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ADAPTATIONS FOR EGG EATING IN THE SNAKE *ELAPHE CLIMACOPHORA* (BOIE)

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INTRODUCTION

Special adaptations for egg eating in snakes have so far been known in only two genera: *Dasypeltis* and *Elachistodon*. The skeleton of the snakes of both genera is characterized by reduction of teeth and by series of adaptively modified vertebral hypapophyses, a number of which pierce the esophagus and are instrumental in breaking the shell of the egg. The distribution of these two genera, separated by various authors from other colubrid genera by family or subfamily status, is restricted to the continental Ethiopian region for *Dasypeltis*, and to northeastern India for *Elachistodon*, of which only three specimens are known (Shaw, Shebbeare, and Baker, 1941, p. 66).[1] Eggs are included in the diet of a large number of other species of snakes, but to our knowledge no adaptive modifications have thus far been described for any of them.

This paper, the first of a series of studies projected by the senior author dealing with egg-eating snakes, their habits and adaptations, describes the modifications of the vertebral hypapophyses found in the Japanese species *Elaphe climacophora* (Boie), which is manifestly specialized as an egg-eating snake.

ACKNOWLEDGMENTS

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[1] The authors here refer also to two additional specimens in a private collection, the existence of which appears to be insufficiently verified.

and laboratory facilities, for his suggestions and help during the course of the work and for his critical review of the manuscript; to Mr. A. Loveridge of the Museum of Comparative Zoölogy at Harvard College for permission to dissect a number of specimens in his care; and to Mr. Roger Conant of the Zoological Society of Philadelphia for the gift of a large specimen of *Elaphe climacophora.*

Further thanks are due to Dr. Ernest E. Williams of the Museum of Comparative Zoölogy for checking the dissections and generally assisting with advice and help during many phases of the project; to Mr. Carl F. Kauffeld and other members of the staff of the Staten Island Zoological Society for help in the unfortunately unsuccessful attempts at egg feeding; and to Dr. Paul Benzer of New York City for permission to refer to his unpublished observations on the structure of the hypapophyses of *Dasypeltis.* We are also grateful for comments and suggestions to Dr. P. E. Vanzolini of the Departamento de Zoologia, Secretaria da Agricultura, São Paulo, Brazil; to Dr. J. A. Oliver of the New York Zoological Society; to Mrs. Bessie M. Hecht of the American Museum of Natural History, and to Dr. Karl F. Koopman and Mr. Samuel B. McDowell, both of New York City. Last but not least we express our gratitude to Mr. Samuel B. McDowell for drawing the figures of the vertebrae; to Mr. Lee Bolton who took the photograph for figure 5, and to Mrs. K. K. Mastroianni who typed the manuscript.

MATERIAL AND METHODS

Elaphe climacophora (Boie) is found on all four of the main islands of the Japanese Archipelago, where the species is known by the name of "Awodaicho" or "Blue General." In 1946 during the senior author's stay in Japan, the junior author pointed out to him that the egg-eating proclivities of this form had long been known. At the same time the junior author ventured an opinion that the method of egg crushing used indicated that it probably possessed specializations similar to those exhibited by *Dasypeltis.*

On the suggestion of the junior author, chicken eggs were obtained, and feeding of the largest specimen was successfully accomplished. Four eggs were fed to the snake, two on the first attempt and one each on two succeeding occasions. Since repeated observations made it appear more likely that egg-eating specializations might well be present, an investigation of the anatomy of the form was projected. To facilitate this the senior author brought several live specimens to the United States. These were to be used to obtain a photographic record of the egg-eating sequence and for the subsequent morphological studies. The first aim was unfortunately circumvented by the snakes, which fed rapaciously on birds, young rats, and mice, but perversely refused eggs. For this reason figures 1 to 4 of this paper stem from a series of photographs taken by the junior author in 1940, the plates of which had unfortunately begun to deteriorate.

For the anatomical study, three skeletons were prepared; one (A.M.N.H. No. 67733) of the specimens on which the initial feeding studies were made, one of a specimen that was donated for the purpose by Mr. Conant (A.M.N.H. No. 71296), and the last (M.C.Z. No. 1337) of a juvenile specimen from the Museum of Comparative Zoölogy. The findings on these three specimens were confirmed by internal examinations of A.M.N.H. Nos. 32351, 67888, and 67937.

HABITS

The initiation of the egg-eating process as observed in *Elaphe climacophora* does not differ significantly from that observed in specimens of North American species of *Pituophis*, *Drymarchon*, and *Elaphe*. The snake first examined the egg, with liberal use of its tongue, suggesting that food recognition is accomplished by means of olfaction through the tongue-Jacobson's organs mechanism. Thereafter the snake attempted to seize the egg by biting. No intentional orientation of the snake with reference to the egg was ever observed during the initial seizure of the egg. Whenever the snake bit the egg crosswise (fig. 1), it thereafter worked its jaws around to either of the ends, in a manner similar to that employed in swallowing a small mammal. On a relatively smooth surface the reptile generally had trouble maintaining a grip on the egg, until it was accidentally maneuvered against a fixed object or a coil of its body.

Thereafter engulfing proceeded in a normal manner, the egg being forced into the distending esophagus by the action of the jaws (fig. 2) and thence being propelled further by the contraction of the muscles anterior to it.

It was only when the egg entered the posterior esophageal region that the snake's behavior differed from that of one of the

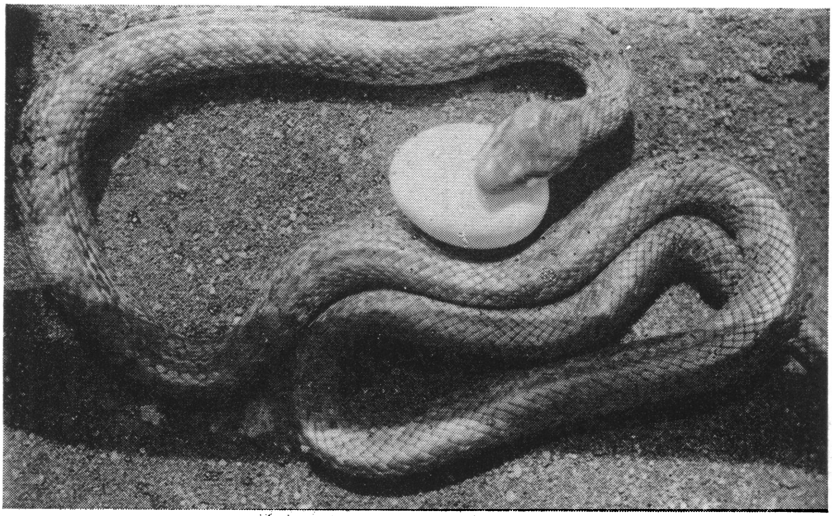

FIG. 1. *Elaphe climacophora* seizing egg.

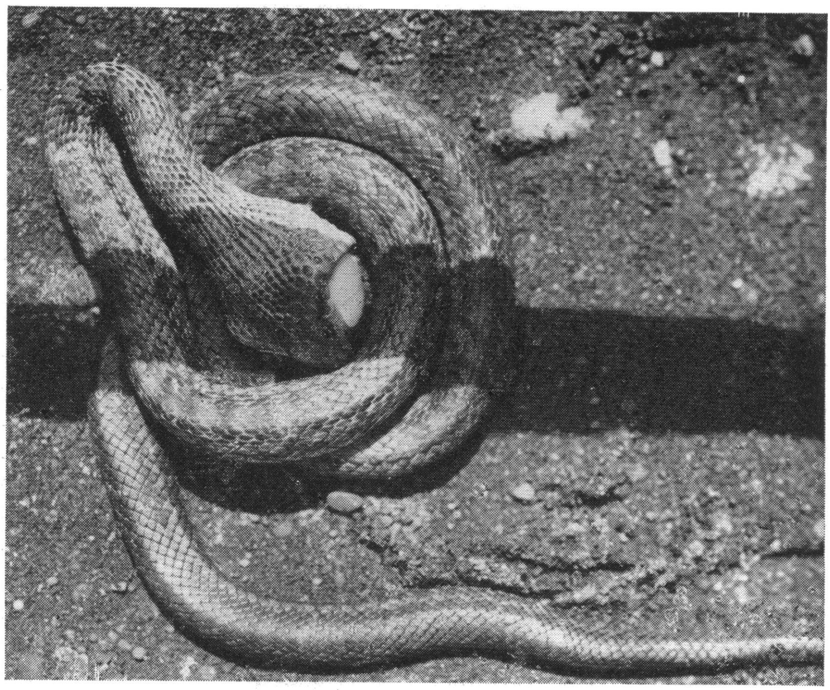

FIG. 2. Egg being engulfed by specimen.

above-mentioned North American species. When the egg reached this location, about 6 to 8 inches from the tip of the snout in the 5-foot 5-inch specimen observed (A.M.N.H. No. 67733), those portions of the body immediately anterior and posterior to the egg were thrown into S-shaped loops, these holding the egg in position and seeming to subject it to considerable pressure (fig. 3). The pressing of the body against the ground described by Ditmars (1949, p. 212) for *Pituophis m. melanoleucus* was, however, not observed in *Elaphe climacophora*.

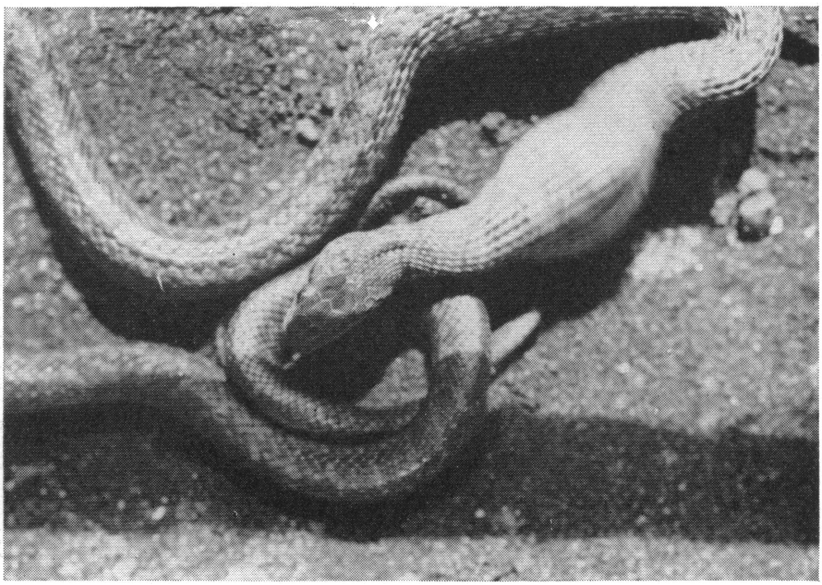

FIG. 3. Instant of egg crushing.

The final fracture of the egg shell, accompanied by a distinctly audible sound, appeared to be caused by the forces imposed on the egg by the two S-shaped loops slowly moving towards each other. The photograph shown in figure 3 appears to have been taken at the exact instant of the egg's breaking, as indicated by the fuzzy outline of the region containing it. The entire process took approximately 20 minutes for the first egg fed to our specimen, and seven minutes for each of the eggs fed thereafter.

Both egg content and broken shell are passed down the alimentary canal (fig. 4), as *Elaphe climacophora* swallows the shell with the egg. This is contrary to the method of egg swallowing observed in *Dasypeltis*, which regurgitates the shell (Smith, 1849, text for pl. 73; FitzSimons, 1912, pp. 104, 106; Rose, 1950, pp. 256–257), although in accordance with the egg-eating habits of other North American species of *Elaphe* (Ditmars, *supra cit.*). After approximately four days the shell is expelled in fragmentary condition from the alimentary canal.

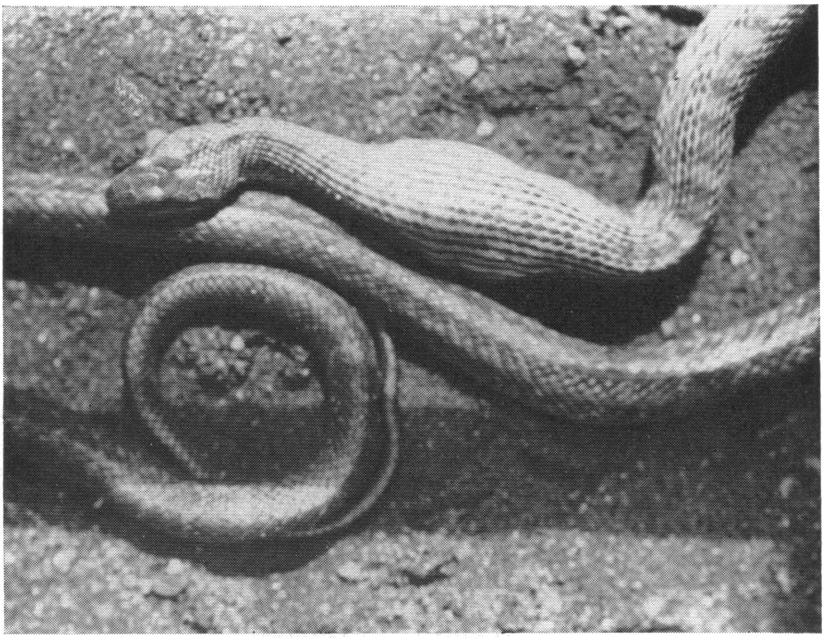

FIG. 4. Egg with shell passing down alimentary canal.

ADAPTATIONS

ESOPHAGUS: The observations discussed above show quite clearly that the breaking of the egg occurs in the posterior esophageal region of the snake, and, therefore, internal examinations were started here. In this region the esophagus occupies a position along the apex of the roughly triangular body cavity, and upon being opened the anterior hypapophyses appear as bumps under its lining. No penetration of the esophagus proper was noted, although the protuberances formed by the hypapophyses could be seen and felt without undue pressure on the thin esophageal lining.

When teasing the esophagus away from its dorsal attachment was begun, it was found that it was quite securely bound to the muscles lining the inside of the ribs, the attachment proceeding down to about one-half of their total height. This strong dorsal attachment occurs from the anterior end of the specimen to the point where the series of anterior hypapophyses ends. Beyond, the alimentary canal rotates towards the left side of the body cavity, and finally assumes a position along its left ventral side.

Examination of the esophagus under the microscope reveals that its wall is slightly heavier along the middorsal line, with faint reënforcing rings of tissue present in certain instances. After removal of the esophagus the tips of the hypapophyses readily became apparent. They appeared between the muscles overlying the vertebrae and were separated from the esophagus only by a very thin layer of tissue. These tips did not, however, penetrate the muscle sheath in a straight line, but rather presented a staggered pattern, with each hypapophysis offset a small amount from the mid-line of the snake.

VERTEBRAL COLUMN: Figure 5 shows a side view of the anterior part of the vertebral column of a specimen of *Elaphe climacophora* (A.M.N.H. No. 67733). Vertebrae as far back as the forty-

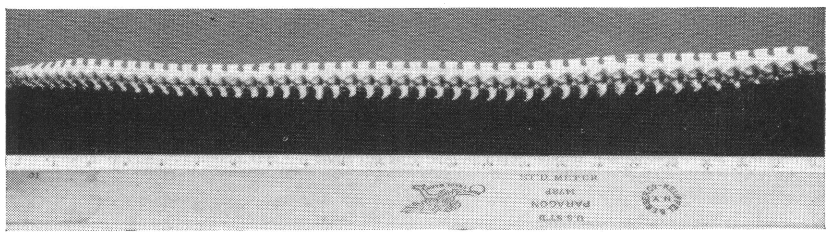

FIG. 5. Side view of anterior portion of the vertebral column of specimen of *Elaphe climacophora* (A.M.N.H. No. 67733) to show variation of hypapophysial shape along the series.

ninth carry hypapophyses in this specimen, the observed range for the species being from 49 to 51, well within the range of other species of the genus. Among those examined so far, the following may be cited for comparison: *E. dione*, 39; *E. guttata*, 48–49; *E. o. obsoleta*, 45; *E. o. quadrivittata*, 48; *E. o. confinis*, 51; *E. schrencki anomala*, 45; and *E. taeniura*, 54–55. All these counts start with the atlas and indicate the position of the posteriormost vertebra with an enlarged hypapophysis.

Figure 5 clearly shows the modification of these vertebrae in a specimen of *E. climacophora*. The majority of the hypapophyses are recurved from their normal backward slope to the point where they assume a sickle shape, with the open part forward. While the first few hypapophyses do not, of course, show the same degree of modification exhibited by those in the region just before the end of the series, they do show a tendency towards modification at their tips, as evidenced by small projections along their anterior edge. It must be noted here that the skeleton of other specimens, while demonstrating the same general configuration, showed considerable variation in several significant structural details, including the degree of knobbing and recurvature.

HYPAPOPHYSES: Before discussing the modified hypapophyses,

FIG. 6. Anterior vertebra of *Elaphe taeniura* (A.M.N.H. No. 62829).

we shall define the norm from which these modifications appear to have departed. For this reason figure 6 showing a typical anterior vertebra of *Elaphe taeniura* (A.M.N.H. No. 62829) is included. The hypapophyses of this east Asian form, similar in appearance to those of *E. guttata* and other North American forms, are about twice as long as broad, straight, and bluntly rounded at their tips and project caudally, as is usual for the hypapophyses of most snakes, at an angle of approximately 60 degrees from the main axis of the spine.

The vertebrae carrying hypapophyses in *climacophora* can be divided into four general categories: anterior, intermediate, modified, and regressing.

The anterior series of vertebrae, which in the specimen described first (A.M.N.H. No. 67733) extends from the atlas-axis complex to about the nineteenth vertebra, shows relatively little modification, except that the tips of their hypapophyses demonstrate evidence of a whitish substance that also forms the knobs on the posterior vertebrae of the series. The first eight are, in fact, unmodified except for this whitish tipping, the nature of which is discussed below. Vertebrae 9 to 18 show various irregular outgrowths of this substance; such outgrowths are generally in the nature of foward-projecting knobs.

The nineteenth vertebra (fig. 7A) is the first to show definite recurving, with a shrinkage of its posterior edge to make up for the growth on the anterior. The next vertebrae, numbering eight in the specimen at hand, form an intermediate series in

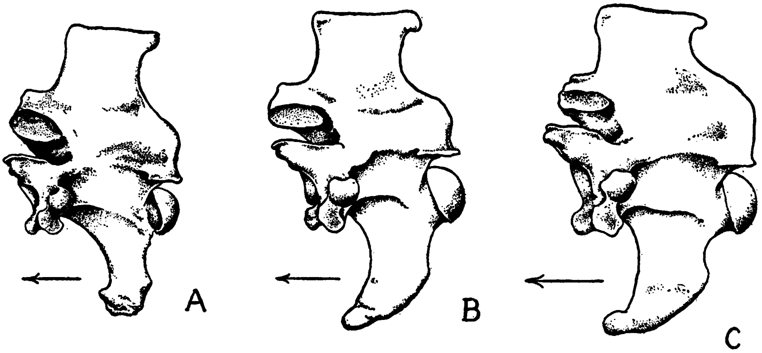

FIG. 7. Anterior vertebrae of *Elaphe climacophora* (A.M.N.H. No. 67733). A. Nineteenth. B. Twenty-ninth. C. Forty-second.

which the development towards the following stage is irregular. In general, the recurvature increases and there exists a tendency towards knobbing of this projecting tip. It must be emphasized, however, that this change is sporadic enough so that several of the vertebrae are more highly developed in this respect than those immediately posterior to them.

The twenty-ninth vertebra (fig. 7B) marks the beginning of the fully modified series extending to and including the forty-fourth vertebra. Here each hypapophysis exhibits a sickle-shaped recurvature that is tipped by a teardrop-shaped knob of dense, white-colored matter pointed forward and downward at approximately a 45-degree angle. Furthermore, the entire end section of the tip is capped by this dense bony matter. This cap is firmly united with the knob and tends to lend a high compressive strength to the structure.

As the end of this series is approached the only further variation to be observed is the increase in size and length that is usual for vertebrae in this region and a further lengthening and upward recurving of the hypapophysis' tip. Figure 7C, depicting the forty-second vertebra of the specimen, clearly shows this tendency. After the forty-fourth vertebra there is a general reduction in size of the hypapophyses, the last and minor one being located on the forty-ninth vertebra.

VARIATION: In addition to the specimen (A.M.N.H. No 67733) just described, two other skeletons were prepared, one (A.M.N.H.

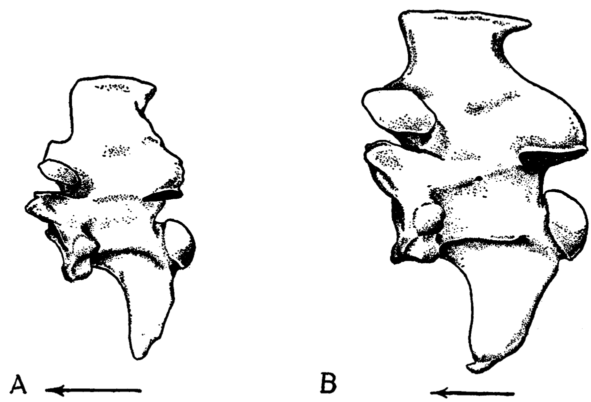

FIG. 8. Anterior vertebrae of *Elaphe climacophora*. A. Thirty-ninth of juvenile (M.C.Z. No. 1337). B. Thirty-ninth of adult (A.M.N.H. No. 71296).

No. 71296) of an adult specimen and the other (M.C.Z. No. 1337) of a juvenile. The bases of the hypapophyses and their general orientation remain identical in these, except that the amount of recurvature is slightly more limited. The real difference lies in the fact that the white tipping is very much reduced, and only rather sketchy indications of the drop-shaped excrescenses occur. In fact, these are entirely absent in the juvenile specimen.

The hypapophyses of the adult specimen (A.M.N.H. No. 71296) seem in general to follow the same organizational scheme as those described above. The anterior and intermediate series, while capped with the white material, show no trend towards knobbing. In this specimen also the hypapophyses of the fully modified series, starting at about the thirtieth vertebra, while recurved almost as much as those of the previously described specimen exhibit only a slight and rather irregular development of drop-shaped knobs. Where present they are of the same general appearance as the others but much smaller. A typical one is shown in figure 8B. The regression section again starts with the forty-fifth vertebra.

The juvenile specimen skeletonized is even further lacking in development of white knobbing. The hypapophyses are generally organized as above and, while definitely exhibiting white tipping, pointing of their ends, and recurvature, they show no evidence of knobbing. It should be stated here that, while this variation may possibly affect the efficiency of the egg crushing, all the specimens examined were definitely specialized for this function, so that the degree of specialization is all that seems involved.

Before the possible and probable reason for this diversity is discussed, it might be well to review what is known regarding the nature of the dense white matter of which these knobs are composed.

Similar material has been described as covering the tips of the hypapophyses of *Dasypeltis*, and a number of authors have offered statements and speculations regarding it. Jourdan (1834, p. 214) is quoted by Hoffman (1890, p. 1421) as stating that these tips are covered with enamel, a similar statement being included in Boulenger's diagnosis of the subfamily Rhachiodontinae (1894, p. 353), while Owen, in his "Odontography" (1845, p. 221), refers to a hard cement capping the extremities. Kathariner (1898, pp. 504–505), in his interesting paper on the anatomy of *Dasypeltis*, which appears to have been largely neglected by subsequent authors, definitely states that specialized bone only and no enamel was found on microscopical analysis of the tips. Gadow (1933, p. 283), without giving a specific reference for the source of this information, also mentions that the "hard apices [are] erroneously stated to be covered with enamel."

In the early 1940's Dr. Paul Benzer of New York City undertook a study of the processes of *Dasypeltis* in order to determine their nature. This work, originating from a different point of view, has never been published, but Dr. Benzer has assured the senior author that his slides of ground cross sections of the hypapophysial tips do not reveal the presence of any enamel. The tips were found to be composed solely of a very hard and dense bone. While it is only fair to point out that an enamel cap of the type generally assumed by previous authors to be present in this case could very easily be chipped off and lost during the preparation of the slides, this finding is what should be expected from a morphological standpoint.

In a consideration of the probable nature of the knobs indicated above, two possible hypotheses arise to explain their variation, namely: genetical determination and phenotypic eburnification.

In case the former hypothesis is correct, the knobs may either be genetically determined individual variations or prove to be racial differences of a geographic nature. In either case, the difference can be considered adaptive and in the latter case due to the relative availability of eggs as opposed to other food in various regions. In the former hypothetical case balanced polymorphism may occur, each of the two hypapophysial conditions being selectively advantageous under certain conditions. Unfortunately, two of the specimens skeletonized lack data, with only the juvenile specimen possessing adequate locality data (from Kanagawa Prefecture, Japan). Furthermore, the present scarcity of material precludes satisfactory analysis of a geographic variation even if such a variation were definitely present.

Of the various tissues of the body, bone is one of the more plastic, inasmuch as it gives a strong reaction to specialized stimulus. It is furthermore known that bone in exposed locations, such as along the cutting edge of incisors with worn enamel, etc., eburnifies, that is, it hardens as a result of usage. In such eburnified bone the general spongy nature of the tissue changes, as the hollow spaces in the cancellous bone are filled in with mineral matter, resulting in a hard, dense structure such as that observed by Dr. Benzer in the hypapophysial tips of *Dasypeltis*.

Unpublished observations of the senior author on the vertebrae of a variety of snakes show that varying types of minor outgrowths that are directionally random are far from uncommon on the vertebral hypapophyses. It may be stated that any such pressure-stimulated growth would naturally take place on the anterior face of the peculiarly recurved hypapophyses of *E. climacophora*. There is therefore the distinct possibility that the degree of knob formation on the tips is related to the amount of egg feeding indulged in by any individual snake, as the shells of avian eggs form by far the hardest of the foods ingested by this species. Another point in favor of this hypothesis is that the hypapophyses of the juvenile (M.C.Z. No. 1337) specimen showed relatively the least amount of tip development, although ontogenetic changes may occur, regardless of other factors.

While it seems probable that either or both of the above hypotheses may offer clues for the future solution of this problem, the analysis thereof must await the acquisition and preparation of additional material. It is intended to present the results of this study in a later paper.

FUNCTION

The preceding discussion of the morphological modifications observed in this species demonstrates a considerable adaptation for eating eggs. In *E. climacophora* the hypapophyses do not exhibit the extreme specialization shown in *Dasypeltis scaber*, where the twenty-sixth to the thirty-second hypapophyses penetrate the esophagus proper, actually barring the egg's further progress and piercing its shell as it is being forced against them. In *E. climacophora* the muscles of the trunk hold the egg in position from both directions, which accounts for the S-curves both anterior and posterior to the egg. The function of these curves is to hold the egg in position while it is being subjected to a considerable compressive stress and is being forced against the hypapophyses. The knobbed or pointed hypapophyses then facilitate crushing by tending to concentrate the stresses at the contact points. Their adaptation to this function is manifest, as their shape permits the transmission of high compressive forces. It is of further interest that the staggering or offsetting of the hypapophysial tips facilitates this contact and may increase the stress concentration.

DISCUSSION

Ditmars (1949) refers to three methods of egg eating employed by snakes: dissolution of the shell by gastric juices (*Elaphe obsoleta lindheimeri*, p. 232), crushing by straight muscular force (*Elaphe vulpina*, *E. o. quadrivittata*, etc., pp. 220, 228, etc.), and by the afore-mentioned crushing of the egg against a hard object external to the body (*Pituophis m. melanoleucus*, p. 212). The effectiveness of these methods would tend to increase in the order in which they are listed, effectiveness here bearing an inverse relation to the size of snake required to swallow an egg of given diameter, which directly determines the muscular effort required for crushing. The first-mentioned method may be disregarded, as the disadvantages of prolonged sluggishness and immobility should be obvious. The method used by *Elaphe climacophora,* while still requiring more muscular effort than the piercing or "sawing" action employed by *Dasypeltis* (FitzSimons, 1912, p. 106) and perhaps by *Elachistodon* (Reinhardt, 1863, p. 202), proves to be markedly more effective than methods mentioned above. The result is to increase the size of the eggs that may successfully be engulfed by a snake of given size.

Maki (1931, p. 100) indicates that *E. climacophora* feeds on rats, mice, and birds and their eggs. This has been borne out by our observations, which were unfortunately based on captive snakes only and hence are prejudiced by the fact that the food habits of captive snakes often bear little or no resemblance to the food habits of the same form in the wild. The adaptation of this form to egg eating has thus not resulted in the exclusive egg diet that characterizes *Dasypeltis,* although it must be remembered that the latter species evolved in an environment in which there is an abundant supply of this specialized food throughout the year (Pitman, 1938, p. 129). It is true, however, that the modifications have endowed *E. climacophora* with a selectively important advantage by allowing juvenile specimens to include another and high energy item in their diet. As previously mentioned, many species of *Elaphe* and of other genera eat eggs, but lack of specialization may restrict[1] egg-eating habits to adults. The basic advantage of further modifications is that they permit juveniles, as well as subadult invividuals, to have a wider choice of food, thus increasing the probability of their attaining adult size.

SUMMARY AND CONCLUSIONS

This paper describes the habits and vertebral modifications for egg crushing of a species of *Elaphe* specialized for the eating of eggs. It is pointed out that considerable variation exists among the three specimens examined, and thus a final decision as to the cause and significance of this variation is precluded at the present time by lack of material, but a number of hypotheses are offered to explain the evolutionary significance of the vertebral modification.

There are possible taxonomic implications in view of the development of similar specialization among related forms and their

[1] It is possible for half-grown snakes to feed on the eggs of the smaller species of birds or to eat those of reptiles, including the small eggs of many lizards.

bearing on the status of the snakes (Dasypeltinae), now placed in a separate subfamily largely because of similar but more extreme adaptive specialization.

It may be of interest to note here that preliminary investigations of the senior author show that similar specialization exists in *Elaphe carinata*, *E. dione*, and *E. schrencki anomala*, among Chinese species of *Elaphe* examined thus far. In *E. carinata* modification of the hypapophyses has progressed to the point of penetration of the esophagus.

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