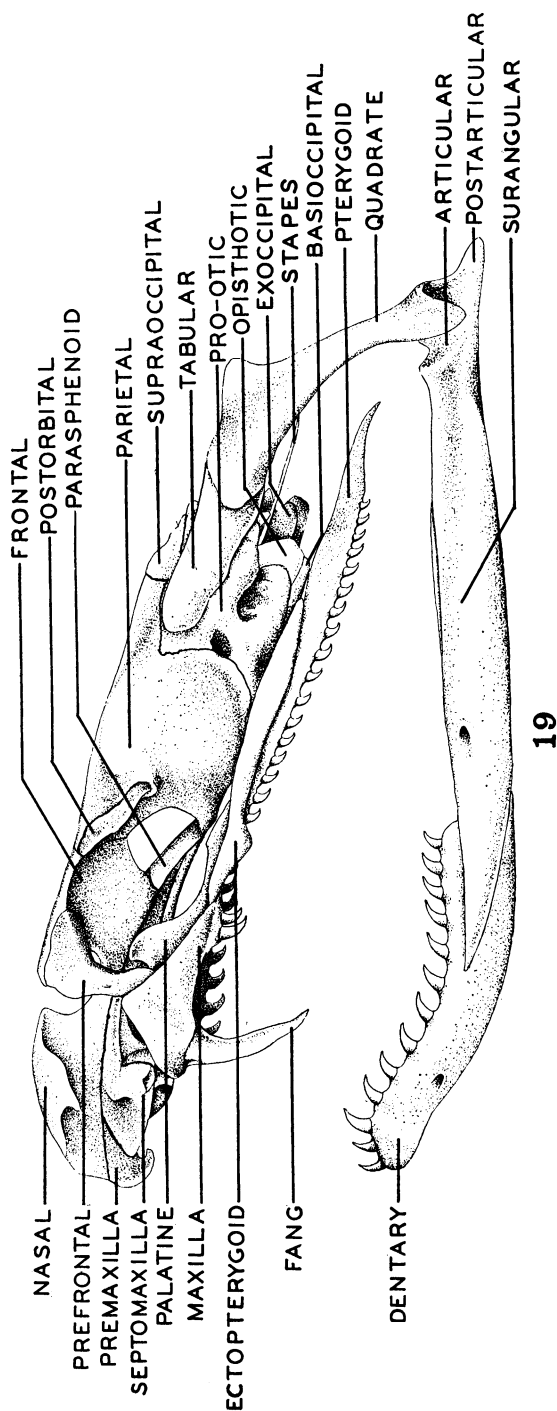FANG
DENTARY

NAJA NIGRICOLLIS

19

Fig. 19. Lateral view of skull (greatly enlarged) of African "spitting cobra," showing position of cranial elements. (A.M.N.H. No. 57812, from Capelongo, Angola.)

derived from five specimens from Cape-longo, Angola, and one from Natal. The data from *N. naja* are given above, and similar data for *N. nigricollis* follow, with the values of the variate stated first and the frequencies of occurrence of these values in parentheses: palatine, 5 (1), 6 (2), 7 (7), 8 (2); pterygoid, 16 (2), 17 (3),

series P is less than 0.01; and for the dentary series P is greater than 0.9.

Therefore, no certainly significant difference in palatine counts is indicated by application of the chi-square test to these inadequate samples, and there is no significant difference in dentary counts. On the other hand, strongly significant differences

NAJA MELANOLEUCA
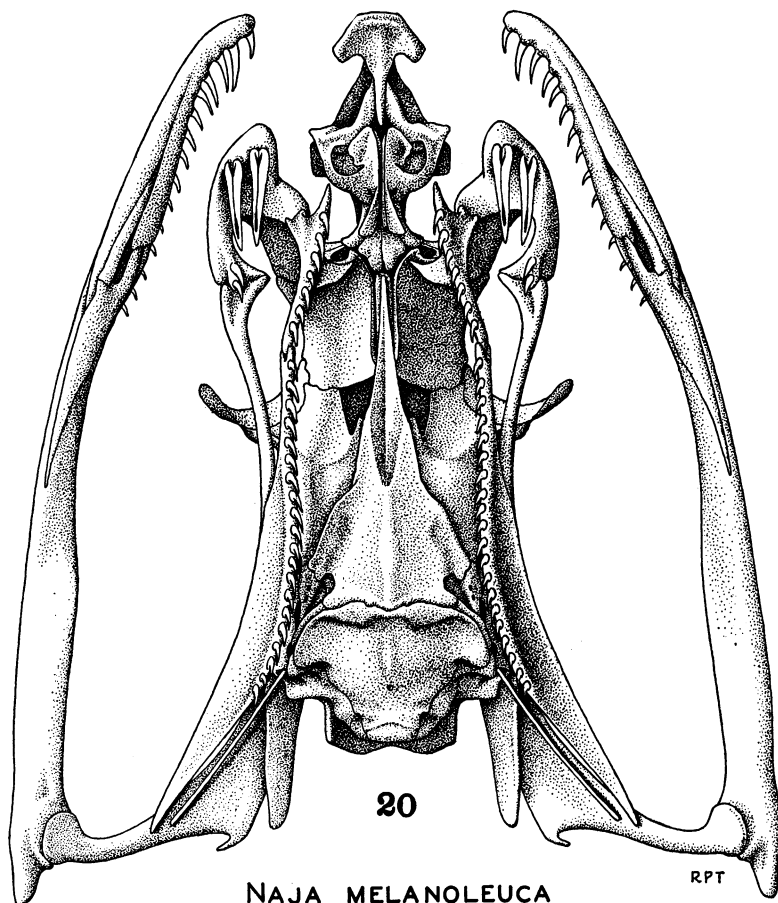
Fig. 20. Ventral view of the skull (approximately × 4) of the cobra inhabiting the African Rain Forests.

18 (7); dentary, 13 (3), 14 (9). In this case the distributions are skewed to the right, in contrast to the distributions of *N. naja*. The significance of differences for the three series, as determined by a chi-square test of an *R*x2 table, gives the following results: for the palatine series P is approximately 0 02; for the pterygoid

in pterygoid counts are indicated for the samples compared, and in all probability differences in pterygoid dentition between the several species of *Naja* could be demonstrated were adequate data available. Such data could profitably be assembled in any monographic treatment of the genus, and it may be inferred that den-

21

HAMADRYAS   HANNAH
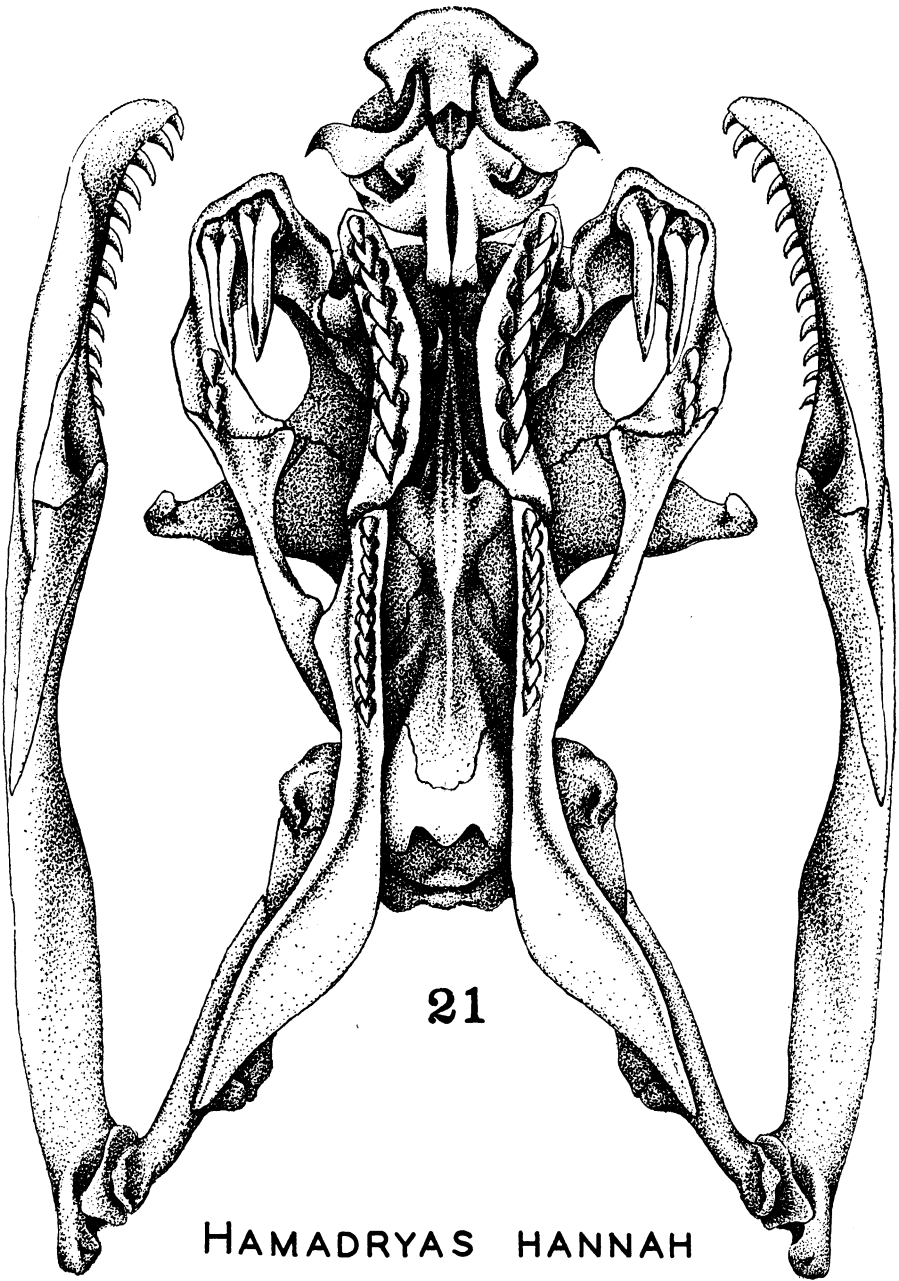
Fig. 21.   Ventral view of the skull (× 2) of the king cobra, showing dentitional characters and cranial elements.

titional characters will often provide useful taxonomic information heretofore neglected in studies of cobras which were based chiefly on pattern and scale characters.

Reference has been made above to the two populations of *Naja naja*, as tentatively interpreted, that exist in Asia. One of these, that inhabiting northern and central India, has no solid teeth on the maxilla (see Fig. 4), whereas the one inhabiting the southern portion of Asia, from lower India eastward, has one solid maxillary tooth. This reduction in teeth at the western ex-

Attention has been called to the fact that with relatively few exceptions, African *Naja* normally have two solid maxillary teeth behind the fangs. On this continent, however, no gradient was discovered in fang characters, although one species possesses fangs modified for spitting, and there are interspecific differences in fang apertures, that of *nivea* being larger than those of three other African species (see Figs. 28–33).

In addition to *N. haje* which ranges into Asia Minor, two cobras from Asia can be

HAMADRYAS HANNAH
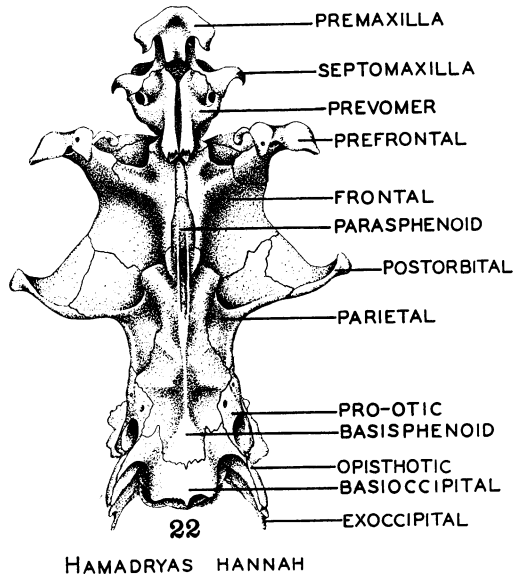
Fig. 22.   Ventral view of skull (× 1) of the king cobra, with jaws removed to show ventral sutures of cranial elements.

tremity of the range of the species is correlated to some extent with fang characters described hereinafter: cobras of the Malay region have fangs adapted for the forward ejection of venom, with the discharge aperture of the fang reduced in size; cobras toward the west in the range of the species have the discharge orifice progressively longer and wider, the orifice largest in the population without solid maxillary teeth in northern India. Thus in *Naja naja* there exists a sort of gradient involving two dental characters.

referred to the African assemblage of the genus on the strength of anatomical characters reported by Eichwald (*supra cit.*) and Thompson (*supra cit.*). These two, *Naja oxiana* and *Naja morgani*, have not been available for examination, but fortunately the maxillary dentition of each has been described, and in the discussion of the status of the forms above presented it is noted that each is reported to possess two solid teeth on the maxilla. *N. oxiana* inhabits the region "from the Oxus River to the eastern shore of the Caspian Sea."
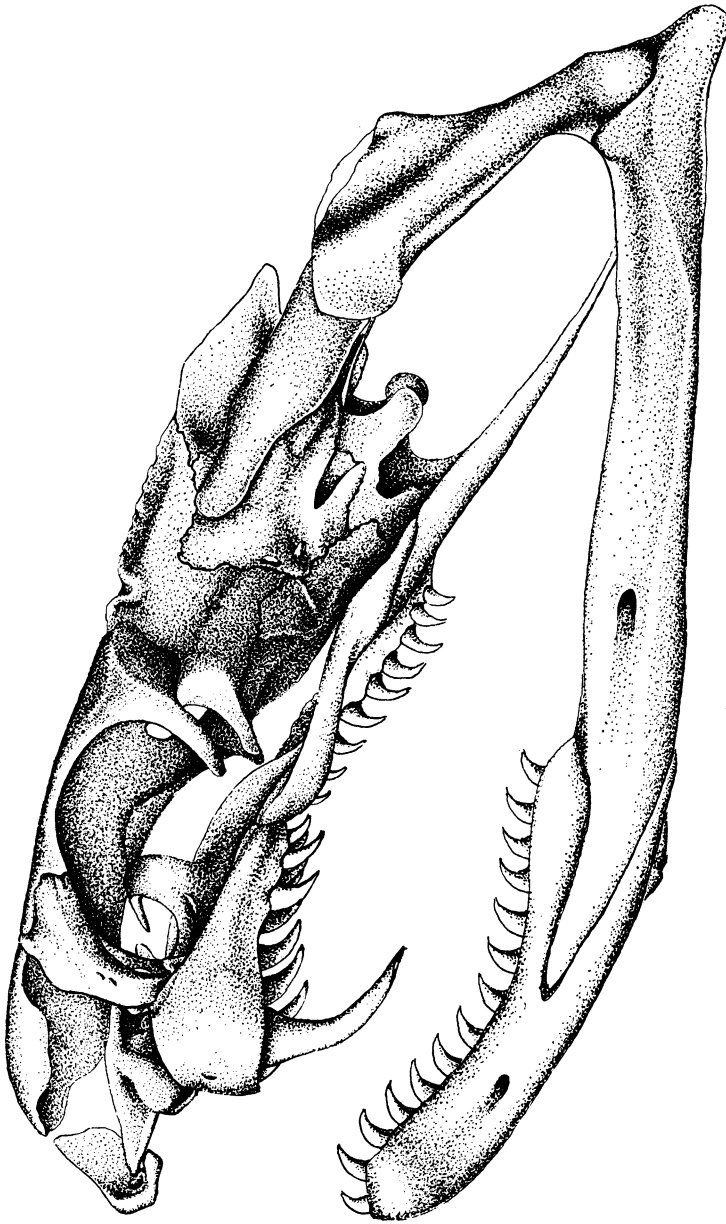
HAMADRYAS HANNAH

Fig. 23. Lateral view of the skull ($\times$ 2) of the king cobra.

24

PSEUDOHAJE GOLDII

25

NAJA MELANOLEUCA

26

BOULENGERINA A. ANNULATA

27
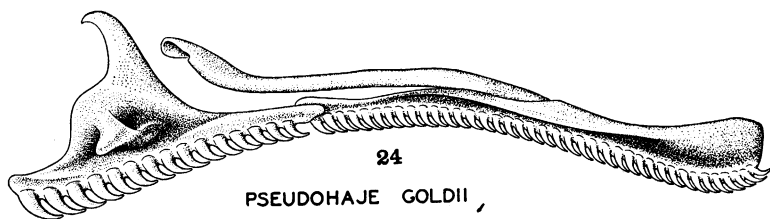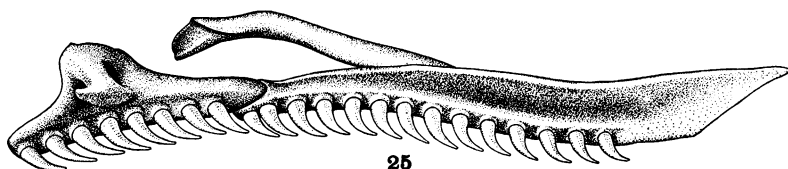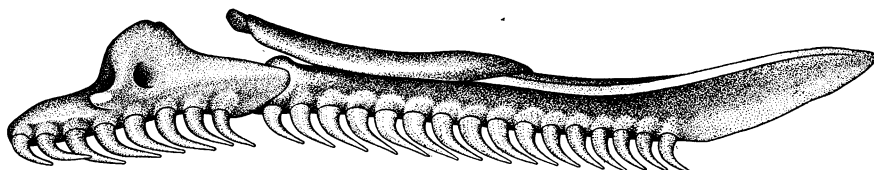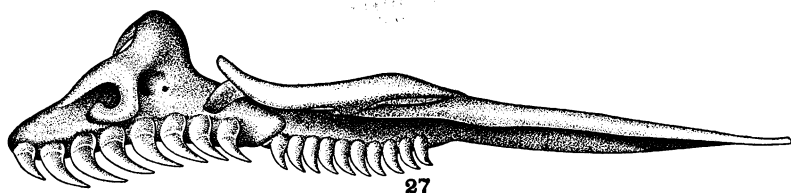
HAMADRYAS HANNAH

Figs. 24–27.   Palatine, pterygoid and ectopterygoid bones of species representing four related cobra genera.   All views from inner side to show variation in position and numbers of teeth and differences in shape of the various elements (approximately × 3, except *Hamadryas* which is enlarged about 1¹/₂ times).

while *N. morgani* is recorded from Persia and Irak.   Assuming that the maxillary dentition of these two forms has been accurately described, their presence in western Asia clarifies the zoogeographical situation.   Even though the areas inhabited by these two species cannot be mapped in de- tail, they apparently fill a gap between Asiatic *Naja* and the range of *Naja haje* which extends from Africa eastward into Asia Minor.   It is further significant that the Middle Miocene *Naja romani* fits into this distributional pattern, having two solid maxillary teeth like other cobras in
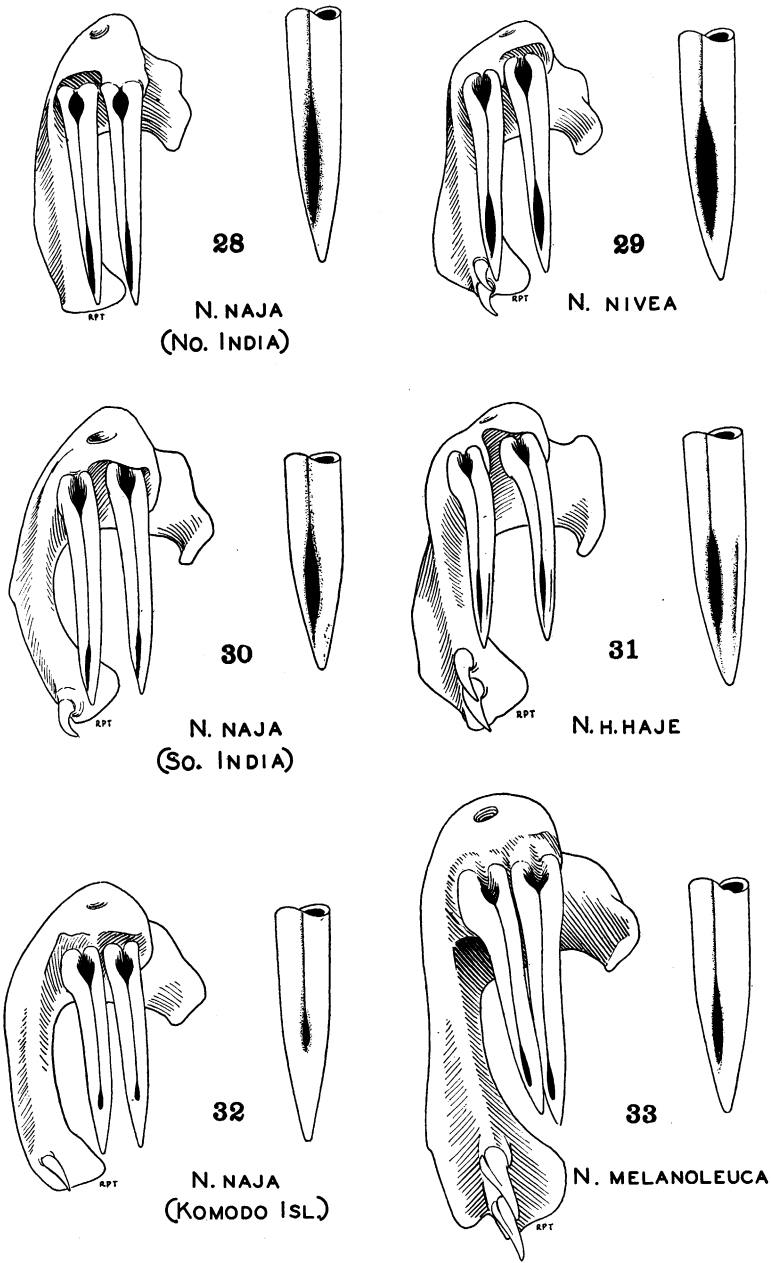
Figs. 28–33. Types of fang aperture (× 10) and maxillae (× 5) in Asiatic *Naja* (left column) and African *Naja* (right column). Note presence of two solid maxillary teeth in African species, in contrast to Asiatic forms of *N. naja*.

DENTAL FORMULAS

$\text{II} + 2$ $\text{II} + 0$ $\text{II} + 1$

MAP No. 4

APPROXIMATE DISTRIBUTION
AND
MAXILLARY DENTITION OF NAJA

N. HAJE
N. NIGRICOLLIS (ADAPTED FOR SPITTING)
N. MELANOLEUCA
N. NIVEA
N. MORGANI
N. OXIANA
N. NAJA (NOT ADAPTED FOR SPITTING)
N. NAJA (NOT ADAPTED FOR SPITTING)
N. NAJA (PARTLY ADAPTED FOR SPITTING)
N. NAJA (ADAPTED FOR SPITTING)
✳ N. ROMANI (MIDDLE MIOCENE)
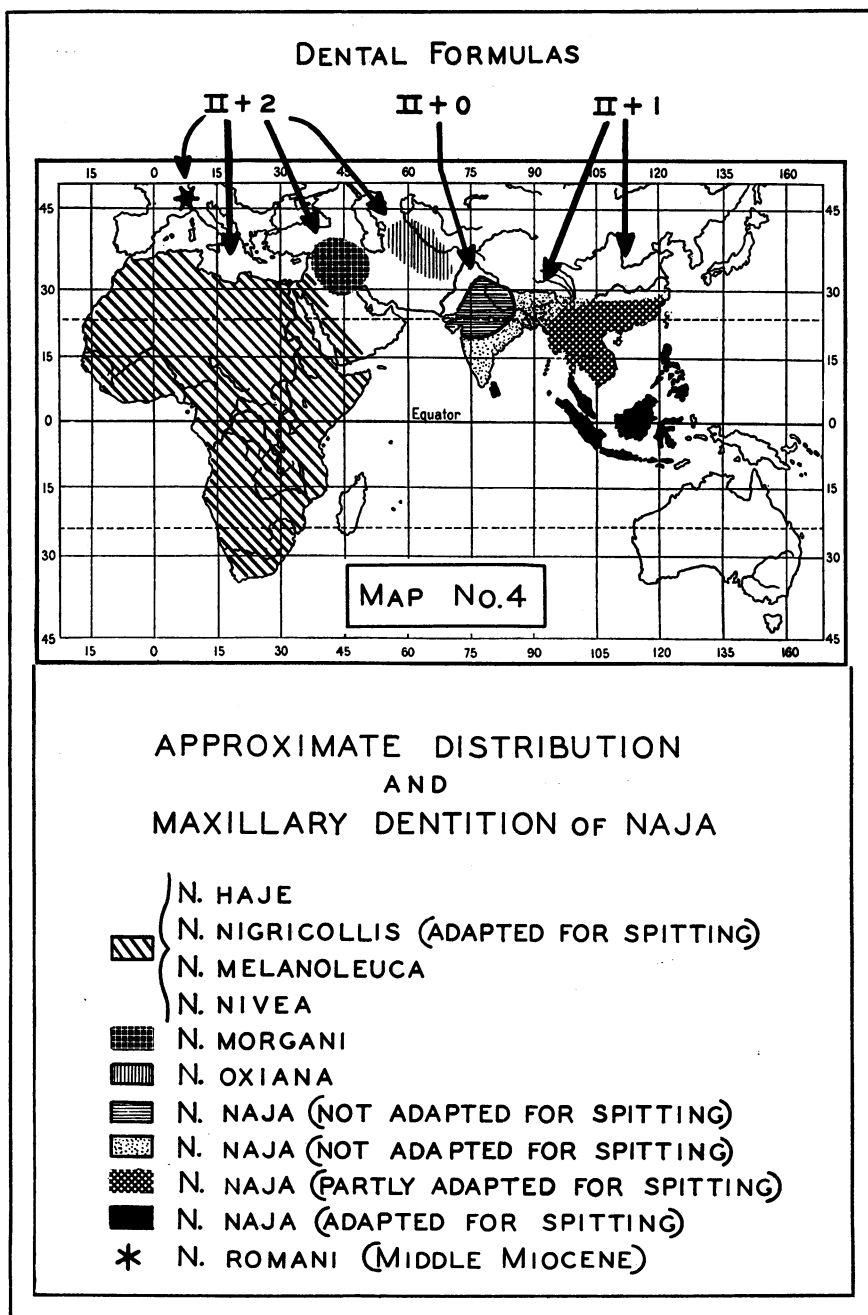
Map 4. Distribution of cobras of the genus *Naja*, with ranges of African representatives of the genus combined, and ranges of Asiatic forms shown separately. Only *Naja nigricollis* among African *Naja* is adapted for spitting, while in Asia only cobras east of India are spitters. Various stages in fang and dentitional characters of *Naja naja* from southern Asia and adjacent islands are indicated by means of cross-hatching. Absence of cross-hatching between ranges of the species in southern Asia indicates gaps in knowledge rather than actual absence of cobras in the areas.

the western portion of the range of the genus.

Thus the cobras of the genus *Naja* seemingly occupy a range probably continuous from the Malay region westward through Asia and most of Africa, while the Sulaiman Range and the Bugti Hills constitute a well-defined physiographic barrier separating cobras with two teeth behind the fangs from those having no teeth or but one tooth. Using Roman numerals to indicate fangs, a plus sign to indicate a diastema, and Arabic numerals to indicate solid teeth in dental formulas, the distributions of snakes of the genus *Naja* and their maxillary dentition are shown in Map 4. The unshaded areas on the map between ranges shown in Asia do not necessarily indicate absence of snakes of the genus *Naja*. Cobras almost certainly inhabit all southwestern Asia, and have indeed been reported in Baluchistan, but the lack of published data concerning dentition makes it impossible to assign such records to the proper species. Other regions are almost unexplored herpetologically, and hiatuses in the range of *Naja* as mapped are indicative of nothing more than gaps in our knowledge of distributions.

Such conclusions as can be drawn concerning the phylogeny, probable origin, and center of dispersal of cobras are limited owing to the paucity of suitable fossil material. Probably it was somewhere in Asia that the family Elapidae originated, and such evidence as is now available suggests that elapids evolved from the same stem as the colubrids at an early period in geological time, at least antedating the Miocene, and probably nearer the Cretaceous. Gilmore (1938) records no fossil Elapidae from North America, none is known from South America (Simpson, 1933, p. 1), and few have been recorded from Europe, while those from Asia are fragmentary and of comparatively recent age. Therefore, it is necessary to look elsewhere for evidence.

Representatives of the family are not present in the recent serpent fauna of Europe, but the family is represented by three closely related genera in the Western Hemisphere, by ten genera in Africa, and by approximately half a dozen on the Asi-

atic mainland, whereas nearly three times this number are represented in Australia and the Malayan Archipelago, the majority of them occurring in tropical or semitropical regions.

With this information it may be speculated that the group had its origin in Asia at a time when the central land mass had a comparatively warm or tropical climate, and that during this early period, or perhaps later during a warmer cycle in the north, in the Miocene or earlier, the ancestral stock became diversified, some forms spreading westward through Europe, while one migratory stock pushed toward the northeast, reaching the Americas via a land bridge. At the same time or possibly earlier, but after the Oligocene since the family is not represented in Madagascar, several forms reached Africa, undergoing secondary dispersal there, while still prior to this, the stock had already reached Australia. The absence of elapids in New Zealand may be the result of present climatic conditions, or it may indicate an earlier isolation of this island. Subsequent to this dispersal, a shift in climatic conditions must have driven the elapids southward, those in Europe failing to survive the rigors of a cooler climate, while those in the Western Hemisphere were forced to migrate southward where the stock evolved several species in comparatively recent times, some of them subsequently moving northward again following the last glacial period. Among American elapids the genus *Micruroides* is probably the most primitive, with one or two solid maxillary teeth, and it remains at the northwestern edge of the range of elapids in this hemisphere. *Micrurus* and *Leptomicrurus*, the only other American elapid genera, lack solid maxillary teeth. In the Old World, the most primitive living elapids are probably those remaining isolated on some of the islands in the Malayan Archipelago, the islands of Fiji, the Solomons and New Guinea, as well as Australia, while those remaining on the Asiatic mainland evolved from stock (or stocks) that was sufficiently eurythermic to spread northward as far as southern China. Many Australian elapids are not unlike colubrids in appearance,

and many possess numerous teeth behind the fangs on the maxilla, whereas no more than four teeth on the maxilla occur in Asiatic or African elapids, further indicative of a more advanced evolutionary state.

Such speculation doubtless represents an oversimplification of the evolution and dispersal of the Elapidae, more than one migration being probable, and it assumes that the genus *Naja* evolved after Australia was cut off from the mainland in late Cretaceous time, elapid stocks having already reached Australia long before the Miocene. This is indicated by the presence of *Naja* as far to the southeast as the Celebes, as well as in the Philippines, and other East Indian islands. Assuming that ancestral *Naja* possessed two or rarely three solid teeth on the maxilla, it appears that they reached Africa in this condition, subsequently evolving four species, all of which retained this dentitional character. To the east of the Sulaiman Range the ancestral stock lost solid maxillary teeth, those in northern India losing all of them, while those to the south and east retained a single, vestigial, solid, maxillary tooth.

Hamadryas, on the other hand, evolved from a more primitive elapid stock that never succeeded in crossing the Sulaiman Range, to judge only by the range of the living form, and while its dispersal paralleled *Naja naja* in southeastern Asia, it evolved along totally different lines. The evolution of the "hood" in *Hamadryas*, *Boulengerina* and *Hemachatus* may be regarded as a modification paralleling the development in some species of *Naja*, since similar parallels exist in colubrids even more distantly related; or the hood may have evolved in an early progenitor, being retained in all four diverging stocks.

Hemachatus may represent a more progressive offshoot of the ancestral *Naja* stock, or possibly it represents an endproduct evolving from some progenitor that reached Africa prior to the advent of *Naja*. Certainly the Elapidae had a comparatively early origin, and their present abundance in Africa, and more especially Australia, does not necessarily indicate origin in either of these two continents.

I do not believe that competition with the more highly evolved Crotalidae or Viperidae accounts for the relatively few elapid genera in Asia or the Americas. Rather it seems more probable that ecological and genetical factors were involved, and that one or both of these families had a somewhat later origin than the relatively stenothermic elapids, perhaps evolving from a more progressive eurythermic ancestral elapid. Mosauer (1935, p. 118) notes that both *Naja* and *Hemachatus* "show viperid muscle arrangement," pointing to the possibility that these genera, and probably others not examined by Mosauer, branched off the stock that finally gave rise to the solenoglyphs. Such zoogeographical evidence as may be assembled suggests that the Viperidae and Crotalidae evolved probably from a common ancestral form in the north, almost certainly in Asia, the earlier forms being adapted for a more temperate climate than their presumed elapid progenitors. Subsequent speciation permitted the dispersal of some forms to the south.

Another possibility remains, namely, that separation of the hemispheres isolated two viperine stocks, the Crotalidae evolving in the Americas and spreading to Asia later, at the same time that many mammalian groups were interchanged between Asia and North America during periods of connection in the Tertiary. The Viperidae, however, must originally have represented a western offshoot, spreading into Europe and Africa, blossoming more spectacularly in Africa where the stock evolved terrestrial, subterrestrial and arboreal groups, adapted for existence in deserts and in tropical rain forests. A similar secondary dispersal and evolution, to some extent paralleling that of the vipers, was achieved by the Crotalidae which migrated northward and eastward to reach the Americas. Nevertheless, the Elapidae survived in Africa, with fewer species but with more genera, implying an earlier origin perhaps, but not indicating that the group suffered from competition with the Viperidae. Elapid genera in Africa have evolved forms that are more or less specialized for terrestrial, subterrestrial,ar boreal and even aquatic habitats. The Crotalidae and Viperi-

dae, with little doubt, failed to reach Australia only because they evolved subsequent to the isolation of this continent. Both groups eventually produced forms that spread into the Malayan Archipelago, although the absence of *Vipera* in the Malay Peninsula and its presence on Komodo and Flores remains unexplained unless we assume an ecological reason for

evidence as exists points to an early origin of the Elapidae, and insofar as the theories outlined above represent a correct interpretation of zoogeographical data, they confirm this conclusion. Additional study of fossils that must eventually become available will certainly throw more light on the problems of serpent evolution, and speculation is perhaps futile at this time.

COLUBRIDAE   HYDROPHIIDAE   ELAPIDAE   VIPERIDAE   CROTALIDAE

ANCESTRAL
ELAPIDAE

ANCESTRAL
COLUBRIDAE

34
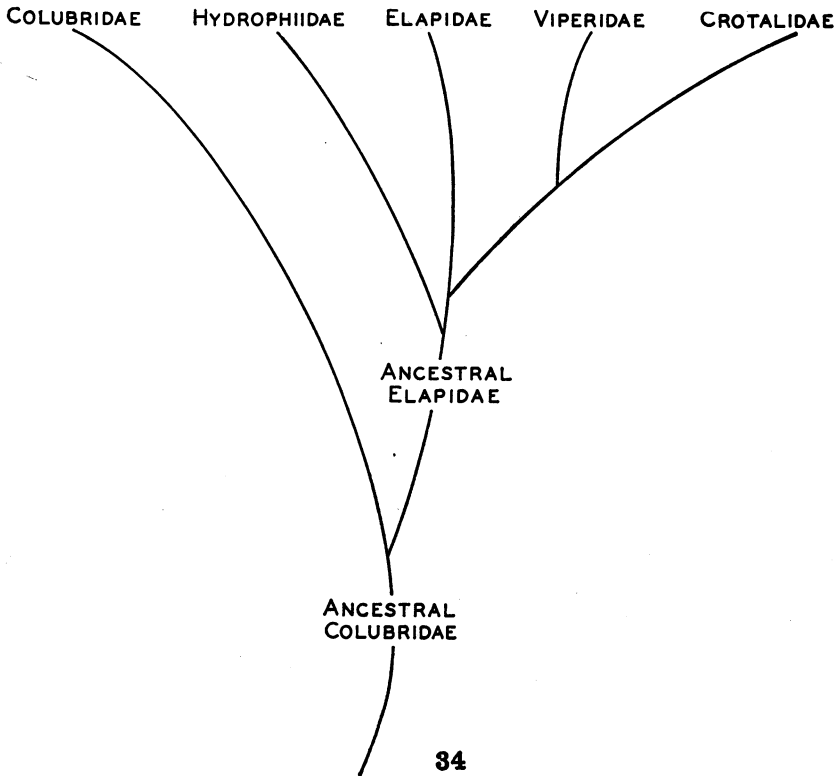
Fig. 34. Tentative schema, indicating probable relationships of the aglyphs, proteroglyphs and solenoglyphs.

its absence on the Peninsula that cannot be demonstrated at present.

This summary of speculative inferences may or may not be confirmed by additional palaeontological evidence, and so far ophthalmological data (Walls, 1942), studies of trunk musculature (Mosauer, 1935) and of osteological and ocular shield characters (Mahendra, 1938) have resulted in somewhat conflicting conclusions. Such fossil

Nevertheless, the hypotheses advanced herein seem to be consistent with such inferences as can be drawn from a study of maxillary dentitional variation in *Naja* and the maxillary dentition of other living elapid genera.

It must be emphasized that summaries of evolutionary phenomena described herein represent hypotheses that are tentative at best, although it seems far more

reasonable, because of similarities in venom apparatus, to derive the Viperidae and Crotalidae, as well as recent Elapidae and Hydrophiidae, from some common ancestral stock that more nearly resembled existing elapids, than to derive the Solenoglypha from the Opisthoglypha as Boulenger (1893, p. 2) preferred. Mahendra (1938, p. 351) feels that Boulenger's opinions "perhaps were formed subconsciously," because whatever criteria Boulenger utilized in erecting his genealogical tree were never explicitly discussed. The results of researches dealing with venoms formerly were used to uphold Boulenger's views with respect to the close relationships of opisthoglyphs and solenoglyphs, but such evidence can no longer be considered confirmatory, snakes indisputably in the same genus having venoms primarily either hematoxic or neurotoxic (Klauber, 1936, p. 209). Venoms seem, therefore, to be of doubtful value in determining the relationships of suprageneric groups.

It may be added that there is much to be said in favor of the phylogenetic arrangement of serpent families presented by Mahendra (1938) except for his decision to disregard the proteroglyph families. I (1940) am quite in agreement with him when he considers the Opisthoglypha to represent an unnatural assemblage, but there seems to be little basis for believing that the Elapidae are polyphyletic in origin. Malcolm Smith (1926, p. vi) intimates that the two subfamilies of the Hydrophiidae, or sea snakes, may possibly have had separate origins, the Laticaudinae in Australia and the Hydrophiinae in the Indo-Malayan region, but whatever the origin of the Hydrophiidae there is little doubt that both subfamilies descended from terrestrial elapid ancestors. Even admitting the possibility of two lines of descent in the Hydrophiidae, it is desirable to recognize proteroglyph families (three of them, if two lines of descent in the Hydrophiidae were proved) as well as two solenoglyph groups, as Walls' (1942) data indicate, confirming osteological and zoogeographical conclusions. It is of little importance whether the solenoglyph groups are designated as subfamilies or families, but I consider it desirable to elaborate the terminal portion of Mahendra's phylogenetic tree somewhat along the lines indicated in Fig. 34.

CRANIAL MECHANISMS ASSOCIATED WITH THE VENOM APPARATUS

Before discussions of fang and dentitional characters are undertaken, several features of the venom apparatus of cobras must be described in order to clarify the treatment of data presented below. Radowanowitsch (1928) has described the poison apparatus of one cobra, *Naja tripudians* (= *N. naja*) in considerable detail with particular reference to the musculature and to the histology of the venom glands. In addition, certain features of the osteology of elapids have been dealt with by several authors. But no discussion of fang growth, of the mechanism of replacement, or of fang structure has been available for cobras or their allies that compares with the meticulous treatment afforded the rattlesnakes of the crotalid genera *Sistrurus* and *Crotalus* by Klauber (1939). Because many features of the venom apparatus in cobras are similar to those of crotalids, additional evidence is provided which confirms the belief that they had a common front-fanged ancestor. Nevertheless there are differences, and it is instructive to compare the two.

The skull elements of cobras as well as those of many other proteroglyphs are the same, with few minor exceptions, as those of viperids and crotalids. The chief differences of cranial osteology between cobras and solenoglyphs lie in the relative size, positions and the nature of the attachments of the individual elements. (See Pl. XLIX, figs. 1 and 2.) The skull of the rattlesnake includes a highly specialized mechanism which enables the snake to tilt the fangs forward and downward, from an inactive position against the roof of the mouth, to a striking or biting position perpendicular thereto. This tilting mechanism (described in detail for *Crotalus* by

LEFT MAXILLA

FANGS

LATERAL VIEW OF SKULL

35

RIGHT MAXILLA

FANGS

PALATINE

ECTOPTERYGOID

PTERYGOID

36

HEMACHATUS HAEMACHATUS
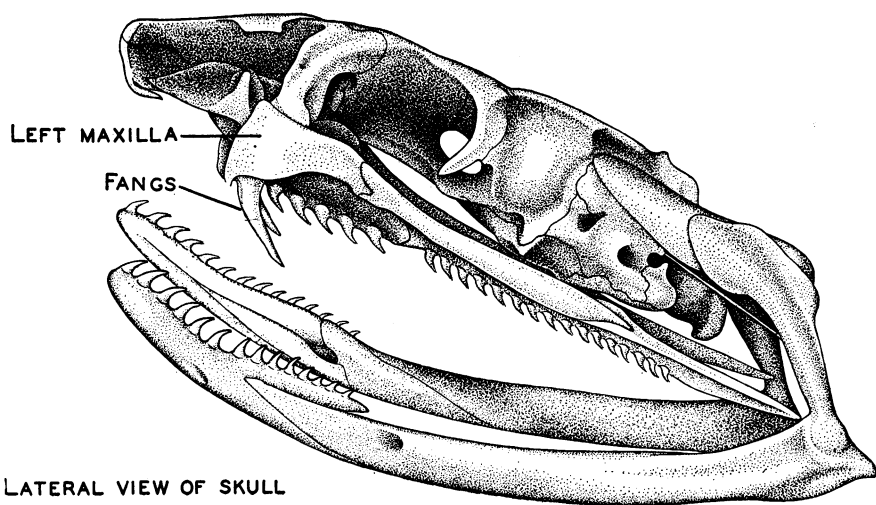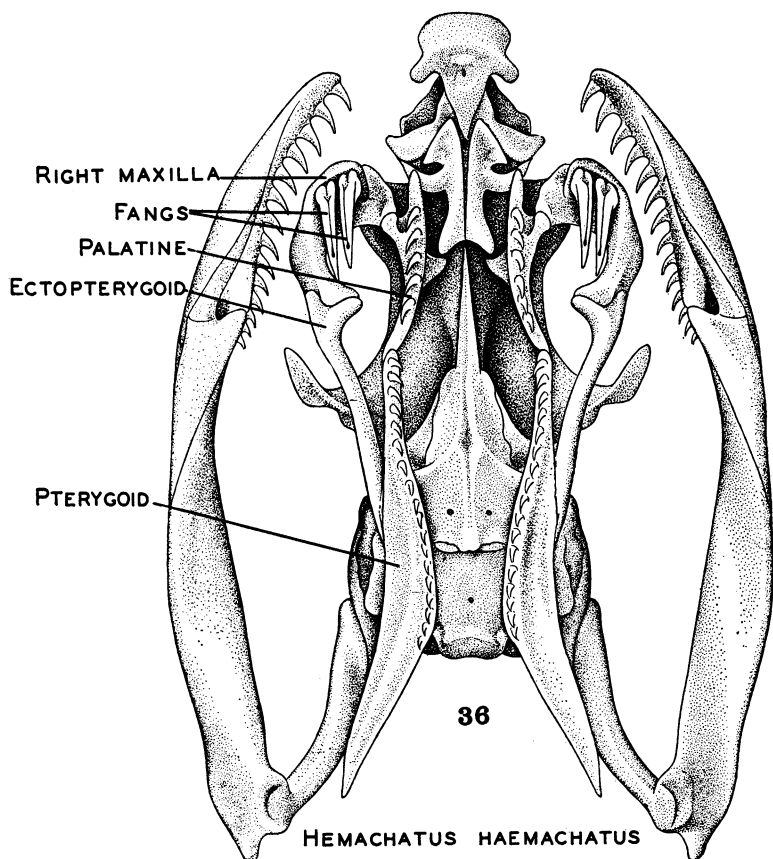
VENTRAL VIEW OF SKULL

Figs. 35–36.   Lateral and ventral views of the skull (× 3) of the rhinghals, *Hemachatus haemachatus*, the most highly perfected of all spitting cobras, showing position of fangs and characteristics of other dental elements.

Klauber, *supra cit.*) involves a slight hinge action where the prefrontal is secured to the frontal (apparently absent in the primitive viper, *Causus*), and a combined sliding and hinge action where the maxilla, the fang-bearing element, engages the prefrontal. In cobras there is no perfected tilting mechanism. The prefrontal is rigidly attached to the frontals (see Figs. 35 and 36 and Pls. XLVIII and XLIX), and the maxilla is not hinged where it is attached to the prefrontal, although muscular attachments to the ectopterygoid and to the posterior end of the maxilla (Radowanowitsch, *supra cit.*) indicate that limited rotation and movement of the maxilla are possible. When the mouth is closed the functional fang on either side extends into a pocket in the gum tissue outside each mandible, but well inside the lips.

The condition in the solenoglyphs may be interpreted as an advancement from that of proteroglyphs, and the changes that have accompanied the evolution and perfection of the tilting mechanism seem to be among the factors that enable rattlesnakes and most other solenoglyphs to possess relatively larger fangs situated farther forward in the skull. Several other differences that result from modifications that have accompanied the perfection of the tilting mechanism in rattlesnakes need not be discussed here, but it may safely be postulated that the two types of dentitional apparatus, that of the cobra and that of the rattlesnake, are correlated with their respective functions. In both, the fangs are well designed for biting, but the strike of the rattlesnake is rapid, the jaws having an opening often approximating 180 degrees immediately prior to the penetration of the fang, so that a stabbing action precedes the bite. Klauber (*supra cit.*, p. 20) points out that "once the point [of the fang] has gained entrance, then both the curve in the fang and the folding action of the maxillary serve to accentuate the penetration produced by the squeezing pressure of the bite, particularly as the fang has a much smaller radius of curvature (about one-sixth) than the hinge distance of the upper jaw." The cobra, having shorter, stouter, permanently erect fangs, relies largely upon a chewing motion immediately following the bite to engage the fangs. There is little if any stabbing action involved in the strike which is not unlike that of many non-venomous snakes (aglypha).

The position of the various elements in the skull, the attachments of the fang-bearing maxilla and the normal position of the fangs of *Naja nigricollis* are shown in Figs. 17–19, and for *Hemachatus* in Figs. 35 and 36.

FANG REPLACEMENT

Owen (1846) made the first extensive comparative study of teeth, and while he describes tooth replacement in many reptiles and devotes a useful chapter to the teeth and fangs of snakes, he makes only the briefest mention of tooth and fang replacement. Mitchell (1861, p. 19) noted that fang succession was regular in rattlesnakes, but he failed to arrive at a correct interpretation of the position and movements of the developing teeth. Later Mitchell was properly criticized by Tomes (1876, p. 380) who presented accurate information concerning fang succession in vipers and rattlesnakes, but Tomes was completely misled so far as cobras were concerned and continued to be misled as late as 1914 (p. 324). He came to the erroneous conclusion that "an arrangement of the successional teeth in a paired series does not exist in the Cobra, in which successional teeth form but a single series," describing such a condition in *Naja*, probably because he had but a single specimen of the Indian cobra from which some of the fangs must have been removed. This is indicated by his figure (Pl. XXXVII, fig. 5) and further corroborated by the presence in collections today of cobras purchased in India that often have had all of the fangs removed. Tomes' section indicates the presence of two fangs behind one socket, however, and the specimen must have been incompletely defanged.

Klauber (1939), in his paper mentioned above, fully verified Tomes' theory of fang succession in rattlesnakes and presented both anatomical and statistical data by

way of proof. Klauber also examined one elapid, *Hamadryas hannah*, and stated that the asymmetrical arrangement of the fangs in the two maxillae indicated a similar method of fang replacement in this genus. This conclusion is confirmed in dissections of *Hamadryas* which I have been able to make, and from an examination of several elapid genera, in particular a large series of *Naja*, it is apparent that a similar mechanism of fang replacement is found in elapids, crotalids and viperids. Furthermore, it is obvious from data presented below that the method of fang replacement is entirely analogous to the method of tooth replacement in aglypha.

As may be noted in Figs. 28–33, two fangs are normally present in each maxilla. It will become apparent from the discussion below that functional fangs alternately occupy the inner and outer sockets of each maxilla. Skulls and dissections of more than 100 cobras reveal that usually one fang is firmly attached while the other may be incompletely formed, or nearly formed, but with the pedestal soft and the fang incompletely anchored; rarely both fangs may be almost equally well anchored. In other words, usually a functional fang and a nonfunctional fang are present in the paired sockets of each maxilla; the non-functional fang may be in any stage of ankylosis, and it may be about to become functional or about to be shed. When fangs of contiguous maxillary sockets are equally ankylosed it may be inferred from Klauber's work on rattlesnakes that both fangs were temporarily functional at the time a cobra in such condition was killed. Klauber found that venom of rattlesnakes was ejected through both fangs in a single maxilla for a brief period when both were firmly anchored.

Behind each of the fangs in the maxilla (only one of which may be firmly anchored) there are normally two or three fangs in progressive stages of growth. Development of the fangs begins posteriorly with what is to become the point, and sometimes there are three recognizable reserve fangs behind a vacant socket, the large one of the three not being in a stage of development that includes the entrance lumen. When a functional fang is completely an-

kylosed the third one behind it is represented by a rudimentary deposit of dentine scarcely recognizable as a fang-point (Figs. 37–38), while a recently ankylosed fang will have only two partly developed fangs behind it, the third having not yet appeared. The actual process of fang replacement obviously cannot be observed, but a number of dissections permits study of the several stages in the process, and correct inferences can be drawn that enable us to understand the entire mechanism.

In dissections it may be seen that each developing fang is contained in a capsule or thin membrane connected with highly vascular tissue located on the inside of the anterior portion of the maxilla. This capsule forms a tube-like extension anteriorly beyond the dentine already deposited in the developing fang within it and contains soft tissue involved in the deposition of additional dentine. The deposition of dentine and the development of a single fang of the reserve series behind one socket may be described as follows:

By reference to Figs. 37 and 38 it can be seen that growth in the fang proceeds from the point to the basal end, the first dentine being deposited in a dorsal position roughly approximating the middle of the maxilla. As the fang takes shape and develops it migrates posteriorly in the maxilla as deposition of dentine continues anteriorly. Simultaneously the fang is slowly moving downward, still in a horizontal position, as rudiments of a new fang appear above it, or later as developing fangs follow it. As the growing fang approaches completion the previously functional fang in the maxillary socket is shed, and the base of the developing fang extends or grows into the vacated socket. At this stage of its growth the fang is still in a horizontal position, but it is evident from numerous dissections of cobras that as the pedestal hardens the fang is gradually rotated until it reaches the functional position, with the main axis of the fang at an angle of approximately 30 to 40 degrees with the horizontal axis of the maxilla. Once the fang is in functional position in the socket, there is evidently a period of unknown interval when

the striated pedestal becomes firmly ankylosed to the maxilla.

The description above, it must be understood, refers to the process of fang growth and replacement for only one of the paired sockets of an individual maxilla. Reserve fangs are present behind each socket as stated above, and similar replacement mechanisms for each are functioning si-

growth of the fangs is also correlated with growth of the organism.

To clarify the above discussion and for further consideration, the following notes have been made on a large adult male cobra (*Naja melanoleuca*, A.M.N.H. No. 12315, from Medje, Belgian Congo). This specimen has an over-all length of 2060 mm. (roughly 6¹/₂ feet). Only one func-
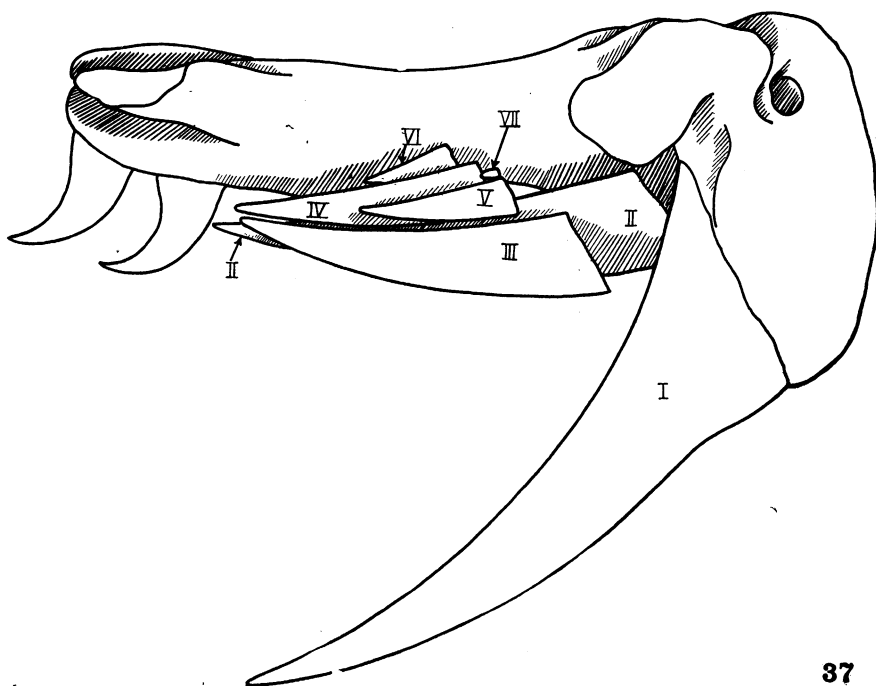
Fig. 37. Left maxilla of *Naja melanoleuca* (A.M.N.H. No. 12315, from Medje, Belgian Congo), viewed from the inner side to show the positions and sizes of the fangs in the replacement series. The Roman numeral I represents the functional fang, and the other Roman numerals indicate the fangs in the order in which they would eventually attain full size, become ankylosed and functional. For actual dimensions see text.

multaneously. However, the two mechanisms are so coordinated that mature fangs in the inner and outer socket, respectively, arrive in place at alternate intervals, with a brief overlap when both are present. Thus a cobra is never without at least one functional fang in each upper jaw. Inasmuch as larger cobras possess larger functional fangs (not precisely in a constant ratio of fang size to total length throughout ontogeny), it may further be inferred that

tional (ankylosed) fang is present in each maxilla in this particular individual, and the distance between fang tips in the preserved specimen was 19 mm. In the right maxilla the functional fang occupies the outer socket while in the left maxilla the functional fang is in the inner socket.

On functional fangs, the pedestal embedded in the socket above the upper lumen cannot be included in fang measurements if they are to be accurate. There-

fore, adopting Klauber's (1939) method, functional fangs and those completed as far as the lower end of the upper lumen have been measured along the straight line distance between the lower edge of this lumen and the tip of the fang. On smaller fangs not completed to include any portion of the upper lumen, measurements represent the over-all straight line distance. Such measurements are reasonably comparable and convenient; made with Vernier calipers under a dissecting microscope they are accurate to approximately one-tenth of a millimeter. Labeling the fangs with Roman numerals in the order in which they appear in alternate sockets of each maxillary bone, the functional and reserve fangs have the following dimensions:

extending into the bone) are approximately 7.6 mm.

(II) The first reserve fang, at the head of the outer series, *in situ* is roughly in a horizontal position, with the basal end in place at the entrance to the outer socket. The fang is tubular and hollow, with the point and discharge orifice well formed and hardened, but with no evidence of the upper lumen.

(III) The second reserve fang (inner series), as well as those above it in each series, is in a horizontal position parallel to but a trifle above No. II of the outer series, and with the point slightly anterior to that of the latter. The point, the discharge orifice and part of the tube are fully formed and hardened.

RIGHT MAXILLA

Inner Series	Outer Series
II—6.6 mm. (completed to include part of entrance lumen)	I—6.6 mm. (functional fang)
IV—4.4	III—5.1
VI—0.3	V—2.1

LEFT MAXILLA

I—6.6 (functional fang)	II—6.3 (not complete to entrance lumen)
III—4.9	IV—3.1
V—1.8	VI—0.7
VII—0.2	

A brief description of each of the fangs of the left maxilla (depicted in Figs. 37 and 38) will add to the information supplied by the dimensional data and the drawings. It may be noted here that the inner series of reserve fangs is separated from the outer series by a thick wall of connective tissue and all reserve fangs are embedded in soft tissue attached to the maxilla. The individual fangs dissected from this tissue may be described as follows, in the order indicated by the Roman numerals:

(I) The functional fang is firmly embedded in the inner socket, with the plane of the outer surface of its basal portion nearly in the same plane as the anterior surface of the maxilla. The pedestal and the portion of the fang above the lower end of the entrance lumen, as noted above, are not included in the straight line fang length measurement, but over-all measurements, from the tip of the fang to the maxillary bone (but not including the pedestal

(IV) The third reserve fang (outer series) lies above No. II, with the point slightly anterior to that of the latter. The point and the discharge lumen are fully formed and hardened, and a portion of the venom canal has been deposited.

(V) The fourth reserve fang (inner series) is represented only by a deposit of dentine that comprises the point and part of the discharge lumen, the upper end of the lumen being hardly closed. The cutting edges are present in normal position. The point is considerably anterior to the point of No. III below it.

(VI) The fifth reserve fang (outer series) consists of only the point below the discharge lumen. It is located somewhat anterior to the point of No. IV.

(VII) The sixth reserve fang (inner series) is represented by a somewhat ovate deposit of dentine. It bears no resemblance at this stage to the point of the fang represented in the fifth reserve fang
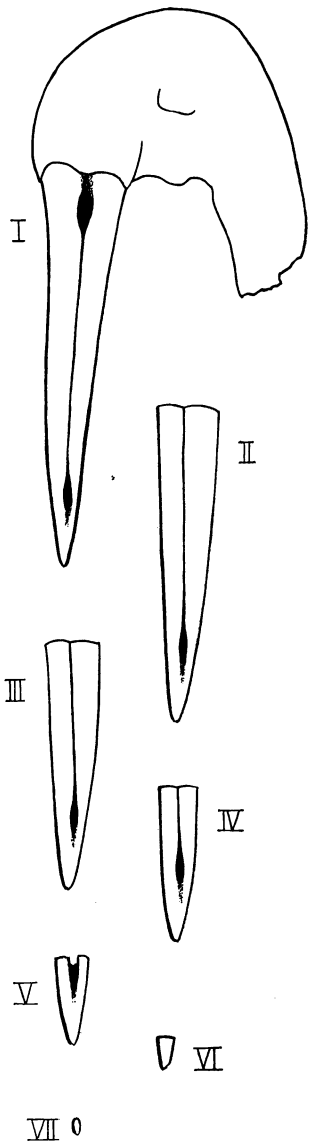
Fig. 38. Anterior view of the fangs of *Naja melanoleuca* from the same specimen depicted in Fig. 37, showing the relative sizes and states of development of the six replacement fangs of the left maxilla. Roman numerals indicate the order in which the fangs will become functional, No. I representing the functional fang. For actual dimensions see text.

(outer series). While it (a sixth reserve fang) is present in the left maxilla of this large specimen, it frequently cannot be found in smaller cobras and is not present in the right maxilla.

It may be observed from the dimensions given that all three fangs, completed as far as the entrance lumen in the specimen, have essentially identical measurements from entrance lumen to tip. Also it is apparent from a consideration of the data presented above that the mechanism of fang replacement in each maxilla is so coordinated that growth of the developing fangs permits alternate occupancy of the inner and outer sockets. But it is also manifest that the replacement mechanism of the left maxilla is not coordinated with that of the right maxilla, the functional fang being in the inner socket of one side and in the outer socket on the other in the particular specimen from which this description is drawn. Likewise, the first reserve fang of the right maxilla is obviously somewhat more advanced than the left in its state of development.

However, the asymmetrical arrangement of functional fangs found in this large specimen of *N. melanoleuca* is neither typical nor atypical, the arrangement of fangs in normal adult cobras being probably a matter of chance. Nevertheless, of 102 cobras of various sizes for which suitable data are recorded, 69 had functional fangs either both inside, or both outside, while the remaining 33 were asymmetrical, with one fang inside and the other one outside. Using the symbol "O" for outer and "I" for inner, the data concerning fang positions may be analyzed in tabular form, the right side being indicated by the right-hand column in the two asymmetrical groups, as follows:

Species	I-I	O-O	O-I	I-O
Naja naja	18	9	8	11
Naja melanoleuca	13	7	3	4
Naja nigricollis	12	5	4	2
Naja nivea	1	2	0	0
Naja haje	2	0	0	1
Totals	46	23	15	18

These data suggest that for the sample available there is a definite tendency for

cobras to possess functional fangs in symmetrical arrangement, with a significantly high proportion of the specimens examined having both inner sockets in use. However, total length, when considered in conjunction with these data, discloses the fact that many specimens in the "I-I" category are juveniles. Further analysis is indicated, and it is instructive to compare the figures recorded for various size groups. All cobras do not attain comparable sizes, *N. haje* and *N. melanoleuca* reaching maximums well in excess of 2000 mm., whereas other species probably do not attain this length. Therefore, it is reasonable to suspect that juveniles of different species are not of similar sizes at birth. Among the *Naja* tabulated, juveniles are represented in but three species, the minimum over-all lengths in these being *N. melanoleuca* 535 mm., *N. nigricollis* 305 mm. and *N. naja* 332 mm. Thus, while it is apparent that comparable sizes may not represent precisely comparable ages, for practical analysis data for various species of *Naja* may be combined and tabulated by size groups. For this purpose only 86 specimens may be used since, of the 102 cobras mentioned above, some were represented only by skeletal material or were otherwise unsuitable. Arbitrarily dividing these 86 specimens into four groups on the basis of over-all measurements and with the symbols used above, the following tabulation permits further analysis, with asymmetrical individuals combined in one column, regardless of right or left fang positions:

test, as Klauber (1941, p. 11) suggests for data of this sort. This test permits comparison of observed frequencies with the theoretical frequencies that would be met if no synchronism of fang replacement mechanism were involved. Employing this test (with Yates' "correction for continuity") we find that P is about 0.004 for Group I, and 0.009 for Group II, but for Group III P is about 0.32 and for Group IV, 0.28. In other words, the presence of synchronism of the fang replacement mechanisms in left and right maxillae is indicated for the two smaller size groups. But for Group III the odds are about 32 out of 100 or only about 3 to 1 that synchronism is present, while in Group IV, the chances are 28 out of 100, and such figures are usually considered to be without significance.

Inasmuch as the four groups are drawn from a non-homogeneous sample, comprised chiefly of *N. naja*, *N. melanoleuca* and *N. nigricollis* but with two other species represented, the results are not so adequate as they might be had a single large series of one species from one locality been available.

Nevertheless, the sample indicates that cobras of the smaller size groups tend to have functional fangs in symmetrical arrangement. But as cobras increase in size, and inferentially also in age, synchronism of the fang replacement mechanisms in the right and left maxillae is gradually lost. It is doubtful whether the arrangement of fangs in adult cobras is not purely a matter

	Groups	I-I	O-O	I-O	Percentage Symmetrical	Percentage Asymmetrical
I.	300– 599 mm.	10	5	2	88	12
II.	600– 899 mm.	10	7	4	81	19
III.	900–1199 mm.	9	2	6	65	35
IV.	1200–2399 mm.	12	7	12	61	39

Tabulation of this sample in terms of percentages indicates a definite but not entirely regular trend toward symmetry in the smaller Groups I and II, but questionable symmetry in Groups III and IV. The significance of the differences in symmetry in the four groups can satisfactorily be ascertained by means of a chi-square

of chance, as it undoubtedly is in adult rattlesnakes. Klauber (1939, p. 7) reports that "of 210 specimens [*Crotalus*] 111 had an asymmetrical arrangement, with one inside and one outside socket in use. In the other 99 cases the functional fangs were either both in the outside, or both in the inside positions, there being 52 with both

outsides functional, and 47 with both insides."

Because the use of the fangs in rattlesnakes involves a rapid stabbing action, the strike, followed by biting, while cobras normally engage their fangs by means of a biting or chewing action not preceded by any rapid stabbing motion, it is possible that synchronism of the fang replacement mechanisms is retained for a somewhat longer period in cobras. It is impossible to say whether this is actually the case, however, and two assumptions would be involved: (1) that rattlesnakes, because of their more strongly recurved fangs and their rapid strike, more frequently break or injure their fangs, and (2) that this injury or breakage affects the mechanism of fang replacement. Thus, while the actual factors involved in the gradual loss of synchronism in tooth replacement are not known, it may be speculated: (1) that there is an inherent tendency for the fangs on the right or the left side to be replaced more rapidly than on the other, or (2) that injury or breakage of a functional fang in the normal use of it may either retard or accelerate its replacement. Either of these phenomena would result in loss of synchronism in the paired replacement mechanisms.

It was noted above that the majority of very small cobras had both fangs in the inner position. This suggests that juveniles may emerge from the egg with their functional fangs so arranged. Unfortunately no adequate series of cobras recently emerged from the egg has been available to determine this. Rattlesnakes differ from *Naja* in being ovoviviparous, as well as in having movable maxillae, but since the fang replacement mechanism is obviously so similar, I have sought information concerning juveniles in this genus, in order to determine the validity of the assumption that the embryo has fangs in a symmetrical arrangement. For this purpose I have utilized two series of *Crotalus basiliscus*, one consisting of twenty-four specimens, possibly of a single litter, obtained by Mr. J. H. Batty in Escuinapa, Sinaloa, and a second consisting of twelve specimens born in the Staten Island Zoo-

logical Garden. All these specimens possess only the terminal rattle or button and can, therefore, be identified as juveniles of somewhat comparable age. Those born in the zoological garden were only a few days old when preserved.

In preserved specimens it is a simple matter to determine which fang is ankylosed in the socket by first removing the investing tissue and then lifting each fang with a dissecting needle; the unattached fang is easily lifted without moving the maxillary bone. Of the twenty-four specimens in the Sinaloan series, twenty-one had the inner fang in each socket firmly ankylosed, while three were asymmetrical. Of the twelve specimens born in captivity, all had only the inner fangs ankylosed. The outer fangs were present in all cases and developed as far as and including the entrance lumen (see description of cobra fangs above, or of rattlesnake fangs, Klauber, 1939). There was marked difference in size, however, in entrance-lumen-to-tip measurements, those in position in front of, but not attached to, the outer sockets being about 38 per cent longer than the inner, ankylosed fangs, which approximated 3 mm. in length. In the three cases where the outer fang was ankylosed on one side, the larger fang, therefore, was functional ahead of the smaller one, indicating that ankylosis of this fang was abnormal. At least it is a reasonable assumption that the longer first reserve fang (normally that in the outer position) allows for considerable growth of the snake before that fang is anchored and becomes functional. It also follows that abnormal ankylosis of one outer fang of a juvenile *C. basiliscus*, resulting in asymmetrical positions at birth, provides the snakes with one long fang and one short fang, possibly a severe handicap that might interfere with the serpent's survival.

For additional information bearing on the question, two embryonic *Crotalus horridus* were dissected. Neither inner nor outer fang was ankylosed or hardened in these specimens, but it was apparent in all four maxillae that the inner fang in each maxilla was more advanced in position than the outer. Extending the investigation to include the Viperidae, twenty-five

juvenile *Bitis lachesis* (*arietans* auct.) were examined. These specimens were born in the New York Zoological Garden; most of them were kept alive for a period of approximately six weeks; some died before the end of the period, and a few (actual number not recorded) were preserved at birth. Of this series, nineteen had both functional fangs in the outer sockets, four had them in the inner sockets, and only two had functional fangs in the inner and outer sockets. It may be postulated that the majority of these specimens, with six exceptions, had survived for a sufficiently long period to have undergone one fang replacement.

While there are evidently abnormalities, all information derived from several species, including elapids, crotalids and viperids, points to a symmetrical arrangement of the fangs at the time of birth, with both of them in the inner sockets. Since paired elements or organs of vertebrates are normally symmetrical at birth, even though asymmetry may be normal later (in the flounder among fishes, or the male narwhal among mammals, for examples), it is not astonishing to find snakes conforming to this rule.

Returning to the discussion of cobra maxillae, it is apparent that the inner socket is located somewhat anterior to the outer socket, but when two fangs are almost equally ankylosed in adjacent sockets the tips of the two fangs tend to extend a similar distance. (This is not shown with proper precision in some of the drawings of skulls.) Still, entrance-lumen-to-tip measurements of fangs indicate similar dimensions for those completed to the upper lumen in any adult snake, and therefore the difference in position of sockets must be compensated for, in the pedestal portion of the fang. Also the point of the fang of the outer socket is directed slightly inward, while that of the fang in the inner socket is swung outward, so that despite the thickness of their respective pedestals and the narrow partition of bone separating the two sockets, the points of the fangs tend to converge when two fangs are approximately equally well anchored. Thus the puncture points of fangs in right and left

maxillae of an individual snake are not spaced appreciably farther apart, regardless of whether the functional fangs are both in the inner or outer maxillary sockets.

A sufficient number of maxillae will, of course, show fangs in all stages of ankylosis. It is apparent that after one fang has become ankylosed in a socket, resorption of the bone surrounding the pedestal takes place in the alternate socket. During the period when both fangs are firmly ankylosed, this condition being quite exceptional, it can be determined which fang is about to be shed only by examining the reserve fangs. Obviously the fang having the most fully developed reserve fang behind it will be the first to be shed.

It may be noted that, on the whole, the mechanism of fang replacement in cobras is essentially identical with that described for *Vipera* by Tomes (1876) and by Klauber (1939) for *Crotalus*, although Klauber found seven fangs, one functional and six developing, in a single maxilla, whereas in *Naja* only six and rarely seven can be demonstrated. It might be suspected that the number of reserve fangs is correlated with relative fang length. However, that this is not the case may be seen by reference to another large elapid, *Pseudohaje* (Figs. 39–41). This genus is related to *Naja*, but a specimen of *P. goldii*, 2175 mm. over-all, slightly larger than the *N. melanoleuca* described above, had fangs but 3.6 mm. in length, and seven reserve fangs, including inner and outer series, were easily dissected from other specimens. Seven reserve fangs have also been found in *Hamadryas*, while *Hemachatus* possesses the same number as *Naja*, perhaps indicating closer relationships.

An incidental observation indicates that the whole mechanism of fang replacement can be destroyed or extirpated. Some specimens examined, those apparently purchased from native dealers in India, lack fangs. Dissections show both sockets of individual maxillae to be vacant and partly filled with abnormal deposits of bone, with no traces of any reserve fangs in the investing tissue.

The amount of time a functional fang remains in place before it is shed is not

known.   Fangs of rattlesnakes have been reported (Wiley, 1929, p. 9) to be shed "on an average of every twenty days," but Klauber (1939, p. 13) questions the value of observations made on captive specimens. Wall (1921, p. 495) makes the doubtful

ber's belief that such observations on captive specimens are of limited value, and the "drawing" or forcible removal of a fang would provide no satisfactory data unless it were known when the fang had become fixed on the socket; even then
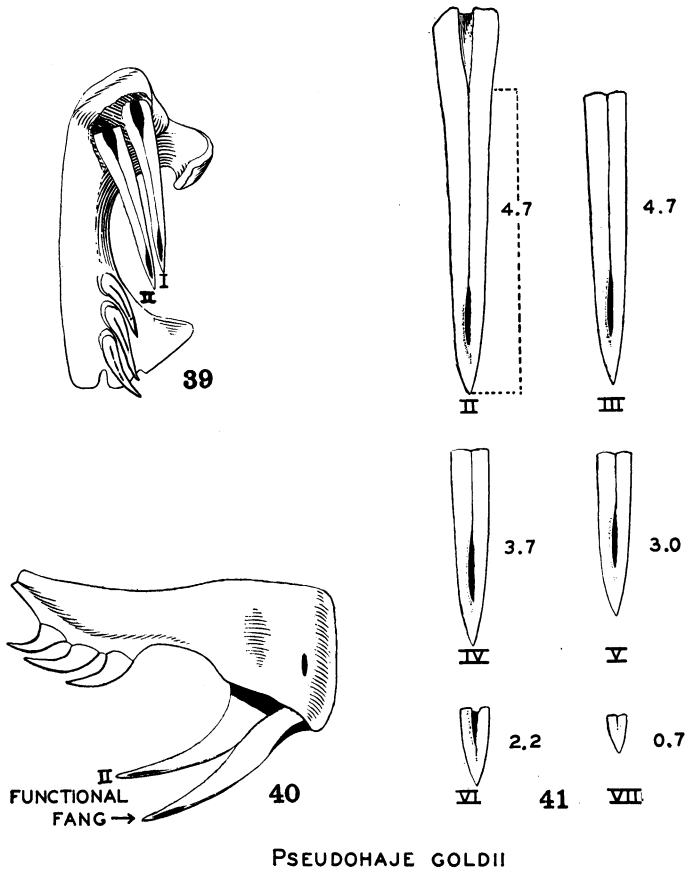
PSEUDOHAJE GOLDII

Figs. 39–41.   Ventral and lateral views of the right maxilla (× 5) of *Pseudohaje goldii*, and anterior view of the fangs of the replacement series.   Roman numerals indicate the order in which the fangs would become functional, No. I representing the functional fang and No. II the first fang in the replacement series.   The position of the first replacement fang is indicated, and figures to the right indicate measurements in millimeters of the respective fangs from a specimen 2365 mm. in total length.

statement concerning *Naja naja* that "there are usually two fully operative fangs in each maxilla, but these are shed singly at intervals, and from Fayer's experiments eighteen days was the shortest period that elapsed between drawing them and the fixation of a new one."   I concur in Klau-

forcible removal, in all probability, would inhibit normal replacement.   Also "two fully operative fangs in each maxilla" are certainly the exception rather than the rule. Wiley's statement, too, is ambiguous as it is not clear whether fangs are shed from one maxilla (with two sockets) every

twenty days, or from a single socket. In fact, she may have meant that rattlesnakes shed a fang from any one of four sockets (two in each maxilla) at average intervals of twenty days.

The most serious problem remaining concerns the mechanism whereby the communication of the duct from the venom gland shifts from the entrance lumen of one fang to that of another as a new fang comes into place, and for a time simultaneously carries venom to both fangs. In dissections of elapids, it is impossible to demonstrate direct connections of the duct to the upper lumen in the fang. Rather the duct terminates in a cavity surrounded by muscular tissue and, by inference, it may be assumed that an anatomical arrangement similar to that which West (1895, p. 821) describes for a hydrophiid proteroglyph is present in elapids (and probably in crotalids and viperids as well).

West points out that a fold partitions the basal portions of the two fangs so that the venom passes to each tooth by a separate route. West was obviously unaware of the alternate functioning of each fang, however, although his fig. 14 of Pl. XLVI points to the possibility that the "two large cushions of muscular tissue" which project into the terminal cavity of the duct, one in front of each fang, operate to close one or the other of the passages leading to the fangs. His figure may indicate that one of the fangs in the maxilla sectioned was connected with the cavity, while the other was not. Had he realized that usually only one fang at a time conducts venom, he might have interpreted his figure to explain the anatomical mechanism which permits use of the fangs alternately, or of both of them temporarily during the interval which precedes the shedding of one.

Since West's work appears to have been generally neglected, although his plates and text provide a useful basis for further research dealing with the problem in solenoglyphs as well as proteroglyphs, his description of the duct and its terminal connections may be quoted in full.

"The *poison-duct* is of rather large calibre, and small tubules open into it along its whole course from the gland to the teeth,

though they become much fewer in number anteriorly. As the duct nears the poison-fangs it becomes sinuous, bends suddenly inwards at the anterior extremity of the maxilla, and on reaching a point just anterior to the bases of the two grooved teeth it enlarges, enclosing a more or less considerable transverse vertical cavity. Into this cavity project two large cushions of muscular tissue, one in front of each tooth. The two cushions are precisely similar and quite distinct from each other, the vertical slit between them being the only communication between this cavity, enclosed by the enlarged termination of the poison-duct, and that enclosed by the folds which closely surround the teeth. The muscular tracts extend a short distance parallel to the teeth down the inner edge of the fold. The fibres are arranged in such a manner that contraction would lessen the cavity at the termination of the duct, widen the passage between the two muscular cushions, and also bring the folds into closer approximation with the outer faces of the teeth. This ensures a free passage for the poisonous secretion from the duct to the bases of the grooved teeth. There is also a fold partitioning off the two grooved teeth from each other, and the secretion passes down one side to one tooth and down the other side to the other."

Tomes (1914, p. 318) reports that in elapids venom is sometimes spilled down the outer edges of the tooth instead of being expelled through the venom canal, and he explains this as being due to the nature of the attachment of the venom duct. However, loss of venom, except through the fang, is certainly the exception rather than the rule. His report must have been based upon an abnormal specimen, quite probably one of commercial origin which may have been defanged in such a manner that the first replacement fang failed to make a normal connection with the duct.

REPLACEMENT PATTERNS OF FANGS AND TEETH

Whatever problems remain to be solved as far as the relationships of venom ducts and fangs are concerned, and regardless of minor differences in the number of replace-

ment teeth, or possible differences in the interval between fang shedding, it is evident that the fundamental mechanism of fang replacement is the same in the Viperidae, Crotalidae and Elapidae. In fact, it can be demonstrated that a similar mechanism of tooth replacement is present in the Colubridae and Boidae. Furthermore, inferences that may be drawn with the data now assembled suggest that the process of fang replacement in the proteroglypha and solenoglypha is essentially the same in all platynotid reptiles, and it probably represents a pattern that had its origin in a pre-Cretaceous lizard ancestor (see Figs. 42–45).

In the course of work leading to a statistical study of teeth in a colubrid genus (unpublished), I have had occasion to examine nearly 1000 maxillae, and an additional 500 from various other snake genera have been examined in connection with other taxonomic problems. When maxillae were removed and adhering soft tissue scraped from the bone, it was noted that not infrequently teeth were present only in alternate sockets, the others having been removed with the tissue. Moreover, only with the greatest care was it possible to remove a bone with all teeth in place, and even then it was obvious that alternate teeth were incompletely ankylosed. Perusal of several additional skulls cleaned by dermestid beetle larvae disclosed a similar condition in serpents of several families, and precisely the same observation can be made on snakes cleared and stained. The significance of this observation became more fully apparent when developing teeth in the replacement series were examined.

The reserve maxillary and dentary teeth, like the fangs, are embedded in connective tissue investing the inner side of the maxilla and dentary as both Owen (1845) and Tomes (1875) realized. The latter prepared sections of the jaw of a "common snake" to show the position of the replacement series, but unfortunately, individual sections do not supply data that are readily interpreted unless sections through contiguous sockets are compared. Thus Tomes overlooked an essential phenomenon in connection with replacement mech-

anisms. If maxillae are removed carefully, it is possible to leave the replacement teeth embedded in the thin layer of connective tissue investing them. When the wet tissue of an alcoholic specimen dries upon exposure to the air, the replacement series below each socket are plainly seen (see Fig. 37), and with a dissecting microscope it can be observed that the series below alternate sockets are composed of alternating numbers of teeth, commonly three below the even-numbered teeth, for example, and four below the odd-numbered, or *vice versa*. Furthermore, the teeth in any two contiguous sockets are staggered, in respect to both size and position. The situation is illustrated in the section of a maxilla of an African colubrid, *Gastropyxis smaragdina* (Fig. 42), a species with sockets spaced far enough apart so that the teeth in the reserve series do not overlap to the extent observed in most snakes. Similar phenomena, however, can be demonstrated with the maxilla or mandible from any colubrid. The specimen illustrated was removed from the preserved specimen with all teeth in place in the section of the bone shown, but the teeth, having only three reserves following them, are obviously of recent occupancy in their sockets and are incompletely ankylosed. It should be noted in referring to Fig. 42 that the replacement series lie posterior to the socket which they eventually occupy. The tooth germ, as it progresses in the soft tissue on the inner side of the maxilla from being the youngest in the series to being the oldest, moves downward, forward and finally outward and upward into the socket vacated by its predecessor.

The identical arrangement is present in the Boidae and represents the normal method of solid tooth replacement on the maxilla of such elapids as *Denisonia melanura*, which possess five solid teeth at the posterior extremity of the bone. The posterior portion of the maxilla of this species is depicted in Fig. 43 where it may be noted that the even-numbered teeth in this instance are firmly ankylosed, whereas the odd-numbered teeth are in place but not firmly anchored. However, it can be seen that the anterior tooth, No. 1, is in a more
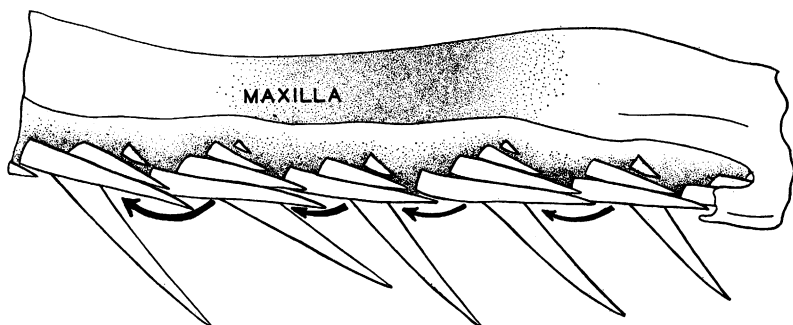
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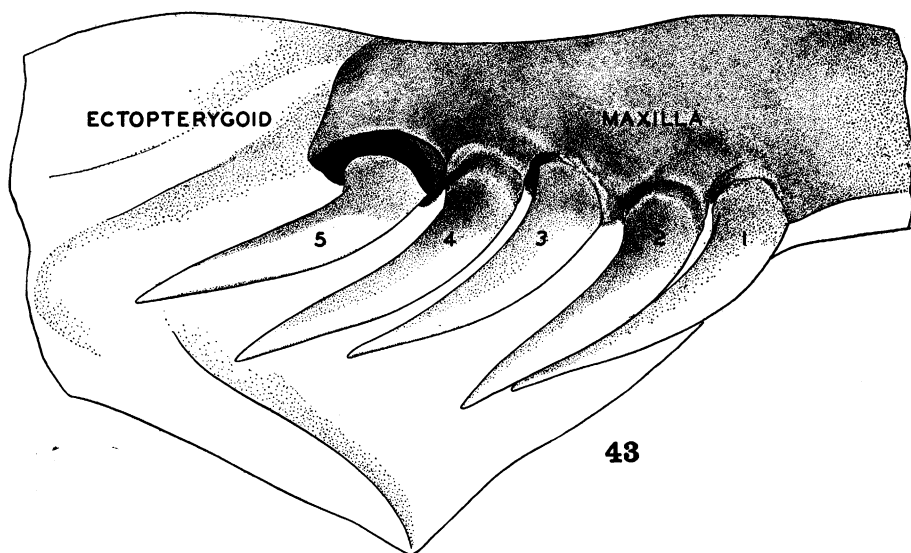
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Fig. 42.   Inner side of middle portion of the right maxilla (× 20) of a colubrid (*Gastropyxis smaragdina*, A.M.N.H. No. 45925), showing the location and number of replacement teeth above each socket.   Note alternating numbers of replacement teeth and their position in the investing soft tissue posterior to the sockets which they would eventually occupy.   Arrows indicate the direction followed by a maturing tooth as it moves into position in a vacated socket.   In this section of the jaw the odd-numbered teeth are completely ankylosed, while the even-numbered teeth (those having three replacements behind them) have recently moved into position in the socket and are not yet solidly anchored.

Fig. 43.   Posterior portion of the right maxilla (× 20) and anterior end of the ectopterygoid, removed from an elapid (*Denisonia melanura*, A.M.N.H. No. 44981).   Lateral view from outer side, showing teeth Nos. 2 and 4 ankylosed in their respective sockets, and teeth Nos. 1, 3 and 5 in progressive stages of ankylosis.   Black areas indicate absence of bone.

advanced stage of ankylosis than No. 3, while the latter is further advanced than No. 5. In this case it seems clear that replacement occurs from front to back, and it may be inferred that the teeth were shed in the order, 1, 3, 5. With information provided by the study of additional maxillae it can be assumed that when Nos. 1, 3 and 5 had become firmly ankylosed, Nos. 2 and 4 would have been shed, in that order. It is of interest to note here that Parrington (1936, p. 110) found evidence of alternate tooth replacement in Mosasaurs, starting "at the back of the jaw in the odd-numbered teeth."

It is apparent, then, that teeth in any given series are shed in two successions, one involving the even-numbered teeth, and the other the odd-numbered; one group is completely replaced, in smaller series at least, before shedding is initiated in the alternate group. Thus, if the teeth in any given series are reduced to two, as in the case of the specialized teeth (or fangs) in the anterior portion of the maxilla of solenoglyphs and proteroglyphs, the mechanism resulting will permit alternate occupancy of paired sockets, precisely as demonstrated in cobras, rattlesnakes and vipers. However, series of teeth on a single bone, but separated by a diastema, are not replaced by coordinated mechanisms. In the specimen of *Denisonia*, for example, the outer fang was incompletely ankylosed, while the first tooth in the posterior series of solid teeth was in the same condition. It may be added that solid teeth in the replacement series lie roughly parallel to the bone above and behind their respective sockets, but the curvature at the anterior end of the maxilla in elapids and the spatial requirements of the enlarged fangs preclude a similar position for them. Thus, the fangs in the replacement series lie approximately perpendicular to the anterior curved portion of the bone to which they will eventually become attached, and parallel to the lateral posterior portion. The positions of the developing fangs and their attendant spatial requirements suggest a mechanical reason for the diastema posterior to the fangs, there being insufficient room for replacement series along the lateral inner surface of the maxillary bone. *Ultrocalamus*, which lacks a maxillary diastema, has relatively short fangs, the smallest in proportion to total length of any elapid examined.

Several details involved in the replacement of teeth in snakes remain to be investigated, but it can be pointed out at this time that teeth on the maxilla, palatine, pterygoid and dentary are replaced in nearly identical fashion, but that more developing teeth, totaling five or six, are commonly present in the reserve series above each alveolus of the palatine and pterygoid series than are present below those of the dentary and above those of the maxilla. Moreover, the replacement teeth of the dentary and maxilla are located on the inner side of the bone, whereas on the palatine and pterygoid they are on the outer side.

In order to find out how widespread the pattern of tooth replacement described might be among reptiles, representatives of a few families of lizards have been examined. In many of them, the Iguanidae and Cordylidae, for example, replacement of teeth did not seem to be entirely regular, although a pattern involving successive shedding of every fourth or fifth tooth is indicated by the material on hand. With the Varanidae, and probably the Helodermatidae, however, a pattern similar to that in snakes is apparent in the skulls of three species available, alternate teeth being firmly ankylosed. Fortunately, the skull of a *Varanus komodoensis* in the American Museum collection had been prepared in such a manner that the replacement teeth of one dentary were still adhering to the bone. This specimen, a section of which is depicted in Fig. 44b, shows clearly that replacement series are staggered in development just as they are in snakes. The maxilla of the same specimen is depicted (Fig. 44a) to show the ankylosis of alternate subpleurodont teeth, the replacement series having been removed.

Patterns of tooth replacement apparently represent a fertile field for investigation, particularly since they may aid in elucidating some of the problems of phylogenies. Pending further investigations,
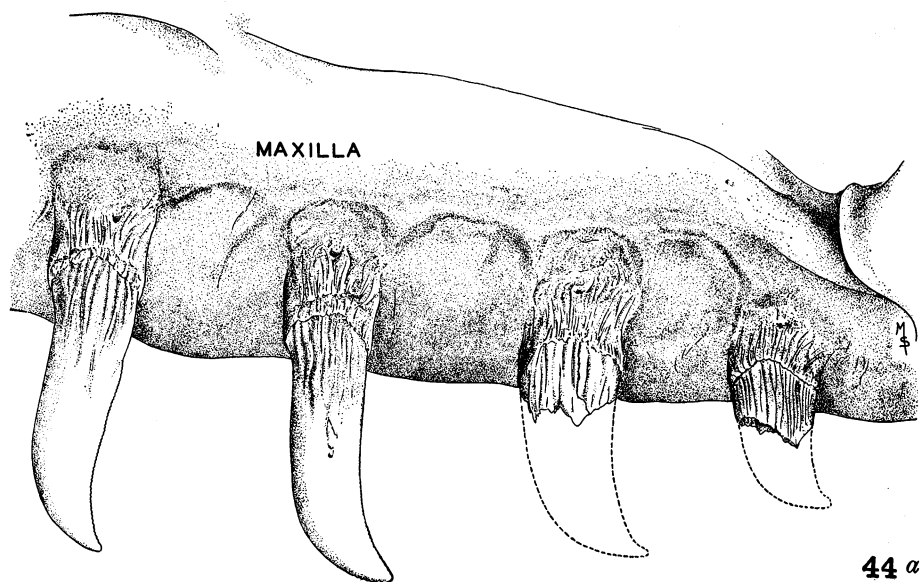
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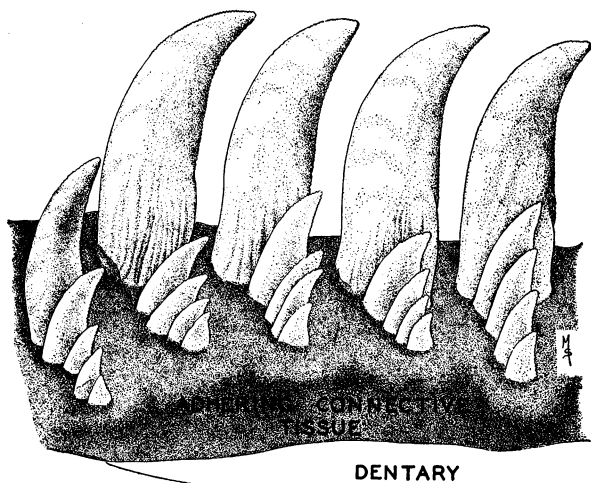
44 *b*

Fig. 44.   Sections of the right maxilla and dentary of an adult specimen of *Varanus komodoensis* (A.M.N.H. No. 37912) as viewed from inner sides.   The maxilla (a) shows alternate sub-pleurodont teeth ankylosed, and intervening "sockets" vacant, with replacement teeth removed.   The dentary (b) was prepared in such a manner that many of the replacement teeth are left embedded in the dry connective tissue adhering to the bone.   The anterior tooth, on the left side of the figure in the section of the jaw depicted, is approaching the functional position prior to ankylosis.   Note alternating sizes of first replacement teeth, indicating alternate use of contiguous "sockets."

preferably extended to include fossils, the similarity of replacement patterns in snakes and varanids suggests confirmation of Camp's (1923, p. 418) conclusion that the "Serpents are believed to have arisen from anguimorphid lizards," closest to the platynotid stock of which *Varanus* is the only recent saurian representative (see Camp's chart, p. 333). The material at hand, however, does not indicate the presence of similar replacement patterns in all Anguimorpha.

The recent papers by Cawston (1941a, 1941b and 1942) seem to indicate only that he has not examined any extensive series of snake skulls. Reserve fangs as well as teeth may be found in all stages of growth and in all intermediate positions between their earliest appearance and their final position ankylosed in the socket. Yet Cawston (1941a, p. 224) states, "If the reserve fangs of Proteroglypha were for replacement there should be evidence of possible replacement of the fangs of opisthoglypha, but these latter fangs appear to be irreplaceable." In the same paper, however, he makes the statement that "In the Boomslangs [the opisthoglyph, *Dispholidus*] it is usual to find two of these fangs anchylosed to the cartilage [*sic*] and the third less firmly attached," showing that

precisely the same pattern of tooth replacement reported above for other colubrids is present in opisthoglyphs. Fangs of opisthoglyphs are unquestionably replaced.

Elsewhere (1940, p. 46) I have pointed out that in opisthoglyphs alternate occupancy of paired fang sockets is the rule, and it seems obvious that whether a rear-fanged snake has two, three or four fangs on the posterior portion of the maxilla, only alternate fangs will be ankylosed at one time, except during a brief transitional period between sheddings when all of them are anchored. Thus, the fact that all opisthoglyphs have a minimum of two fang sockets indicates quite clearly that alternate use of functional fangs is provided for. It is furthermore significant that no snake known has fang sockets reduced to less than a pair.

Apparently because he could not understand how a replacement fang might become attached to the venom duct, Cawston comes to the ludicrous conclusion that unankylosed fangs, because they are not attached to the bone, have no known function! His other ideas, insofar as I have been able to interpret them, appear to be based upon nothing approaching scientific evidence; it would be idle to discuss them at greater length.

FANG PROPORTIONS

In order to undertake satisfactory comparisons of proportionate fang lengths, several factors must be taken into account. First, it must be determined whether sexual dimorphism is involved in fang lengths, and second, the amount of individual variation must be ascertained. Individual variation in this instance is complicated by the fact that two body parts rarely maintain a fixed ratio throughout the ontogeny of an animal, and if we are to compare fang lengths with other parts, or with the total length of a snake, it is preferable to calculate regression coefficients. Unfortunately this requires that a considerable number of measurements be available for each species, and that individuals of many sizes and ages be represented. The material available for cobras does not entirely

fulfill these requirements. However, some notion of the type of the regression line involved and the extent and nature of the dispersion can be indicated roughly by means of a scatter diagram. This procedure has been followed in the case of three species represented by samples exceeding seventeen specimens.

It can usually be demonstrated among vertebrates that the size of the head is proportionally larger in juveniles and smaller in adults. There are no precise data available for cobras or other elapids in this respect, and in the case of some of the smaller species, particularly subterrestrial forms, it is extremely difficult to measure the length of the head with accuracy owing to the absence of any sharp line of demarcation between the head and

the neck. In this study of elapid fangs, therefore, as a matter of convenience, I have used the total length as the datum for comparison with fang length. Since Klauber (1939) provides total length and fang length data for rattlers and some other pit-vipers, this procedure affords ready comparison of ratios for the Crotalidae and Elapidae.

fangs are broken at the tip, and in such cases the first reserve fang can be dissected out and measured, since it is always completed on one side, at least as far as the entrance lumen. Only slight differences in length between right and left functional fangs were noted in any specimen with both fangs complete, and more often than not the differences were less than 0.1 mm.;

BODY-FANG LENGTH RELATIONSHIP
18 CHINESE NAJA NAJA
MALES ● FEMALES, X

FANG LENGTH IN MM.

LENGTH OF BODY IN METERS
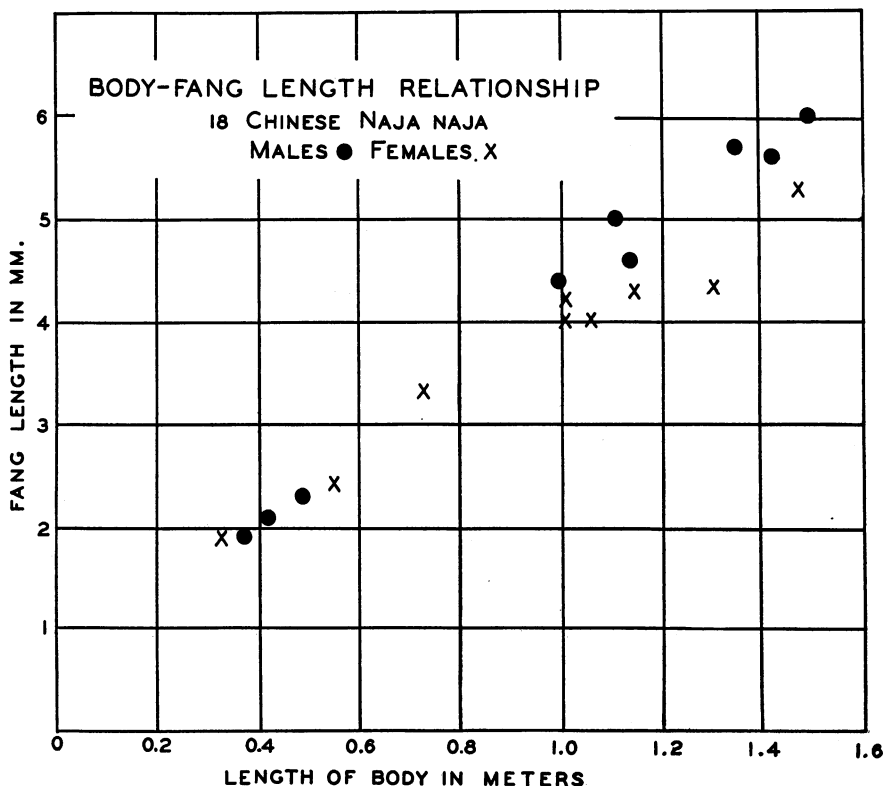
45

Fig. 45. Scatter diagram showing correlation of fang size with total length in Chinese *Naja naja*, with some indication that adult males have relatively slightly larger fangs than adult females.

I have likewise followed Klauber (*ibid.*, pp. 20–21) in the method of fang measurement, utilizing the straight line distance from the lower end of the entrance lumen to the tip of the fang as a criterion of length. Measurements were made with Vernier calipers under a dissecting microscope with a magnification of 30 diameters. This permits accuracy to 0.1 mm. In cobras it often happens that one or both

only occasionally was the difference as great as 0.2 mm. Similarly, with the method of measurement used, the length of the first reserve fang was approximately the same as either of the functional fangs. In recording data, therefore, sufficient accuracy was provided by measuring either the first reserve, or any functional fang that had not been broken.

The results of this investigation are

Fig. 46. Scatter diagram illustrating relationships of fang length and total length in two African species of *Naja*, with a spitting cobra (*N. nigricollis*) compared with a non-spitter (*N. melanoleuca*).

partly summarized in two scatter diagrams, Figs. 45 and 46, in which it will be noted that some evidence of sexual dimorphism is indicated for *Naja naja*. On the basis of the small sample comprised only of eighteen Chinese cobras, the adult males tend to have slightly larger fangs than adult females, whereas the juveniles have fangs of similar proportions regardless of sex. On the basis of such a small sample, however, sexual dimorphism in proportionate fang lengths cannot be considered proved.

trated. Aside from possible taxonomic implications, therefore, it has been of interest to calculate ratios of total body length to fang length. While these are not presented in Table III with any intention of proving the existence of differences between various species of *Naja*, it seems probable that some differences could conclusively be demonstrated with more extensive series. Simple mean body-fang ratios as well as a scatter diagram (Fig. 46) produce rather strong evidence that *Naja*

TABLE III.—FANG PROPORTIONS IN COBRAS AND OTHER ELAPIDS
(ALL MEASUREMENTS IN MILLIMETERS)

Species	Number of Specimens	Body Length Range	Fang Length Range	Mean Body	Mean Fang	Mean B/F
Naja naja (China)	18	332–1490	1.9–6.0	966	4.0	244
Naja naja (Komodo Island)	3	885–1055	3.0–3.4	955	3.3	292
Naja naja (Siam)	3	375–1240	1.9–4.8	930	3.1	239
Naja naja (northern India)	2	1037–1195	4.3–5.3	1116	4.8	232
Naja haje	4	1350–1580	4.6–5.3	1435	4.9	292
Naja melanoleuca	27	335–2172	1.9–6.6	946	3.1	309
Naja nivea	1	—	—	1530	4.6	310
Naja nigricollis	22	305–1535	1.4–6.0	1080	4.4	250
Hamadryas hannah	1	—	—	3055	8.0	381
Hemachatus haemachatus	9	730–1140	3.1–4.2	933	3.6	257
Pseudohaje nigra	2	1810–1889	3.2–3.4	1850	3.3	560
Pseudohaje goldii	4	660–2365	1.5–4.8	1520	2.8	523
Boulengerina annulata	4	865–1910	3.3–5.1	1641	4.6	361
Boulengerina christyi	1	—	—	474	1.6	296
Elapsoidea sundevallii	10	265–475	0.8–1.4	362	1.0	355
Aspidelaps lubricus	2	500–645	1.5–2.5	573	2.0	286
Dendroaspis jamesoni	3	1858–2490	6.4–8.0	2166	7.3	292
Dendroaspis viridis	3	2000–2125	6.5–7.2	2045	6.7	306
Dendroaspis angusticeps	3	1120–2260	3.0–6.5	1967	5.4	365
Bungarus multifasciatus	1	—	—	1110	2.5	444
Maticora bivirgatus	1	—	—	1060	2.6	408
Ultrocalamus preusii	2	465–560	0.6–0.8	512	0.7	732
Apistocalamus pratti	1	—	—	450	0.9	500
Toxicocalamus stanleyanus	1	—	—	532	0.9	591
Elaps lacteus	3	415–465	1.2–1.3	442	1.3	349
Micruroides euryxanthus	4	401–456	0.7–1.0	419	0.8	510
Micrurus fulvius	3	700–817	2.1–2.5	747	2.3	324
Leptomicrurus narducci	3	473–660	1.1–1.4	576	1.3	431

Even less conclusive evidence is indicated for *Naja nigricollis*, while in the case of *Naja melanoleuca* there is no indication whatever of any difference between the sexes, and males and females are not plotted by separate symbols.

For practical purposes it is of interest to know something of the lengths of fangs in various species, since occasionally a physician in treating a case of snake bite may be aided by having some knowledge of the depth to which a fang has pene-

nigricollis possesses relatively longer fangs than *Naja melanoleuca*, for instance, and since *nigricollis* has fangs adapted for "spitting," the additional length might conceivably represent a modification correlated with its more obvious morphological adaptations (see discussion hereinafter). Nevertheless the meager data provided in Table III suggest that while both *N. nigricollis* and *Hemachatus*, the two African "spitters," have longer fangs in proportion to their total lengths than any other Afri-
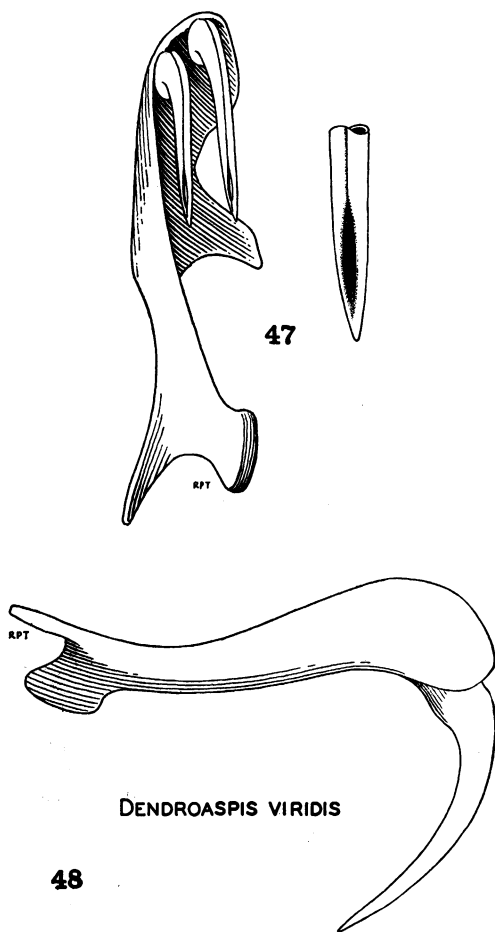
DENDROASPIS VIRIDIS

Fig. 47. Ventral view of the right maxilla (× 5) and anterior view of the distal portion of the fang (× 10) of the green mamba, *Dendroaspis viridis*.

Fig. 48. Lateral view of the right maxilla (× 5) of the green mamba, *Dendroaspis viridis*.

47–48) proportionately thinner and somewhat shorter than those of the average cobra. The fangs of all mambas are relatively slender and situated farther forward in the head than those of any other elapid, while the attenuated body and head of these snakes produce the illusion that mambas have large fangs. The adult king cobra (*Hamadryas*) possesses fangs that are relatively shorter than those of any *Naja* examined with the exception of a few specimens of *melanoleuca*. Snakes of the genus *Pseudohaje* also possess fangs that are much shorter than those of other cobras, in proportion to the total length of the snake, offering confirmation for the belief that these snakes do not belong in the genus *Naja*.

A few additional comparisons of cobras with other members of the family Elapidae indicate on the other hand that, as a whole, cobras, mambas and their nearest allies tend to have relatively longer fangs than the smaller representatives of the family. Burrowing forms, such as *Micruroides* and *Leptomicrurus* of the Western Hemisphere, and *Ultrocalamus*, *Toxicocalamus* and *Apistocalamus*, three closely related genera of New Guinea, probably have the smallest fangs of any front-fanged genera, and it is doubtful whether any of these is capable of inflicting a dangerous bite. However, four specimens of *fulvius*, the single species of *Micrurus* examined, possessed fangs less than 3 mm. in length, and serious results from the bite of this elapid have been reported.

Because many of the smaller elapids are secretive or burrowing in habits it might be argued that small fangs result from the small heads and attenuated bodies, which are often, but not necessarily, associated with a fossorial existence (*Ultrocalamus* may have as many as 361 vertebrae, with a body diameter contained in the total length 113 times). There may be some sort of association of short fangs with truly burrowing habits in elapids and it is of interest in this connection to report a few measurements of fangs in burrowing vipers.

The only fossorial viperine snakes known are all African, and all belong to the genus

can cobras, almost the opposite condition is represented among the various populations of Asiatic *Naja naja* for which there are data. Cobras from northern India, not adapted for spitting, on the basis of these small samples have longer fangs than other populations partly or wholly adapted in fang characters to eject venom forward.

One of the more striking facts brought out in Table III is that mambas, snakes of the genus *Dendroaspis*, which are notably swift and aggressive, possess fangs (Figs.

Atractaspis. These snakes bear no outward resemblance to other members of the family Viperidae, all having narrow heads and relatively slender bodies; not unlike *Ultrocalamus* they may have as many as 376 vertebrae. Some are equipped with cutting edges on the rostral, presumably as an adaptation for a burrowing existence, although they are reported to come to the surface after rains. Despite their specialized habits and habitus, however, these snakes have movable maxillary bones which enable them to rotate the fangs to a horizontal position when the mouth is closed. The fangs of *Atractaspis* have been described as "enormously developed" and "exceedingly long." Just as in the case of the mambas, the relatively narrow head for a viper seems to have given the illusion of great fang size, although actual measurements do not bear out this conclusion. Three specimens of *A. irregularis* from the Belgian Congo and Liberia varied in length from 505 mm. to 550 mm. with fang lengths from 3.6 mm. to 4.1 mm. Fang lengths are contained in total lengths 124 to 140 times. An even more elongate species than the latter, *A. heterochilus*, is represented in American Museum collections by a specimen 830 mm. over all, nearly the maximum for the genus, and this specimen has fangs 6.3 mm. in length. The ratio of total length to fang length provides a figure of 132, comparable to those of *A. irregularis*. This is not a long fang in terms of comparison with total length and falls within the range reported by Klauber (1939, p. 45) for rattlesnakes, in which the fang length is contained in the body length from 80 to 165 times, averaging closer to 120.

Using the total length as the datum for comparison of fang lengths there is little doubt but that viperids of the genus *Bitis* exceed all other living snakes in relative fang length and probably in actual fang length as well. A series of ten puff adders, *Bitis lachesis* (*arietans* auct.), ranging in size from 743 mm. to 995 mm., had fangs 9.7 mm. to 14.3 mm. in length, with fang length contained in body length 60 to 83 times. In fang size, the heavy-bodied *Bitis gabonica*, or Gaboon viper of the

African Rain Forests, exceeds all others, a specimen 1300 mm. long having fangs of 29 mm., contained in the total length only 45 times. The skull shown in Pl. XLIX (fig. 2) has fangs 25 mm. long, and the stocky skeleton itself (Pl. L) measures 1380 mm., probably somewhat less than the total length of the snake in life. The fangs are relatively shorter than those of the 1300-mm. specimen. Pitman (1938, p. 70) reports a specimen of *B. gabonica* 6 feet (approximately 1830 mm.) in length, and another specimen 5 feet 8$^{1}/_{2}$ inches long which "had fangs nearly two inches in length." Using Klauber's method of fang measurement, which excludes the pedestal and represents straight-line distance, the body/fang ratio of 45 reported above applied to the specimen 1830 mm. long would indicate presence of fangs approximately 41 mm. long in such an individual. If the fang were measured along the curve, a 6-foot specimen of *B. gabonica* would, indeed, have a fang approximating 2 inches in length, but straight-line distance from the lower end of the discharge aperture to the point would be closer to 1$^{3}/_{4}$ inches.

The king cobra, *Hamadryas*, has been reported to reach a length slightly in excess of 18 feet, which unquestionably represents the maximum size attained by any venomous snake. Klauber (1939, p. 57) reports a specimen 3830 mm. long with fangs of 10.1 mm., comparing favorably with a specimen at hand which measures 3055 mm. over all, having fangs 8.0 mm. long. Calculations, therefore, would lead us to expect an 18-foot (5490-mm.) king cobra to have fangs only 15 mm. long, or roughly about a third as long as those of a Gaboon Viper 6 feet long.

The Viperidae and Crotalidae, as a result of their movable maxillae and their resulting ability to rotate their fangs to an inactive position, have been able to evolve fangs greatly exceeding in size those of the Elapidae. Among viperine snakes, the most primitive in many respects is *Causus*, or night adder, represented in Africa by four species. Snakes of this genus prove to have, in proportion to total length, the smallest fangs of any viper examined. Of twenty-one Angolan specimens of *C. rhom-*

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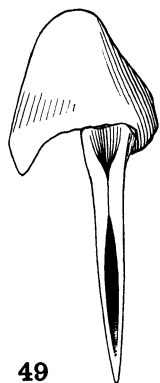
CAUSUS RHOMBEATUS

Fig. 49. Anterior view of the right maxilla (× 10) and functional fang of the African night adder, *Causus rhombeatus* (A.M.N.H. No. 62690). The comparatively crude fang of this viper is no longer in proportion to the total length of the snake than those of some elapids. The functional fang of the specimen depicted is ankylosed in the inner socket, the alternate socket being vacant.

beatus which ranged in size from 190 mm. to 590 mm., fangs ranged in size from 1.1 mm. to 2.6 mm., the ratios of total length to fang length ranging from 158 in juveniles to 245 in adults, the fangs of adults thus being no longer than those of Chinese *Naja naja*. The fang (Fig. 49) of these small vipers is relatively crude in comparison with those of other members of the family, including the putatively primitive *Azemiops* of southeastern Asia. An examination of the skull of *C. rhombeatus* indicates that there is no hinge action where the prefrontal engages the frontal, although the maxilla unquestionably can be rotated nearly as much as in any other viperid. *Causus* cannot, in any sense, be considered an annectant form intermediate between the Viperidae and Elapidae, and the ancestral stocks of these two families must have become completely differentiated early in the Tertiary.
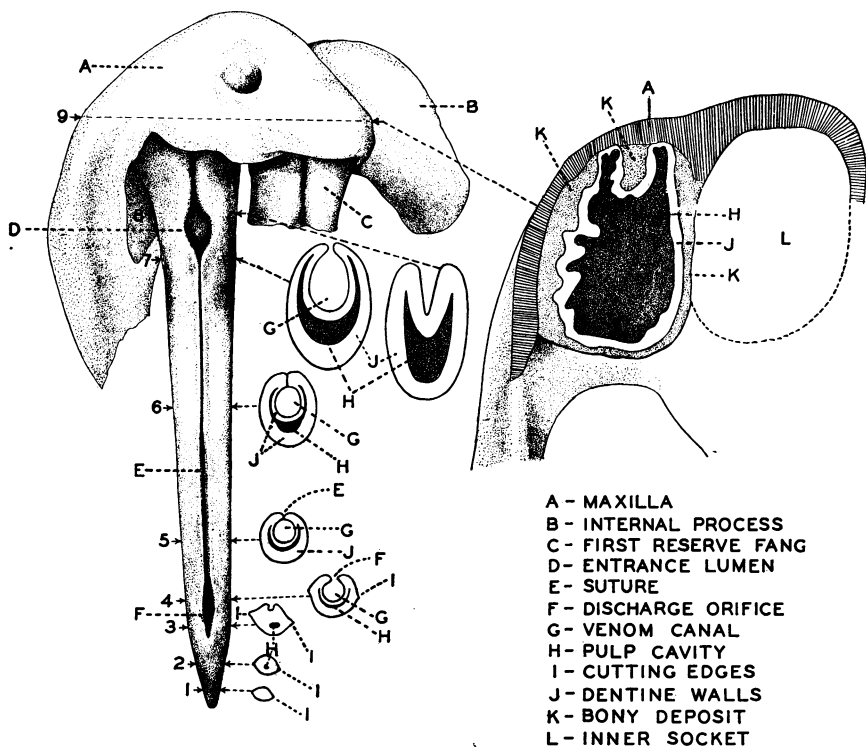
MORPHOLOGY OF COBRA FANGS

From an evolutionary viewpoint, the fangs of cobras represent teeth that have become modified in structure and specialized in function for the conduction of poison secretions. They may be described briefly as recurved, elongate-conical structures containing a tube with an entrance lumen at the base and a discharge orifice at the point, both apertures being located on the external surface of the curve. Such brief description omits many important details, as the presence of a suture on this external surface and the internal structure suggest that this tube, the venom canal, has arisen as an invagination of the external wall. However, it is obvious from the reserve series described above that this invagination does not occur during the ontogeny of the fang. Growth of the structure as a tube proceeds from the distal end to the base by the accretion of particles and terminates in the ankylosis of the fang in the socket, as mentioned above (Figs. 37–38). Therefore, it must be assumed that the venom canal has evolved through progressive modifications of solid teeth in ancestral elapids, and the presence

of the suture or weld in recent cobras must be interpreted in terms of phylogenetic implications.

For purposes of description, the fang, as viewed externally, may be divided arbitrarily into two parts: (1) the broad pedestal which includes the portion of the fang above the entrance lumen, and (2) the elongate portion which includes the entrance lumen, the venom canal and the discharge orifice (see Figs. 50 and 51). More detailed structure of the fang can be ascertained by an examination of longitudinal and cross sections produced by removal of the fang substance with a whetstone. By reference to Figs. 50 and 51, it may be seen that dentine walls separate the fang internally into (1) the pulp cavity and (2) the venom canal.

The pedestal is irregularly oval in cross section, with lateral walls that are corrugated on the sides where they engage the temporary bony substance deposited in the socket during ankylosis. Anteriorly, a groove-like continuation of the venom canal of the elongate portion extends onto the pedestal and is embedded in the bony

A - MAXILLA
B - INTERNAL PROCESS
C - FIRST RESERVE FANG
D - ENTRANCE LUMEN
E - SUTURE
F - DISCHARGE ORIFICE
G - VENOM CANAL
H - PULP CAVITY
I - CUTTING EDGES
J - DENTINE WALLS
K - BONY DEPOSIT
L - INNER SOCKET

50 ANTERIOR VIEW AND CROSS SECTIONS OF FANG

MAXILLA

SOLID TOOTH

PEDESTAL

BONY DEPOSIT

PULP CAVITY

DENTINE WALLS

ENTRANCE LUMEN

VENOM CANAL

DISCHARGE ORIFICE
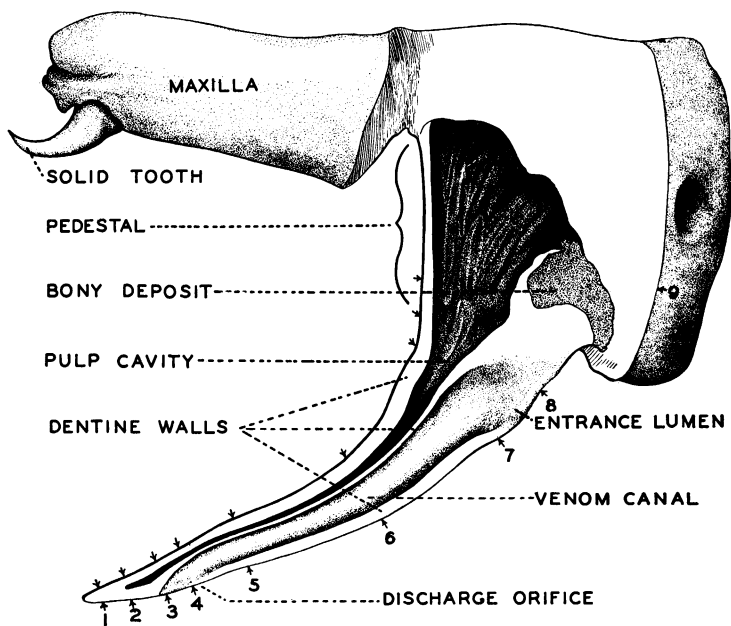
51 LONGITUDINAL SECTION OF FANG
CHINESE NAJA NAJA

Figs. 50–51. Longitudinal and cross sections, illustrating internal morphology of cobra fangs.
Numbers indicate levels of cross sections illustrated.

substance at the front of the socket, thus insuring firm attachment with the bone of the anterior portion of the maxilla. On the inner side of the pedestal the wall is striated and relatively thin, with little bony substance deposited on it. Thus the pedestal is engaged in the socket chiefly at the sides and front, with weaker attachment at the rear.

As can be seen in sections, the pedestal contains a large pulp cavity behind the invaginated continuation of the venom canal. The internal surface of the pedestal walls is striated, additional reinforcement being provided therefrom, and cross sections reveal the lateral and anterior walls to be thickest. That is, the walls most firmly attached to the bony substance of the socket are slightly thicker than the posterior wall (see Fig. 50). The pulp cavity extends from the interior of the socket through the pedestal and into the elongate portion of the fang, diminishing in width toward the distal end in longitudinal section (Fig. 51). It is roughly U-shaped in cross section, but the arms of the U become progressively less apparent distally. The pulp cavity, however, extends into the very point of the fang, becoming slightly enlarged distally to the discharge orifice of the venom canal.

Cross sections of the elongate portion of the fang show the venom canal to be a round tube that occupies a position within the arms of the U formed by the pulp cavity. The suture along the anterior surface of the fang is apparent in such sections, although union is complete, except where the walls diverge from the line of the suture to form the entrance lumen at the proximal end, and at the discharge orifice on the distal end. The walls of the venom canal are continuous with those of the outer wall, however, so that in effect the pulp cavity separates an inner tube from an outer tube. Where the pulp cavity is not apparent in cross sections just above the discharge orifice it can nevertheless be demonstrated as a plane of separation if the fang is split. Distally to the discharge orifice the remainder of the tapering pulp cavity is oval in cross section, and the walls of the venom canal fuse with the outer walls dis-

tally to the orifice. Thus the closed end of the outer tube extends slightly beyond the inner tube, and its walls come together to form the point of the fang. On the basis of the characters at the distal end of the fang, cobras may conveniently be divided into two groups, and the detailed structure of the discharge orifice and the point of the fang can profitably be described separately for each group.

NON-SPITTING COBRAS

Non-spitting cobras, or those having what approximates the usual sort of elapid fangs, possess characteristics of the discharge orifice and fang point that are to some extent associated with the suture mentioned above. This suture or weld in the venom canal is readily apparent on the anterior of the fang as a shallow groove that extends from the entrance lumen to the discharge orifice. Fangs moistened with water can easily be split longitudinally by pressing a sharp edge of a razor into the suture. On non-spitting cobras the suture does not follow the median line of the front of the fang but swings slightly outward so that the discharge lumen tends to be on the outer edge of the point. Below the discharge orifice, that is, distally to the termination of the weld, the venom canal is continued as an open groove which extends onto the point. On fangs of adult cobras there is a faint ridge paralleling the groove just beyond its inner edge, and a similar but well-developed ridge on the inner side of the fang not far behind the outer edge. The position of these ridges varies from species to species or even from population to population in *Naja naja*, as may be seen in Figs. 56–66. These structures correspond to those on the fangs of rattlesnakes that Klauber (1939, p. 14) refers to as "wearing or cutting edges," or as "reinforcement ridges" (p. 57). Presumably they serve as cutting edges facilitating insertion of the fangs when biting action of the jaws forces the fangs into the flesh of prey. Both fangs on a side (that is, a functional fang in right or left socket and the first reserve) have the cutting edges and the discharge orifice in similar positions, but those of the opposite maxilla are on the reverse side;

the flow of venom, therefore, is directed slightly outward and downward from the functional fang in each maxilla as will be explained below.

Fangs of various elapids not known to be spitters have fangs of the sort described above; these include the African species, *Naja nivea*, *Naja melanoleuca* and *Naja haje*. Such fangs are also characteristic of two forms now included under *Naja naja* in Asia, and while I have not been able to examine specimens of *Naja morgani* and *Naja oxiana*, neither of these has been reported to eject venom under normal circumstances, and there is little doubt but that they too fall into this group of cobras. (See Figs. 28–33 and Map 4.) Snakes of the elapid genera *Hamadryas, Boulengerina, Pseudohaje, Elapsoidea, Aspidelaps, Demansia, Pseudechis, Glyphodon, Ultrocalamus* and *Dendroaspis* have been examined, and the apertures of the points of the fangs are similar to those of cobras described above. However, there are differences between species in the relative size of the discharge orifice, with comparatively little intraspecific variation in adults. These differences can be observed in Figs. 52–54.[1]

Spitting Cobras

Spitting cobras, or those species of *Naja* and *Hemachatus* that forcibly eject venom in the manner described in some detail under the topic of their behavior, possess fangs in which the suture is approximately on the median line of the anterior surface of the curve. As in non-spitters the suture terminates distally in the discharge orifice, but below the aperture there is no groove continuing from the venom canal onto the point of the fang, and the aperture is in the middle of the distal end rather than on the
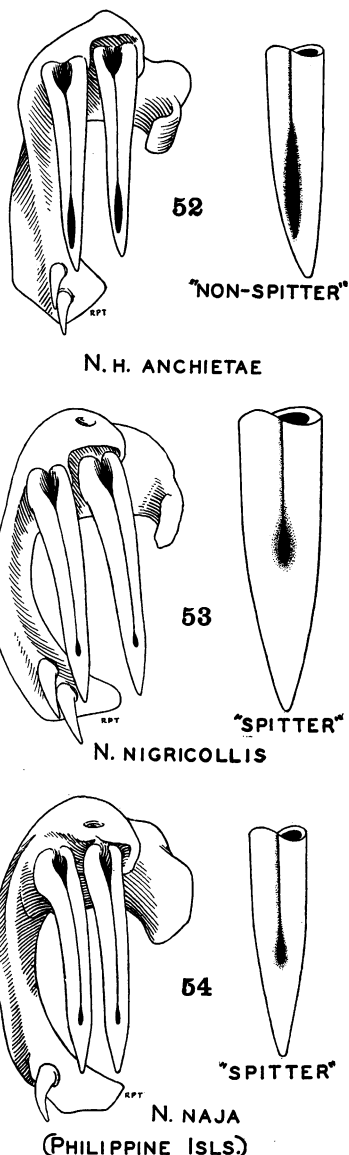
[1] It is difficult to depict maxillae of different species, or even specimens of the same species, in exactly corresponding positions, and in drawings of anterior views of the fang it is not possible to indicate the relative length and width of the fang with accuracy owing to the curvature. Since two fangs are commonly present in the maxilla, both have been depicted in drawings, with darker shading around the socket of the non-functional fang to indicate incomplete ankylosis. Usually the two fangs of a maxilla were not in the same plane, but they have been depicted as though they were to facilitate the artist's work and to provide uniformity. Within limitations imposed by these conditions, the figures presented in this paper are reasonably accurate representations of the fangs and maxillae of the species portrayed.

52

"NON-SPITTER"

N. H. ANCHIETAE

53

"SPITTER"

N. NIGRICOLLIS

54

"SPITTER"

N. NAJA

(PHILIPPINE ISLS.)

Figs. 52–54. Ventral views of the maxillae (× 5) and anterior views of distal portion of fang points (× 10), contrasting fangs of a non-spitter (Fig. 52, *Naja haje anchietae*, A.M.N.H. No. 51860, from Capelongo, Angola) with those of two spitters (Fig. 53, *Naja nigricollis*, A.M. N.H. No. 51806, from Capelongo, Angola; Fig. 54, *Naja naja*, A.M.N.H. No. 32874, from "Philippine Islands"). Note similar adaptations in the fangs of two spitters from widely separated regions.

outer side. In non-spitters the discharge orifice appears as an elongate opening, but in spitters the orifice is more or less tear-shaped in outline, the lower edge of the opening appearing rounded while the upper end of the opening terminates where the walls of the venom canal meet on the suture (see Figs. 28–33, 52–55).

The description above refers particularly to the fangs of South African *Hemachatus haemachatus*, to *Naja nigricollis* (including all races examined) and to *Naja naja* inhabiting the East Indian islands and the adjacent mainland (see Map 4). Fangs from specimens of a series of *Naja naja* from the provinces of southern China, as well as a specimen from northern Burma, are all similar, the aperture being more elongate than in cobras from the Malay Archipelago. Toward the west, in southern Asia from Burma to India, a transition from a tear-shaped orifice in Malayan cobras to an elongate orifice in Indian cobras is indicated in the specimens available. Essentially all of the intermediate stages between spitters and non-spitters, as far as fang modifications are concerned, are represented in Asiatic specimens (see Figs. 28, 30 and 32). Descriptions of point and discharge orifice characters in three specimens will serve to illustrate the more important steps in the progressive modifications of fangs culminating in those adapted for the forward ejection of venom:

1. A.M.N.H. No. 39397, from Siwalik Hills, Punjab Province, India. Orifice on outer edge of fang, pronounced groove extending onto point. (Not adapted for spitting.)

2. A.M.N.H. No. 58524, from Tasu Bum, northern Burma. Orifice nearly in middle of fang, terminating more abruptly distally in shallow groove extending only short distance onto point. (Partly adapted for spitting, and almost identical with the fangs of Siamese and Chinese cobras.)

3. A.M.N.H. No. 12865, from Singapore, Straits Settlements. Orifice in middle of fang, rounded at lower edge, groove on point replaced by slight bulge. (Adapted for spitting.)

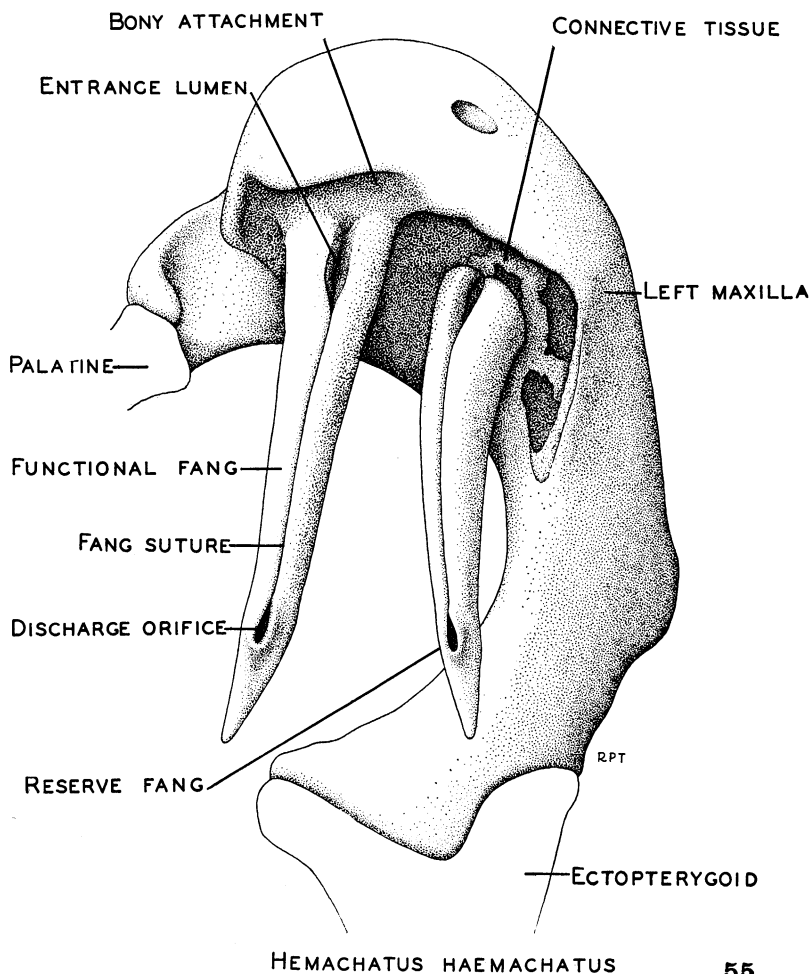It has not been possible to show the ex-

tent of variation within populations graphically, but an attempt has been made to indicate the regions where intermediate fang conditions occur on Map 4. Twenty-four specimens of *Naja nigricollis* have been examined, and all are nearly identical as far as the modifications of the apertures and points of the fangs adapt them for spitting. Similar modifications are found in the fangs of East Indian *Naja naja*, but there are minor differences between these *Naja* and *Hemachatus* when the terminal portions of the fangs are compared. The lower edge of the discharge orifice in *Hemachatus* is raised more pronouncedly, as may be seen in Fig. 55, to form a sort of projecting lip on the aperture.

The cutting edges described for non-spitters are present on most spitters, but instead of being located on the sides with the outer one more toward the front of the fang than the inner, they are shifted to approximately equal positions, cross sections of the fang point being symmetrical or nearly so. (The relative positions of venom canal and the cutting edges in various species may be seen by reference to Figs. 56–66.) Viewed from the side the point is asymmetrical in spitters, the anterior surface of the point being nearly in the same plane as the curve of the fang above the aperture, while the rear surface in outline is on a slight angle with the curve of the plane of the posterior surface as a result of a bulge behind the discharge orifice.

This description will be clarified by reference to Figs. 67 and 68 which permit contrast of longitudinal sections of fangs of a non-spitter and a spitter. These figures demonstrate the difference between the distal termination of the venom canal in the two types.

FUNCTIONAL SIGNIFICANCE OF DIFFER-
ENCES BETWEEN FANGS

An examination of the fangs of various cobras suggested that certain species, particularly the ones most often reported as spitters, were capable of ejecting the jet of venom at an angle of approximately 45 degrees with the tangent of the curve at the end of the fang, whereas others ejected the venom downward. To test this experi-

BONY ATTACHMENT   CONNECTIVE TISSUE

ENTRANCE LUMEN

LEFT MAXILLA

PALATINE——

FUNCTIONAL FANG——

FANG SUTURE——

DISCHARGE ORIFICE——

RPT

RESERVE FANG——

——ECTOPTERYGOID

HEMACHATUS HAEMACHATUS   **55**

Fig. 55. Ventral view of the left maxilla (× 10) of the ringhals, *Hemachatus haemachatus* (A.M. N.H. No. 49947), showing details of external fang structure and positions of the functional fang and first reserve fang. Note projecting lower lip of discharge orifice.

mentally the fangs of several species of co-bras were thoroughly cleansed, and, by in-serting a hypodermic needle in the entrance lumen, water was forced through the venom canal with a syringe. The approximate results for four species are shown in Figs. 69–72. The fangs of *Naja melanoleuca*, *Naja nivea* and *Naja haje* all ejected the fluid along the plane of the curvature and slightly outward (not forward) from the direction of the point of the fang. The fang of *Naja nigricollis* directed the jet of

water almost perpendicular to the tangent of fang curvature, and this was found to be true as well of fangs of *Naja naja* from the Malay Peninsula, from the Philippines, from Sumatra and from Komodo. *Naja naja* from China directed the jet only slightly outward from the plane of the fang, closely resembling *N. naja* from Burma and Siam which ejected fluid at an angle of hardly 30 degrees from the tangent of curvature at the end of the fang. With *Hemachatus* there were consistent results
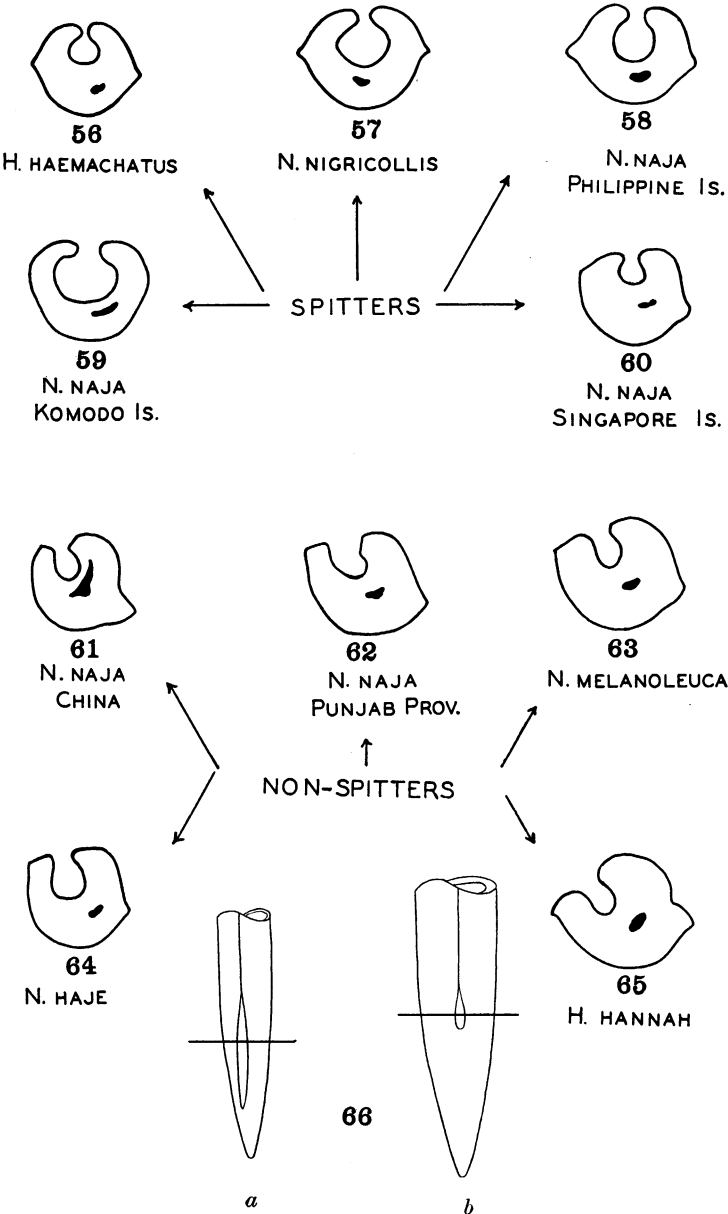
Figs. 56–66. Cross sections of the distal portion of the fangs of various cobras, showing positions of the venom canal, pulp cavity and cutting edges. (See legend on Fig. 50.) Distal portions of the fangs of a non-spitter (left) and a spitter (right) indicate approximate levels of cross sections.
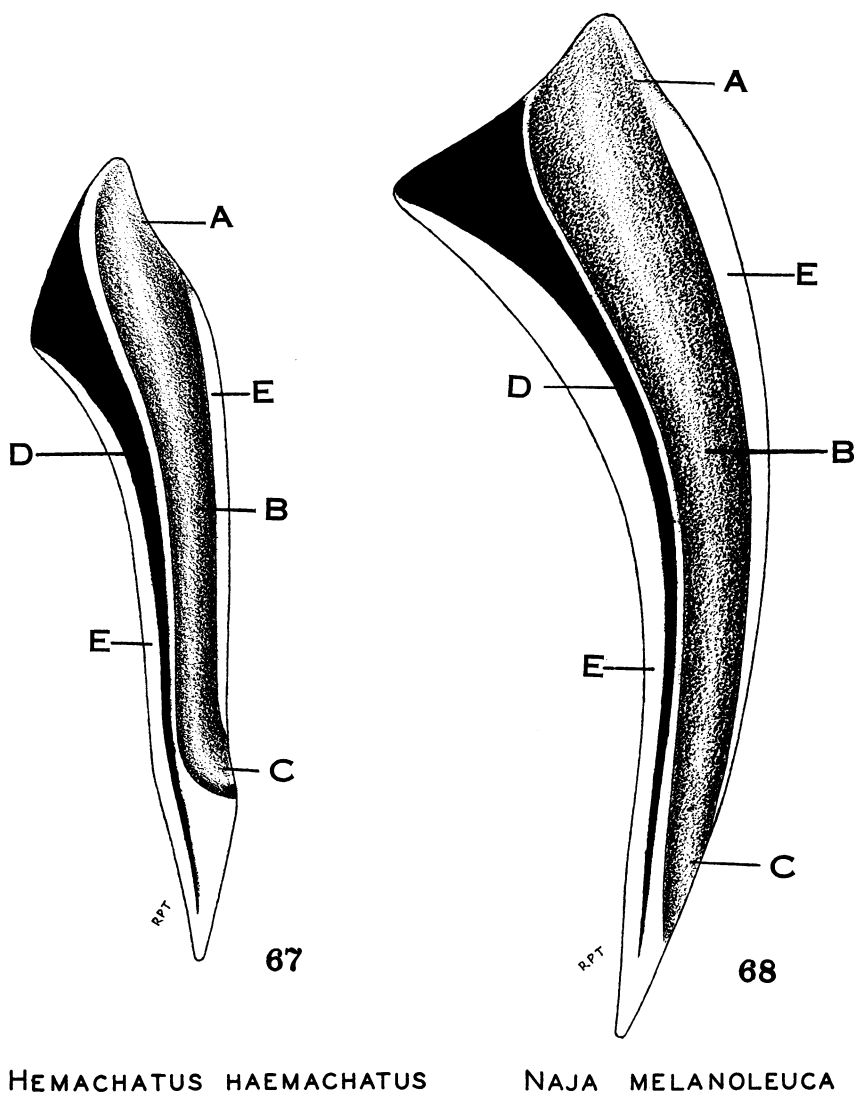
Figs. 67–68. Longitudinal sections of fangs, contrasting the fang of a spitting cobra (Fig. 67) with that of a non-spitter (Fig. 68). A, entrance lumen; B, venom canal; C, discharge orifice; D, pulp cavity; E, dentine.   Drawing made from fangs split along anterior suture, × 15.

with four fangs tested; all directed the jet not only outward but slightly upward with respect to the tangent of curvature.

Thus the modifications in the discharge orifice of fangs are, in part at least, correlated with the known habits of cobras. The species that habitually eject venom as a protective measure prove to be the species that have fangs adapted for the forward ejection of venom, as will be discussed below in more detail. By reference to Fig. 19 showing the skull of *Naja nigricollis*, it will be seen that the fang in normal position has the point directed inward rather
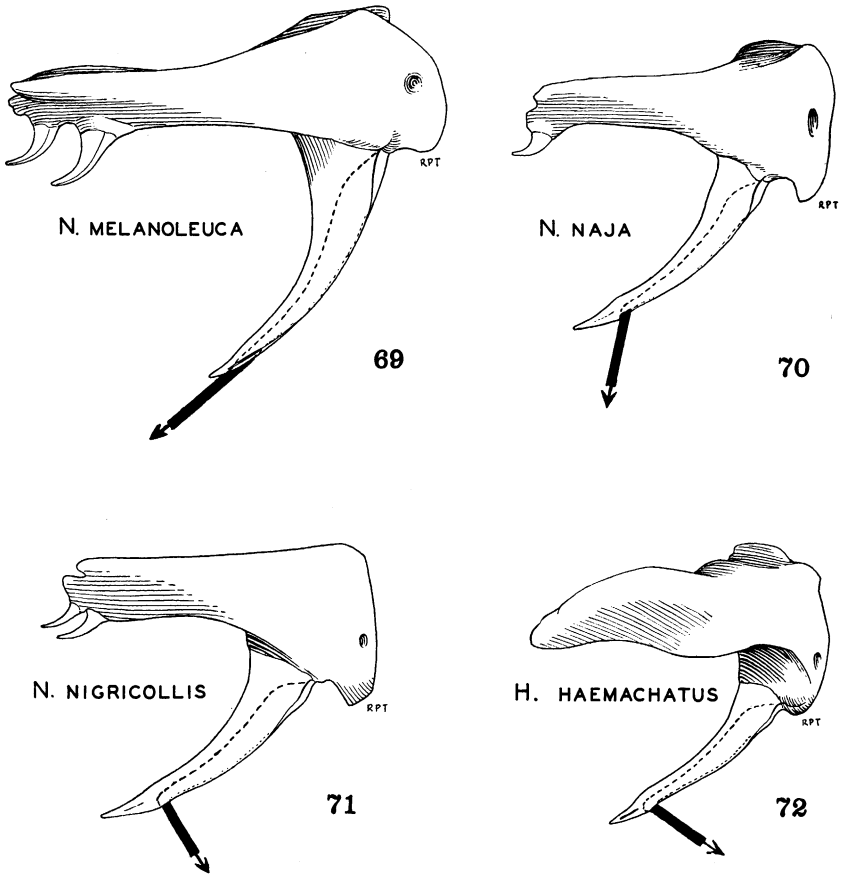
Figs. 69–72. Lateral views of representative types of fangs attached to maxillae. Dotted lines indicate position of venom canal. Arrows indicate the direction of liquid ejected from various fangs, as determined by experiment with removed maxillae. Fig. 69. *Naja melanoleuca*, a non-spitter from Africa. Fig. 70. *Naja naja*, a Chinese cobra partly adapted for spitting, but not reported as a spitter. Fig. 71. *Naja nigricollis*, the most widely distributed spitting cobra in Africa. Fig. 72. *Hemachatus haemachatus*, the South African "ringhals," the most perfectly adapted of all spitting cobras.

than perpendicular to the horizontal axis of the skull. That *N. nigricollis* can and does eject venom from the mouth cannot be doubted, as the accounts quoted under the discussion of the behavior of spitting cobras amply testify.

Radowanowitsch (*supra cit.*) clarifies the situation by his description of the cranial musculature, as he indicates that slight rotation of the maxilla is possible in *Naja*. Thus it may be inferred that the spitting cobra manages to eject twin jets of venom outward and upward by relatively slight

movements of the maxilla, bringing the point of the fang into a position nearly perpendicular to the main axis of the head, while movements of the head and neck permit the snake to direct the jets in any given direction.

It has been possible to obtain information from published reports concerning the posture of cobras while spitting, but most satisfactory has been the information kindly placed at my disposal by Mr. Henry C. Raven. The cobra depicted in Fig. 73 was sketched from a photograph secured in

northern Rhodesia by Mr. Raven who came upon the snake early in the morning as it was eating a frog. At the approach of Mr. Raven and his assistant, the snake dropped the frog, assumed a posture with the hood spread, the head raised from the ground and began to "spit." While his assistant attracted the cobra's attention

ferent, more erect, defense posture than *Naja nigricollis*, and it may be postulated from the results of experiments with fangs, mentioned above, that this cobra need not elevate its upper jaw to the extent that *N. nigricollis* does. Both *Hemachatus* and *N. nigricollis* are apparently able to direct the ejected venom with considerable accuracy

ARROWS INDICATE APPROXIMATE
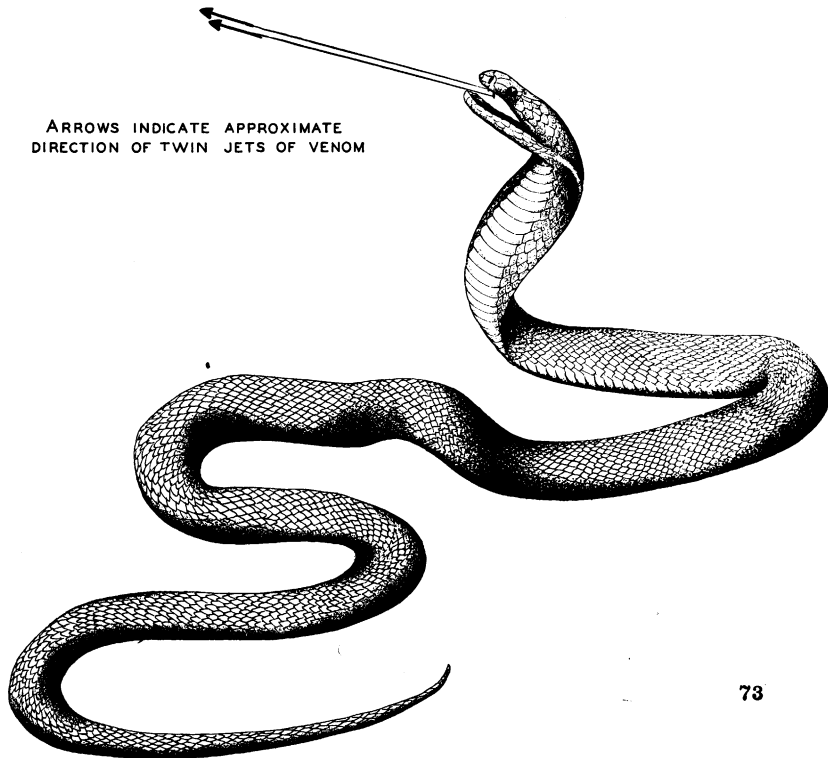DIRECTION OF TWIN JETS OF VENOM

73

Fig. 73.   Posture of African cobra, *Naja nigricollis*, when "spitting" or ejecting venom toward an enemy.   Drawing based upon photograph of a cobra in the act of spitting secured by Mr. Henry C. Raven at Kafue, northern Rhodesia.   Venom was being directed toward an assistant when the photograph was taken.   Note slightly uptilted head.

Mr. Raven secured a photograph of the snake from the side. The result shows clearly that the head was slightly elevated, and the white fang-sheath or *vagina dentis* is apparent through slightly parted jaws. The direction of the venom jets indicated on the drawing represents conclusions drawn from study of the photograph and from the inferences that can be drawn from the nature of the fangs and skull.

Hemachatus (Pl. L) has a somewhat dif-

by means of head and neck movements, as the photographs in Rose (1929, Figs. 113–114) indicate. Cobras can eject venom from any position, and do not necessarily assume the typical defense posture. Rose (*op. cit.*, p. 170) states that the ringhals ". . . may show off another item of its remarkable repertoire by rolling over on its back and shamming dead. . . though apparently innocuous, one eye at least is always directed toward the enemy who will attempt

a closer examination of the 'corpse' at his peril."

The adaptations of the fang that enable a cobra to eject venom effectively do not preclude its use for the normal function of fangs, namely, the hypodermic injection of venom. Fangs of spitters thus serve a dual purpose: (1) they provide effective protection from mammalian, and quite possibly avian, enemies, and (2) they provide means of killing prey rapidly and efficiently. The ejection of venom into the eyes of an approaching enemy has the obvious advantage of preventing attack; snakes that must inject their venom follow-

ing a hit or strike must always undergo the risk of being bitten or trodden on by an enemy. This disadvantage is partly overcome, to be sure, by the rapidity of the strike of vipers and pit-vipers, such snakes being able to launch the head forward suddenly, inflicting a bite on an attacker and recoiling before the enemy has had an opportunity to launch an assault. Thus it has often been questioned whether a mongoose could successfully engage in combat with a viper, although the mongoose is known to be an enemy of cobras. It seems doubtful that such mammals could successfully prey upon spitting cobras.

BEHAVIOR OF SPITTING COBRAS

Using the terminology for cobras adopted in the taxonomic discussion, the literature dealing with spitters may now be reviewed as pertinent to the study of fang modifications. The term "spitting" I continue to use with the explanation that it carries an erroneous connotation, for as used to describe cobras it does not imply any manipulation of the lips. Photographs and other data presented above indicate that the mouth is slightly opened and that venom is forcibly ejected in a minute jet from each fang. True spitters are able to eject venom for several feet as a deliberate defensive action. Vipers or other venomous snakes may eject venom when being handled, or upon striking wire mesh their fangs may be engaged and venom ejaculated for several feet. Such ejection of venom is, however, not "spitting" in the sense that the adjective is used in connection with cobras.

ASIATIC SPITTING COBRAS

As noted in the introduction, Boie's name *sputatrix* for a Malayan cobra indicates that some knowledge of spitters was available more than a century ago, and descriptions of the spitting phenomenon have appeared from time to time since. All reports by competent authorities indicate that in Asia the spitting habit is confined to certain populations of *Naja naja* inhabiting the region east of India. The

king cobra (*Hamadryas hannah*) has never been reported to spit, although numerous persons have reported encounters with this large and aggressive elapid.

The account of Goring Jones (1900, p. 376) concerning the behavior of a Burmese spitting cobra (*Naja naja*) near Mandalay, Burma, may be quoted in full as a typical description of a field encounter: "Yesterday evening as Lieut. Gibson of our regiment was going to his quarters to dress for Mess he saw a snake at which he proceeded to throw a stone. He then called for a light and a stick, and as he was bending down with the light to look for the snake, it made a dart at him but fortunately missed its aim. Some of the poison or saliva, however, was ejected into Lieut. Gibson's eye, causing instant and great pain, and the eyelids and parts round swelled up quickly to the size of a large hen's egg. The snake was killed, and was found to be a small black cobra about 3 feet 4 inches in length. Lieut. Gibson went to the hospital and after a painful night recovered his eyesight."

In light of more carefully reported observations on captive specimens it seems doubtful whether the snake actually "made a dart at" Gibson, although forward movement of the head often has been mentioned apparently in an effort to account for the ejection of venom. Wall (1921, p. 466), supposedly upon the basis of his knowledge

of the snakes of Ceylon, mentions the fact that "a hospital attendant trying to dislodge a cobra that had taken refuge in the wall of his garden, had a jet of venom ejected into his face." He adds that in "our Society's rooms it is a matter of common observation that cobras 'spit' at spectators, and leave a spray on the glass." His statement that "the venom ejected is shaken off the fangs and carried forward by the vehemence of the thrust," may represent either speculation or careless observation, but, pending opportunity to examine cobras from Ceylon, I have included the island in the range of spitters (Map 4).

Shaw and Shebbeare (1930, p. 27), discussing cobras in Bengal and Sikkim, report that, striking and failing to reach its object, "the snake ejects drops of venom, or a spray," but there is nothing at all in the accompanying text to indicate that this was observed in local snakes. Ouwens (1916, p. 4) reports that as a defense mechanism the cobra raises the anterior part of the body, expands the hood and "hisses and spits at the aggressor before attacking," while Boulenger (1912, p. 202), quoting Ridley, asserts that "when annoyed the cobra sits up in the well-known manner and makes a very curious snorting noise, holding its mouth open in the form of a circle [?] and every now and then spitting its poison at its opponent." Such accounts are of little if any value, but Kopstein's papers (1930, p. 351; 1932, p. 250) supply precise information for Asiatic cobras. He states definitely that the venom of Javanese specimens is ejected for a distance of two meters, but that if washed from the eyes immediately there is but a slight burning sensation. If the venom is not removed quickly, however, he states that it is likely to cause temporary blindness.

Kopstein's detailed notes are of particular interest. He reports that a freshly caught cobra, measuring 1.5 meters, spat while being lifted out of a container. Some of the venom struck Kopstein in the eyes, whereupon he immediately noticed a "burning pain." As a protective measure in further attempts to move the cobra he held a glass plate in front of the snake.

Soon the plate was covered with drops of venom of various sizes which he washed off in salt solution and injected intramuscularly into a "Reis-vogel" which died a few minutes afterward. Later he continued the experiment of holding the glass plate in front of the cobra for a quarter of an hour during which time the snake continued to spit until the "amount of accumulated liquid was astonishing." Kopstein suspects that toward the end of the period some of the ejected liquid may have originated elsewhere than in the venom glands, perhaps being forcibly expelled from the trachea.

All the above accounts concern cobras in the East Indies, the Malay Peninsula, Burma and Ceylon. There appear to be no reports of Chinese cobras spitting, although spitters have been reported from the Philippine Islands (Taylor, 1922, p. 262). For mainland India west of Bengal there seem to be no definite reports of cobras ejecting their venom, although Prater (1923, p. 160), in his discussion of the snakes of Bombay Island and Salsette Island, states that cobras are "able to spit out venom, but unless exceedingly aggravated they do not practice this habit." Whether he has drawn this conclusion from observation of local cobras, from the literature or from experiences with cobras elsewhere is not certain.

These accounts, to which others might be added, suggest that the ejection of venom, while not uncommonly observed in the true cobras (*Naja*) of southeastern Asia, represents a defensive behavior not always elicited in individual specimens. Dunn (1927) failed to observe spitting behavior in cobras on Komodo Island, although the fangs of the specimens he collected show definite modifications adapting them for the purpose.

AFRICAN SPITTING COBRAS

On the continent of Africa nearly every cobra, including one species of *Pseudohaje*, has been reported by one author or another as a spitter. When it has been possible to make an accurate identification of the species, however, it has invariably proved to be either *Naja nigricollis* or *Hemachatus haemachatus*. The several accounts re-

viewed indicate that both are especially prone to spit when confronted at close quarters, particularly if wounded. There is not the slightest first-hand evidence that *melanoleuca, nivea* or *haje* spit, although these names or their synonyms have been included in numerous discussions of spitters, even including that of Boulenger (quoted by Curtis, 1911). Mistakes in field identifications are probably responsible, as the most widespread African spitter, *nigricollis*, occurs within the range of every other African cobra, and it is notably variable in coloration.

In addition to numerous field accounts of spitting by *Naja nigricollis* (Loveridge, 1928a, p. 58, and 1928b, p. 107; Corkhill, 1935, p. 25; Hobley, 1910, p. 38; Boileau, 1912, p. 134; Scholefield, 1912, p. 61; Werner, 1908, p. 62), there are the more detailed observations on captive specimens made by Ditmars (1931, pp. 167–172) and the useful review and report of experiments by Koch and Sachs (1927, p. 155). Ditmars (p. 168) describes the spitting of *nigricollis* as follows: ". . . the performance is accomplished with the jaws slightly parted and the venom comes directly from the openings at the tips of the fangs. The performance is very quick. . . . The snake rears and it may instantly spring to the pose. Facing the object of anger it looks intently into one's face. . . . If it seeks to direct the poison upwards it curves its rearing pose backward, thus directing the head upwards. The ejection of the poison is an instantaneous operation. The jaws are slightly opened and closed so quickly as to appear like a snapping motion and during this action the poison leaves the fangs. There is no dribbling or spilling of the fluid. It issues in twin jets and the jaws of the snake are clear of it when the feat is accomplished. There is every indication that, at the instant the snake prepares to eject the poison, it contracts the temporal[1] muscle

over each gland, thus producing pressure to force the toxic fluid a considerable distance. This flies with such force that its impact can be distinctly heard against ordinary glass five feet away. At the instant of the ejection the snake emits a sharp hiss. This ejection of air might be an accompanying token of anger, or it may assist the travel of the poison."

Loveridge (*supra cit.*) reports that when collecting an exceptionally large *N. nigricollis* in Tanganyika, "It spat between a dozen and twenty times and its venom was in no way exhausted right to the end." Accounts differ concerning the maximum distance venom is ejected; Ditmars (*loc. cit.*) says 12 feet, but Loveridge gives the approximate figure of 6 feet. Probably size and other factors are correlated with the distance to which individual specimens expel venom. Sachs experienced some difficulty in making a captive specimen spit after it had been caged for several weeks, but noted that when venom was ejected it came forth in two separate jets. He and Koch recovered the venom ejected on a

"This organ [the poison gland], which is really a salivary gland, and the analogue of the parotid gland in mammals, including man, consists of a body and a neck. The body is much the shape and size of an almond kernel, and consists of (1) a thick fibrous capsule or jacket, (2) the glandular or poison secreting substance proper, and (3) a duct running centrally in the long axis of the gland. The capsule gives off numerous fibrous septa, which pass into the glandular substance and divide it into numerous chambers or pockets (the poison lakes of Bobeau). Each pocket is lined with poison secreting cells, and carries in its walls blood vessels, which convey the blood which the poison cells depend upon for their activity. After a period of activity, the pockets, which converge forwards and inwards towards the axis of the gland, become distended with poison, and this is poured into the central duct. At the posterior pole the gland ends in a downward projecting lobe. The fibrous capsule dips into the gland, just in front of this lobe, to form a furrow for the attachment of an important muscle, the masseter. This muscle originates from the postfrontal [postorbital] bone and the ridges on the parietal, and is somewhat fan-shaped. Its fibres converge, and pass first backwards over the superior and internal surfaces of the gland, then downwards behind its posterior pole, and finally forwards to be attached to the furrow, or dimple in front of the lobe. The muscle, in fact, embraces a large part of the gland surface, and in contraction squeezes it much in the same way as the hand operates on a bicycle horn, the result being that poison is driven forwards into the duct to pour finally into the mouth. The neck of the gland consists of a sheath which is the direct continuation of the capsule surrounding the body, but is much thinner. Centrally is the poison duct, and intermediate between the sheath and the duct a series of mucous glands. These are placed at right angles to the axis of the duct, and discharge their mucous into that channel, where it mingles with the poison proper. In section the gland appears to the naked eye much like a sponge."

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[1] This muscle has been variously referred to as the "temporal" or "masseter" but does not appear to be entirely homologous with these mammalian structures. Dr. Edwin H. Colbert informs me that it is more properly designated as the capiti-mandibularis superficialis. (See also Adams, 1919, Ann. N. Y. Acad. Sci., XXVIII, pp. 51–166.) Wall's (1921, p. 478) description of the venom gland of *Naja naja* provides a basis for a clearer understanding of how the venom is expelled through the fangs, as follows:

glass disk, dissolved it in water and placed it on the cornea of the eye of a 500-gram rabbit in order to observe the effects. A day later they found the eye covered by a thick, viscous "pseudediphtheritic" membrane. The animal was practically blind, the eye having subnormal turgor. Three days later the eye watered strongly, the membrane had become green, although the animal ate and drank normally. Two months later the inflammation had subsided, but the cornea was changed into a large scarred leucoma. The pupil had grown to the interior corneal surface, and as far as Koch and Sachs could observe there was no pupillary reaction. The animal was practically blind in the poisoned eye.

Later Koch smeared the contents of a freshly excised venom gland on the cornea of a 3-months-old rabbit, obtaining essentially the same results. In this case, however, the findings were determined more accurately, because the excised eyes of the rabbit were fixed in formol, embedded and sectioned. The histological examination disclosed complete degeneration of the corneal epithelium, alteration of the ciliary body and partial vascularization of the cornea. Koch and Sachs conclude that poison spitting constitutes an effective weapon for the cobra, as proved by the "dreadful and rapid action" the venom had on the eyes of the mammals tested. That it is used by cobras in defense against mammals other than man may be surmised, and Koch and Sachs cite the case of a hunting dog that howled in pain and ran away when a cobra ejected venom into its eyes. Later it became blind because it could not be treated at once.

Since the fangs of cobras that habitually spit are adaptively modified for the forward ejection of venom, it might be assumed that spitters have likewise evolved a venom particularly effective when directed into the eyes of mammalian enemies. The venom of *Naja nigricollis* has not been available, but I have been able to perform some simple experiments with the venoms of two elapids, *Naja nivea* and *Hemachatus haemachatus*, of a viperid, *Bitis arietans*, and of a crotalid, *Crotalus atrox*. Approxi-

mately equal amounts of the desiccated venom of each of these species were dissolved in 1 cc. of tap water. Two drops of the dissolved venom of each snake were placed in each eye of individual rats. The rats thus treated with the venom of *Hemachatus* and of *N. nivea* died within fifteen to twenty minutes. Experiments were repeated with additional rats on three successive days, and on the third day only a single drop of venom was placed in one eye. In every case, regardless of whether venom was placed in one eye or both, the rat evinced immediate pain and succumbed in less than an hour. The opaque cornea reported by Koch and Sachs was not observed in any rat, perhaps because the systemic effects resulted in death before any local destruction of tissue became apparent or because the effects of the venoms used may differ from those of the venom of *Naja nigricollis*.

Rats treated in a similar fashion with the venom of *B. arietans* and of *C. atrox* demonstrated no signs of pain, and no apparent ill effects were observed later. Even a stronger solution of the venom of each of the two solenoglyphs failed to produce any symptoms in the rats, although two of the four rats thus treated were subsequently subjected to the venom of *Hemachatus*, and both of them were dead within twenty minutes.

These rather crude experiments indicate that the venom of a non-spitter, *N. nivea*, may be nearly as effective as that of a spitting cobra, *Hemachatus*. Potentially, therefore, any cobra is capable of using its venom defensively by directing it into the eyes of an enemy, provided it could evolve the necessary behaviorial and fang adaptations to do so. Inasmuch as neither the venom of *Crotalus atrox* nor of *Bitis arietans* seemed to be absorbed through the conjunctiva, these physiological properties of the venom might account for the fact that no viperid nor crotalid apparently has ever evolved spitting habits comparable to those known for cobras.

Dr. David I. Macht (*in litt.*) informs me that "the venom of *Naja naja* is readily absorbed through the eye into the system, producing poisonous effects on cats and

rabbits." Some small stocks of the venoms of *Hemachatus* and *Naja nivea* have been turned over to him for further experimentation, and he has generously permitted me to report the results of some preliminary investigations which indicate that the venom of *Hemachatus* is more readily absorbed through the eye than the venom of non-spitters so far tested. Thus *Hemachatus* seems to be specialized in both fang and venom modifications.

The spitting habits of the ringhals (*Hemachatus*), essentially the same as those of *Naja nigricollis*, are mentioned by Rose (1929, p. 169) and described in some detail by FitzSimons (1912, p. 189). Rose

states that the venom may be ejected for a distance of six or seven feet, and that the snake aims at the eyes, even when these are high above the snake, as in the case of man. Noyes (1934, p. 1477), probably on the basis of casual observation, states that he has "never known the ringhals to spit at an object outside the range of his spray of pure venom," which, if borne out by experimentation, implies considerable size discrimination. Such ludicrous statements as that of French (1942, p. 50) that "two streams of saliva or mucus are forcibly ejected through the nostrils" of the ringhals doubtless result from faulty observation.

DISCUSSION OF SPITTING ADAPTATIONS

Among the accounts cited above, in no case has any cobra, other than *Naja nigricollis*, *Naja naja* and *Hemachatus haemachatus*, been observed to spit under conditions where the identity of the snake was beyond question. Therefore, it seems relatively certain that only those cobras with fangs having the discharge orifice modified for the forward ejection of venom are capable of using such methods of defense. It is perhaps astonishing that the adaptive modifications of fangs in spitting cobras have not been noted heretofore, particularly when observations on captive specimens made it apparent that venom was expelled outward, whereas the fangs were directed downward. As long ago as 1818 Thomas Smith obtained a cobra from Madras, India, and provided a fairly accurate description of the fangs of *Naja naja*. But he had a specimen that was not a spitter, as indicated by his figures and confirmed by information at hand concerning the fangs of Indian cobras.

Judging from the accounts cited, *Hemachatus* spits with slight provocation when encountered in the field, while *N. nigricollis* seems to resort to this defense more commonly when wounded or cornered. Only occasional specimens of Malayan *N. naja*, on the other hand, spit, despite provocation, and many specimens have been secured by collectors who have failed to

observe the phenomenon. Specimens in the American Museum collections were secured on the Island of Komodo by E. R. Dunn who failed to note any attempt of the cobras to spit as noted above, although to judge from the fangs they could have. Clifford H. Pope collected twenty-five Chinese cobras (referred by him, 1935, p. 348, to *Naja naja atra*) for the American Museum, and he notes (p. 353) that "Instead of showing fight when teased, they constantly attempt to escape, and only adopt a defensive attitude as a last resort." Even when placed in a cage with a mongoose they failed to spit, although dissections reveal that twenty of the specimens still on hand are uniformly partly adapted for spitting, and quite similar in fang structure to cobras from Burma where spitting has been reported. Among a score or so of cobras from the Malay region received by the Staten Island Zoological Park in 1936, none ever spat, although these specimens, too, prove to be adapted for such defense as far as fang structure is concerned. I am indebted to Mr. Carl F. Kauffeld for the gift of one of these specimens which raised its head, spread its hood and hissed loudly when annoyed by attempts to get it to pose for a photograph, although it never ejected venom.

The failure of such cobras to spit may be

explained perhaps by assuming the inheritance of suitable fang structure unaccompanied by any neural mechanism enabling the snakes to perform or to integrate the necessary muscular actions that accompany the act of spitting. Such an explanation is suggested by variation with the series of Asiatic cobras, the fangs of those from the southeastern portion of the continent being better adapted than others, whereas *Naja nigricollis* and *Hemachatus haemachatus* are uniformly well adapted. Alternative explanations, less probable in light of Pope's experiments, may be suggested by reference to other genera. It is well known, for example, that occasional specimens of *Crotalus* fail to vibrate their tails, although all normally possess rattles on the tail in adult life. Such failure on the part of some snakes, then, may be ascribed to individual differences in the state of excitability, or whole populations or even species may be less excitable than others.

Another explanation may be concerned with the nature of the cue necessary to elicit the defense reaction of spitting in cobras. It has been a common observation that bull snakes (*Pituophis*) can be handled, frequently without any manifestation of alarm. But if a dog sniffs at the head of one the snake frequently reacts immediately, hissing loudly and striking with the mouth opened wide in an obvious attempt to intimidate the animal. Elsewhere (Bogert, 1941) I have reported the defense reaction of rattlesnakes in the presence of certain ophiophagous ophidian enemies, whereas the presence of many non-snake-eating ophidians failed to elicit the response. In this case the rattlers apparently reacted in a characteristic manner only when certain odors were present. Thus it remains a possibility that spitting cobras in eastern Asia have evolved the habit of defensively ejecting venom in response to some particular enemy or enemies, and their failure to spit, even when teased by man, is indicative only of an inadequate or improper stimulus.

Barbour (1922, pp. 36–38) compares the protective usefulness of spitting by cobras with the usefulness of the rattling of rattlesnakes, suggesting that in both cases the result is a particularly efficient means of protection against "hordes of grazing ruminants." However, if we assume that such protective behavior as spitting has evolved primarily for protection against the larger hoofed animals, it is difficult to see why cobras of the Malay Peninsula and the adjacent islands are adapted for spitting whereas those of India are not, grazing ruminants being more or less of equal prominence in each region. This does not, however, completely invalidate Barbour's[1] assumption, and the fact that cobras partly adapted for spitting fail to expel their venom when introduced into a cage with a mongoose may indicate that spitting is elicited only in the presence of larger mammals. But even this speculation would not entirely account for the failure of Chinese cobras to spit at man, and it seems doubtful whether they ever spit, despite their partially adapted fangs.

It may be suggested that *Naja naja* throughout its range was once an efficient spitter and that the species is now in the process of losing its spitting abilities, modifications in fang structure that once enabled the snake to spit being lost as a result of disuse. Without upholding arguments for

[1] Barbour's speculations include some interesting ideas not mentioned elsewhere in this paper, and therefore his paper may profitably be quoted at some length: "The African veldt is the only other region in the world where snakes abound and where hoofed animals grazed in numbers comparable with those of the western American plains. Snakes probably found the heavy antelopes equally dangerous though unwitting foes and many antelopes probably suffered from snake bite. No rattle was evolved, however, but some of the common veldt-ranging snakes secured protection in another way. Several common cobras and cobra-allies learned to expel their poison in a fine spray for very considerable distances, and with a fairly shrewd aim at the eye. The poison, of course, is not caustic, the skin is unaffected; prey cannot be secured by this means but the moist eye allows of an absorption so rapid that sharp pain and subsequent photophobia instantly results from the contact. Gardeners who work stooping about shrubbery have come into the Bulawayo hospital with acute conjunctivitis. The Dutch call *Sepedon* the 'Spuw slang' [the ringhals, *Hemachatus*] or spitting snake, a poor name, however, as the saliva is not involved. Natives know the habit and fear spitting snakes. Here again, however, the habit must antedate man's coming, for contact between man and the snakes can hardly be conceived as sufficiently frequent to account for the modification. Moreover, the modification would not have been particularly protective since man would inevitably become increasingly prone to kill the offensive reptiles. Against hordes of grazing ruminants, however, the protection is probably perfectly efficient. The eyes are easily assailed and the injured creature rushes away followed doubtless by its comrades. The snake thus, whether aided by a warning sound or by the infliction of transitory pain, is aided at the time of its most frequent danger."

irreversibility of evolution, it can be pointed out that spitting as a defense mechanism must have considerable survival value, and once the behavioral and anatomical specializations involved in spitting were perfected there is little reason to believe that they would be lost. Therefore it seems more probable that evolution has not reversed direction in this case, but rather has not proceeded to final perfection in such populations of *Naja naja* as that inhabiting China.

Fang structures conceivably could evolve simultaneously with habits as they may have in Malayan *Naja*, or in *N. nigricollis* of Africa, but modification of behavioral patterns would enable only those cobras to eject venom which possessed suitably adapted fangs. Therefore, such behavioral patterns, possibly heritable, could more readily evolve once the fangs had become structurally modified to direct the venom outward. Once structure and behavior had become even partly integrated, the defensive value would be of immense selective importance.

The presence in the Philippines, in Java and in the Malayan Peninsula of cobras that have been observed to utilize their fangs for the ejection of venom for defensive purposes may be, in part, the result of peninsular and insular isolation, since selection proceeds more rapidly where smaller populations are isolated and recessive mutations have a better chance of becoming homozygous. Thus it is conceivable that the imperfectly adapted fangs of Chinese, Burmese and Siamese *Naja naja* represent a preliminary stage in the evolution of well-adapted fangs, requiring: (1) the origin of a behavioral pattern utilizing such modifications for defensive ejection of venom, and (2) a selective advantage of such behavior that eventually results in the elimination of those members of the population having imperfect modifications and retention of those having fang characters better adapted to direct the venom more effectively into an enemy's eyes.

The assumption that fangs partly adapted for the defensive ejection of venom arose through fortuitous modifications prior to the evolution of suitable behavioral

patterns necessary to make them useful need not involve any teleological viewpoint. The amount of variation in fang structures (see Figs. 28, 30 and 32) within existing *Naja naja* shows plainly that several alterations in fang structures have arisen in the course of the evolution of various populations, and a fang partly adapted for spitting may have occurred quite as easily as any other sort of fang. Since modifications of the fang which enable a snake to eject venom forward do not preclude use of the fang for the more usual purpose, namely, the hypodermic injection of venom at the time of the bite, it follows that such modifications are not disadvantageous. Thus, fortuitous genetic changes involving suitable alterations of the discharge orifice of the fang might have been retained for countless generations before the necessary behavioral pattern evolved that placed a selectional value on fang characters. Originally crude, the whole mechanism would then have become improved, perfected and better coordinated through the selectional value of such protective behavior. Inasmuch as cobras referable to the genus *Naja* were present at least as early as the Middle Miocene, and doubtless earlier, several million generations have provided ample grist for the evolutionary mill.

To recapitulate, on the basis of the evidence supplied in descriptions of fangs and in the review and discussions of the literature, the conclusion is drawn that adaptive modifications in the fangs and venom (of *Hemachatus* at least) of spitting cobras are closely correlated with the behavior of such snakes. Cobras having rather typical elapid fangs which direct the venom downward have not been authentically reported to eject venom as a means of defense under normal circumstances, nor is it considered likely that they could do so with efficiency. On the other hand, snakes that utilize such means of defense do not find it necessary to open the mouth widely in order to ejaculate venom. It is problematical whether such cobras have venom glands specialized for the rapid secretion of venom in sufficient quantities to enable them to repeat the defensive action, but the reports by

Loveridge (*supra cit.*) for *N. nigricollis* and of Kopstein (*supra cit.*) for *N. naja* suggest that this may be the case. The venom of any cobra, however, apparently is absorbed through the eyes of mammals, producing poisonous effects. Thus, any species of *Naja* is theoretically potentially capable of evolving fang and behavioral adaptations enabling it to utilize its venom for purposes of protection by ejecting it in the eyes of an attacker.

Modifications in the point of the fang, venom canal and discharge orifice must have evolved by gradual steps. Comparisons of the fangs of spitters and non-spitters indicate that those of the former evolved from fangs not unlike those of the latter, by partial closure of the lower end of the discharge orifice and the loss of the groove below the orifice that extends onto the point of the fang in non-spitters. Intermediate stages are represented only in *Naja naja*, while available specimens of *Hemachatus* and *N. nigricollis* are uniformly well adapted to expel venom for-

ward from the fang. The latter two species are likewise more inclined to use their venom for defense, whereas the spitting behavior cannot be evoked in many specimens of *Naja naja*. Therefore, it appears to be possible that, following an original fortuitous modification, the fangs of spitting cobras have become perfected as a result of small cumulative orthogenetic modifications probably directed by natural selection. The perfected fang structure appears to be integrated with the neural and muscular mechanisms in the most perfectly adapted species, but incompletely integrated in *Naja naja*, the spitter in which fang adaptations are most variable. On zoogeographical and anatomical grounds it can be stated that adaptive fang characters have evolved separately in three distinct but related species. Similar, but in no case identical, fang adaptations are not indicative of close relationship, however, but have resulted from ‛parallel evolution in originally diverging strains of a common ancestral stock.

SUMMARY AND CONCLUSIONS

1. On the basis of the data presented, the genus *Naja* appears to be composed of seven living species, at least three of which can eventually be separated into subspecies when more material is available. Three species are confined to Asia and adjacent islands, while a fourth species ranges from Africa into the contiguous portion of Asia Minor, the Arabianpeninsula. The Asiatic species do not appear to overlap in range, whereas each of the four distinct African species is found within the range of one or more of the other species. One fossil species of the European Middle Miocene is referable to the genus *Naja*.

2. Maxillary dentitional characters permit division of the genus *Naja* into two groups or assemblages. Those east of the Sulaiman Range and the Bugti Hills of India have less than two (normally none or one) solid teeth on the maxilla, whereas six species (or seven including the fossil form) west of this physiographic barrier normally possess two solid maxillary teeth behind the fangs.

3. The genera *Hemachatus*, *Hamadryas* and *Walterinnesia*, despite the fact that they are monotypic, should be retained. *Limnonaja* Schmidt is referred to the synonymy of *Boulengerina* which is thus composed of two species, *christyi* and *annulata*.

4. Fang characters and other dentitional differences are often correlated and provide useful information in connection with taxonomic and phylogenetic interpretations. A speculative summary of phylogenetic inferences is presented, and reasons are advanced for nomenclatorial retention of the family Elapidae. Similarities in the venom apparatus suggest that the living Elapidae, Hydrophiidae, Viperidae and Crotalidae all descended from a single terrestrial elapid progenitor.

5. The chief skull differences between the proteroglypha (Elapidae and Hydrophiidae) and the solenoglypha (Viperidae and Crotalidae) lie in the attachments of the maxilla and prefrontal. Erection of the fangs in the solenoglyphs involves a combined sliding and hinge action where the

maxilla engages the prefrontal, whereas only a slight hinge action is present in the proteroglyphs. Limited hinge action of the prefrontal, where it is attached to the frontal seems to be present in most solenoglyphs but is absent in the primitive viperid, *Causus*, and in all proteroglypha examined.

6. The mechanism of fang replacement, providing for alternate use of paired inner and outer sockets in each maxilla, is essentially the same in solenoglyphs and proteroglyphs, although the number of replacement teeth potentially present behind any given socket varies from genus to genus, within narrow limits. Snakes of the genus *Pseudohaje*, for example, have one more replacement tooth in the process of development than any *Naja* examined. Fang replacement in cobras is described in some detail and while both proteroglyphs and solenoglyphs normally emerge from the egg with functional fangs in the inner positions of each maxilla, synchronism of the replacement mechanisms in right and left maxillae is apparently lost as individuals attain adult proportions.

7. The solid teeth of snakes examined are replaced in much the same manner as the fangs, the replacement mechanism providing for alternate occupancy of contiguous sockets. Usually only the teeth in either the even- or odd-numbered series of any tooth-bearing bone are completely ankylosed. Ankylosis of teeth begins in the anterior of the bone and progresses from socket to socket posteriorly, the tooth in the rearmost socket of either series being ankylosed before shedding of the alternate series is inaugurated. Therefore all teeth in any given bone will be ankylosed simultaneously only for a brief period between ankylosis of one series and the shedding of the other. The replacement mechanisms of adjacent bones, the palatine and pterygoid, are not coordinated, and the last socket of the palatine and the first pterygoid socket may be shed simultaneously. Gaps or diastemas in the series of any single bone similarly result in lack of coordination between the rows of teeth so separated. However, nearly identical replacement mechanisms are present for the teeth of the maxillary, palatine, pterygoid and dentary,

but replacement teeth are located on the inside surface of the maxilla and dentary, but on the outside surface of the palatine and pterygoid. Furthermore, there are more replacement teeth present above the palatine and pterygoid sockets than there are above the maxillary and below the dentary sockets.

8. Relative fang proportions, using total length as the datum for comparison, differ in various elapid species and genera, being smallest in some of the more primitive elapids of New Guinea, which lack a diastema between the tubular fangs and the solid teeth, and largest in some of the cobras. Fang proportions are not the same throughout the life of a cobra, the fangs being relatively larger in juveniles, a condition probably correlated with the proportionately larger head of young cobras. The fangs of vipers and pit-vipers, in general, are proportionately larger than those of elapids, reaching their maximum size in the Gaboon viper, *Bitis gabonica*, while the smallest fangs of any solenoglyph are probably those of the African night adder, *Causus*. Sexual dimorphism in fang length is indicated in adults of only one species of *Naja* for which sufficient data were available; even in this instance the series on hand were not sufficiently large to establish this conclusion.

9. Cobra fangs are essentially similar to those of vipers and pit-vipers in their general morphology. The venom canal is closed in all species of the family Elapidae examined, although the suture, or weld, on the external surface of the fang where the walls of the venom canal meet is more easily seen in proteroglyphs than in solenoglyphs. The fangs of *Naja* are described and figured in some detail.

10. Three species of cobra authentically reported to "spit," or to eject their venom, unquestionably for defensive purposes, possess modifications of the discharge orifice which serve to direct the venom (in single jets from each functional fang) forward instead of downward. The most highly adapted of these is the ringhals, *Hemachatus haemachatus* of South Africa, the fangs of which direct the jets of venom slightly upward when the point of

the fang is perpendicular to the substratum. The African black-necked cobra, *Naja nigricollis*, is nearly as perfectly and uniformly adapted in fang structures as *Hemachatus*, and is reported to resort to "spitting" whenever wounded, or when no avenue of escape permits it to avoid an enemy. Among Asiatic elapids only one species of *Naja* is known to spit, and of those examined, only some populations of *Naja naja* possess the necessary modifications of the fang to permit it to do so. Other populations of *Naja naja* are not well adapted, and a sort of gradient, involving fang structures, is present, Indian *N. naja* possessing fangs which direct the venom downward and slightly outward, while other populations in the southeastern portion of the continent and the adjacent islands have fangs which direct the venom forward. In China, Burma and Siam (Thailand), representatives of *N. naja* possess fangs only partly adapted for spitting, the venom being ejected from them at a slight angle with the point of the fang. However, even cobras adapted for spitting in the Malay Peninsula and in the islands of the Indo-Australian Archipelago do not always eject venom when confronted by an enemy. Therefore it is suggested that fang modifications in some cases may have evolved unaccompanied by the necessary behavioral patterns to make such fangs of practical value in defensive behavior.

11. There is some evidence that modifications of fangs, venom, venom glands and behavioral patterns in *Naja nigricollis* and in *Hemachatus haemachatus* have evolved in an integrated fashion, probably involving the organism as a whole. However, the various degrees of perfection represented in fangs of *N. naja* suggest that modifications of the venom, venom glands, fangs and habits have not necessarily evolved simultaneously but may become intergrated following partial and possibly originally fortuitous modifications of the fang. Subsequent evolution and perfection of the fang and other elements of the "venom-spitting" mechanism of some populations of *Naja naja* may have been directed by natural selection. This involves the assumption that spitting is of protective value, even when habits and morphology are not completely integrated or perfected.

12. Spitting cobras have evolved independently in southeastern Asia, in south Africa and in central Africa. While the three species in all probability evolved from divergent stocks having a common ancestor, similar but not identical venom-ejecting mechanisms in each of the three forms represent homologous adaptations. Similar psychological and morphological modifications are involved which may best be interpreted as parallel specializations differing chiefly in degree of perfection.

<div align="center">LITERATURE CITED</div>

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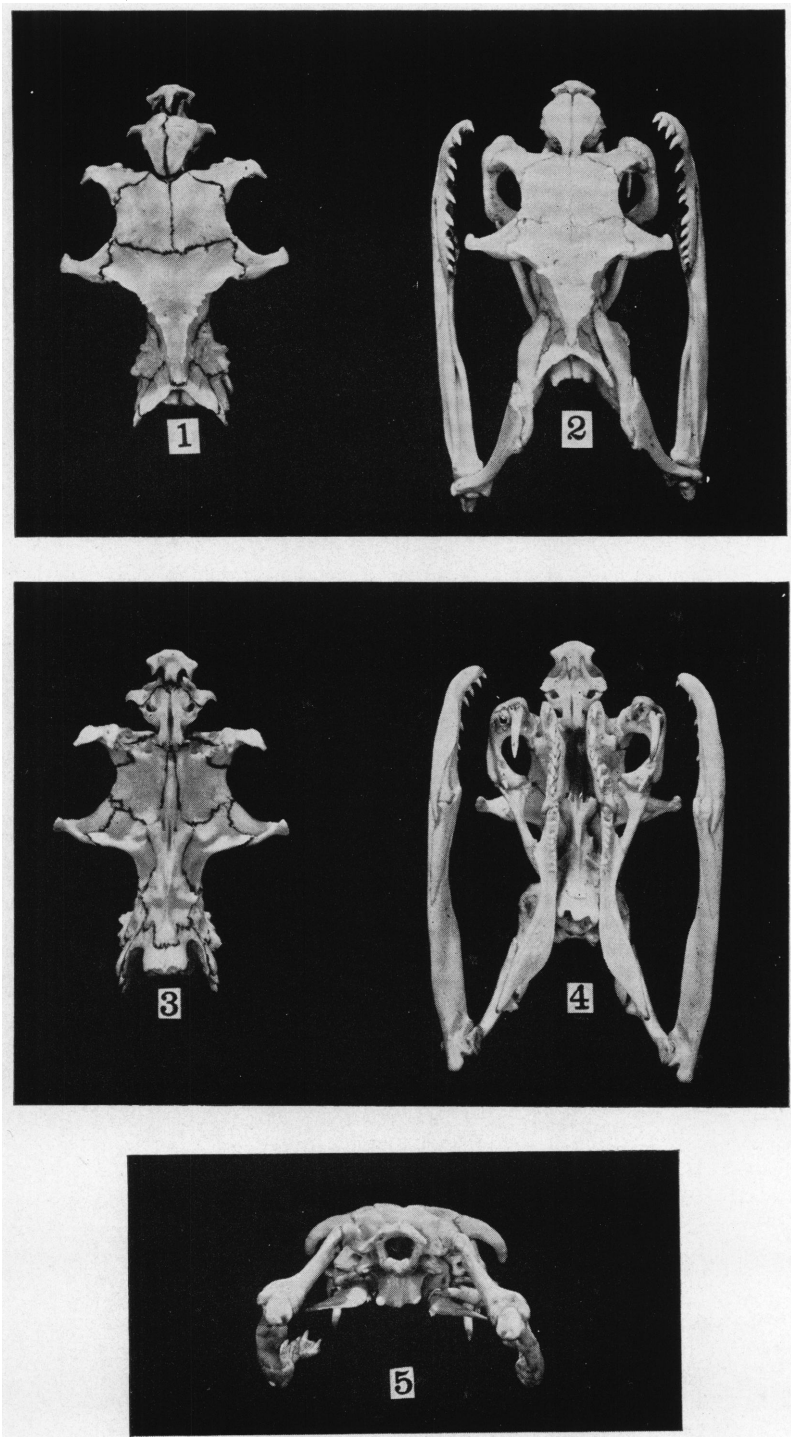
PLATES XLVIII–LI

Elapid skull (fig. 1) compared with the skull of a viperid (fig. 2). Note size and attachment of maxilla and relative size of the fang in each.

Fig. 1. Lateral view of skull ($\times$ 1$^1/_2$) of king cobra, *Hamadryas hannah* (A.M.N.H. No. 32266). Actual length of fangs (straight-line distance from entrance lumen to point), 10.5 mm. Over-all length of specimen in life, approximately 4000 mm.

Fig. 2. Dorsolateral view of skull (slightly reduced) of Gaboon viper, *Bitis gabonica* (specimen on exhibition at The American Museum of Natural History). Over-all length of skeleton, 1380 mm.; straight-line length of fang, 25 mm.