General Skull, Bone, and Muscle Variation in *Agkistrodon* and Related Genera

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Agkistrodon and its related genera, *Calloselasma, Deinagkistrodon,* and *Hypnale,* have in large part been recognized on the basis of integumental and color characteristics. Some taxonomists have expanded such analyses to bone shape (Chernov, 1957; Brattstrom, 1964) and skull proportions (Hoge and Romano-Hoge, 1981) in an attempt to establish the boundaries of these genera. Aspects of the jaw musculature have more recently been consulted (Groombridge, 1986; Mao et al., 1986) when seeking phylogenetic relationships. It is the purpose of this paper to extend the analysis further and to compile information on the dentition, osteology, and myology of representative species within these genera to see if tooth, bone, and muscle variations are consistent with existing generic categories.

Preparation of my contribution and companion contributions in this monograph extended over an especially active and communicative period of research on Asiatic *Agkistrodon* and related genera (Zhao et al., 1979; Sawai and Kawamura, 1980; Zhao, 1982; Nilson, 1983; Chen et al., 1984; Yoshida and Toriba, 1986a; 1986b). A newly named full species has also been recognized, *A. shedaoensis* (Zhao, 1979; Zhao et al., 1979; Zhao, 1980; Jiang and Zhao, 1980), as well as a new subspecies, *A. halys boehmei* (Nilson, 1983). Where characters I examined contribute to the evaluation of Asiatic species, I have tried to include them.

APPROACH

Each of the three categories of skull features was approached in the following manner:

Teeth. The maxilla, pterygoid, palatine, and dentary bones bear teeth. Each maxilla carries two tooth sockets in all species, although usually only one socket is actually occupied at a time by a fang. On the other dentiferous bones, counts of tooth sockets ("tooth counts") were made on skeletons and on preserved specimens (Characters 1-3). Counts were made on both sides, and each was separately entered in the respective tables (1-3).

Osteology. No attempt was made to quantify aspects of skull bone size or shape. Instead, attention was given to aspects of the osteology that have been used previously in the taxonomy of agkistrodontines, namely overall skull proportions (Character 4) and shape of the palatine (Character 5).

(a) *Character 4*—Skull Proportions

This character was introduced by Hoge and Romano-Hoge (1981), and pertained to Old and New World members of the genus *Agkistrodon* (*sensu* Gloyd). I have divided the character into two states.

State 1. Braincase is short and stout; supratemporal bones extend beyond the posterior end of the braincase (Figs. 1A-B).

State 2. Braincase is long and narrow; supratemporal bones are short and do not extend beyond the posterior end of the braincase (Fig. 1C).

(b) *Character 5*—Shape of Palatine Bone

The palatine generally varies in two ways among the genera. First, the number of teeth it bears differs statistically (see Character 3, Table 3). Second, the shape of the bone differs, the feature treated here as Character 5. Chernov (1957) took advantage of the shape of the palatine to place *rhodostoma* into its own genus *Calloselasma,* a genus revived from Cope (1860). Use of the palatine (and other osteological characters) in a taxonomic study of pit vipers was extended by Brattstrom (1964).

The shape of the palatine is influenced partly by the configuration of its articulation with the pterygoid, partly by its overall length, but mostly by the prominence of the choanal process. In the genus *Agkistrodon,* the choanal process is wide and forms a keel-like process atop the palatine (Fig. 2). In *Deinagkistrodon* (Fig. 2) the choanal process is as proportionately tall, but not as wide as in *Agkistrodon.* In *Calloselasma,* the choanal process is tall and slender (Fig. 2). In *Hypnale* this process is low or absent (Fig. 2); further, within *Hypnale,* the posterior articular edge is relatively heightened perhaps incorporating the low choanal process into its dorsal corner.

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TABLE 1. Character 1 — Dentary tooth counts.

	10	11	12	13	14	15	16	17	18	19	20
Agkistrodon intermedius	2	-	-	-	-	-	-	-	-	-	-
A. shedaoensis	1	1	-	-	-	-	-	-	-	-	-
A. halys	-	4	-	-	-	-	-	-	-	-	-
A. strauchi	-	3	-	-	-	-	-	-	-	-	-
A. himalayanus	-	2	-	-	-	-	-	-	-	-	-
A. caliginosus	-	-	1	1	-	-	-	-	-	-	-
A. blomhoffii	-	2	9	4	-	1	-	-	-	-	-
A. bilineatus	-	-	2	-	1	7	5	3	-	-	-
A. contortrix	-	-	1	2	27	69	29	9	2	-	-
A. piscivorus	-	-	-	-	-	1	-	21	38	14	2
Deinagkistrodon acutus *	-	-	-	-	-	2	-	2	3	-	-
Hypnale hypnale **	-	-	-	-	-	1	-	6	4	-	-
H. nepa	-	-	-	-	-	-	-	1	1	-	-
Calloselasma rhodostoma	-	-	-	-	-	-	1	1	2	1	1

*Reported range of 16 to 18 tooth counts by Ma Ji-Fan (1982).
**Reported range of 16 to 19 tooth counts by Wall (1921).

Myology. The lateral jaw musculature was carefully inspected by dissection. Origins, insertions, and gross muscle structure were noted. Terminology follows Haas (1973). At least one representative individual of each species was examined, except for *A. monticola* and *H. walli* which were unavailable. Compared to hard tissues, there are special problems that attend the use of muscles in taxonomic research. Muscles are often altered by fixation and even by the route of inward dissection chosen to expose a muscle. Such distortions can make it difficult for one investigator to use the myological descriptions of another. To avoid this, I include only muscle variation that seemed unaffected by preservation or personal dissection technique.

Four such muscle characters with species-related variation were discovered.

(a) *Character 6*—Insertion of *M. retractor pterygoidei*

The *M. retractor pterygoidei* is present in all advanced snakes and runs from the anterior braincase to the palatomaxillary arch (Kochva, 1962; Haas,

TABLE 2. Character 2 — Pterygoid tooth counts.

	8	9	10	11	12	13	14	15	16	17	18	19	20
Agkistrodon intermedius	2	-	-	-	-	-	-	-	-	-	-	-	-
A. himalayanus	1	1	-	-	-	-	-	-	-	-	-	-	-
A. strauchi	-	-	4	-	-	-	-	-	-	-	-	-	-
A. halys	-	-	2	2	-	-	-	-	-	-	-	-	-
A. shedaoensis	-	-	1	1	-	-	-	-	-	-	-	-	-
A. blomhoffii	-	3	-	3	6	4	-	-	-	-	-	-	-
A. caliginosus	-	-	-	1	1	-	-	-	-	-	-	-	-
A. contortrix	-	-	-	-	-	4	25	48	32	28	11	1	1
A. bilineatus	-	-	-	-	-	-	1	9	5	3	-	-	-
A. piscivorus	-	-	-	-	-	-	9	31	22	11	1	-	-
Calloselasma rhodostoma	-	-	-	-	-	1	1	1	1	1	3	-	-
Deinagkistrodon acutus *	-	-	-	-	-	2	3	1	1	1	-	-	-
Hypnale hypnale **	-	-	-	-	-	-	2	2	3	4	1	-	-
H. nepa	-	-	-	-	-	-	-	-	-	-	1	-	-

*Reported range of 12 to 15 tooth counts by Ma Ji-Fan (1982).
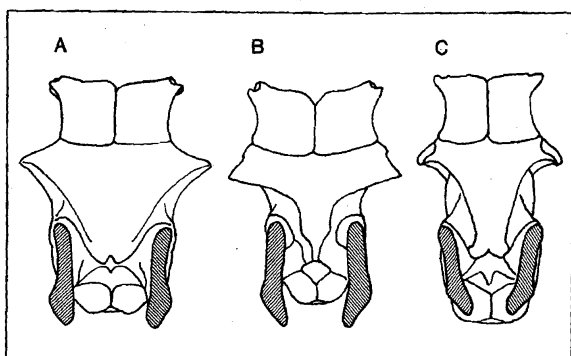**Reported range of 13 to 19 tooth counts by Wall (1921).

FIGURE 1. Character 4—Skull proportions. Dorsal view of skull of New World (A, B) and Old World (C) species. A. *Agkistrodon contortrix*, B. *A. piscivorus*, C. *A. blomhoffii* (after Hoge and Romano-Hoge, 1981).

1973). The course of this parallel-fibered muscle implies that it participates here as in other snakes in retraction of the palatomaxillary arch (Kardong, 1974; Cundall, 1983; Cundall and Gans, 1979; Kardong et al., 1986). Within the agkistrodontine snakes generally, this muscle inserts on the palatine bone. In *C. rhodostoma*, the palatine bone is reduced in size and tooth bearing role. This reduction is further reflected in the reduced insertion of the *M. retractor pterygoidei* to the palatine, thus giving rise to the following character states:

State 1. This, the most common method of insertion of the *M. retractor pterygoidei*, was to three sites: choanal process of the palatine, anterior pterygoid, and medial process of the ectopterygoid.

State 2. In only *C. rhodostoma*, the insertion was to just two sites: anterior pterygoid and medial process of the ectopterygoid. There was no significant direct

fiber insertion to any part of the palatine.

(b) *Character 7*—Origin of *M. levator anguli oris* and *M. pseudotemporalis*

Both muscles originate from the lateral side of the braincase. Both muscles appear broadly to be lower jaw adductors although their insertions differ—*M. pseudotemporalis* to the compound bone, *M. levator*
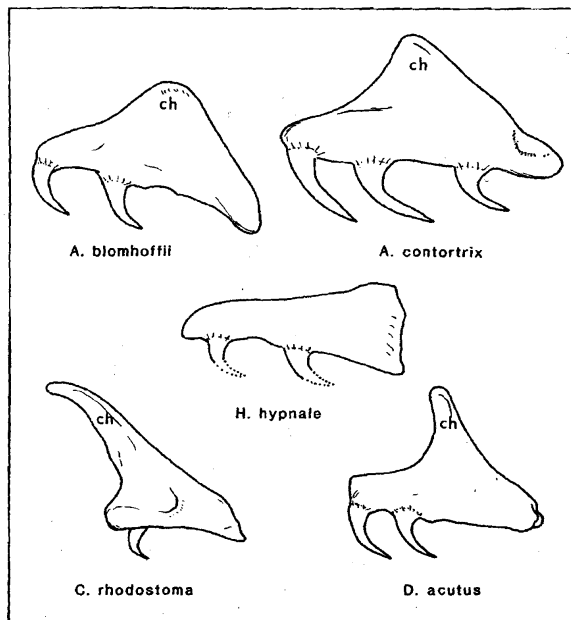

FIGURE 2. Character 5—Shape of the palatine. Medial views of right palatine bone from five species. *Agkistrodon blomhoffii* (CAS 16097), *A. contortrix* (KU 39744), *Calloselasma rhodostoma* (KVK 312), *Deinagkistrodon acutus* (FMNH 25178), and *Hypnale hypnale* (FMNH 119698). Abbreviations: ch, choanal process.

TABLE 3. Character 3 — Palatine tooth counts.

	0	1	2	3	4	5	6
Calloselasma rhodostoma	6	1	-	-	-	-	-
Agkistrodon intermedius	-	-	-	2	-	-	-
A. halys	-	-	-	4	-	-	-
A. shedaoensis	-	-	-	2	-	-	-
A. bilineatus	-	-	-	8	8	2	-
A. blomhoffii	-	-	-	3	8	-	-
A. strauchi	-	-	-	2	1	-	-
A. himalayanus	-	-	-	-	2	-	-
A. caliginosus	-	-	-	-	2	-	-
A. contortrix	-	-	-	8	37	87	-
A. piscivorus	-	-	-	-	2	61	5
Deinagkistrodon acutus *	-	-	-	2	5	-	-
Hypnale hypnale	-	-	-	-	3	2	-
H. nepa	-	-	-	-	1	-	-

*Reported range of 2 to 4 tooth counts by Ma Ji-Fan (1982).

anguli oris to the infralabial gland and dermis of the adjacent integument (e.g., Kardong, 1973). The insertions remained constant throughout the specimens examined herein, but the relative sites of origin differed between species.

State 1. The origin of the M. levator anguli oris lies anterior to the origin of the M. pseudotemporalis.

State 2. The origin of the M. levator anguli oris lies approximately adjacent to the origin of M. pseudotemporalis.

State 3. The origin of the M. levator anguli oris lies posterior to the origin of M. pseudotemporalis.

(c) Character 8—M. pterygoideus

The M. pterygoideus is a complex, pinnate muscle composed of layers of muscle fascicles that insert at specific sites (e.g., Kochva, 1962). It is one of the largest muscles of the jaws. The muscle generally runs from the anterolateral ectopterygoid to the retroarticular process of the mandible. This course places this muscle in a position to exert an influence over lower jaw movement, palatomaxillary arch displacement, and fang positioning.

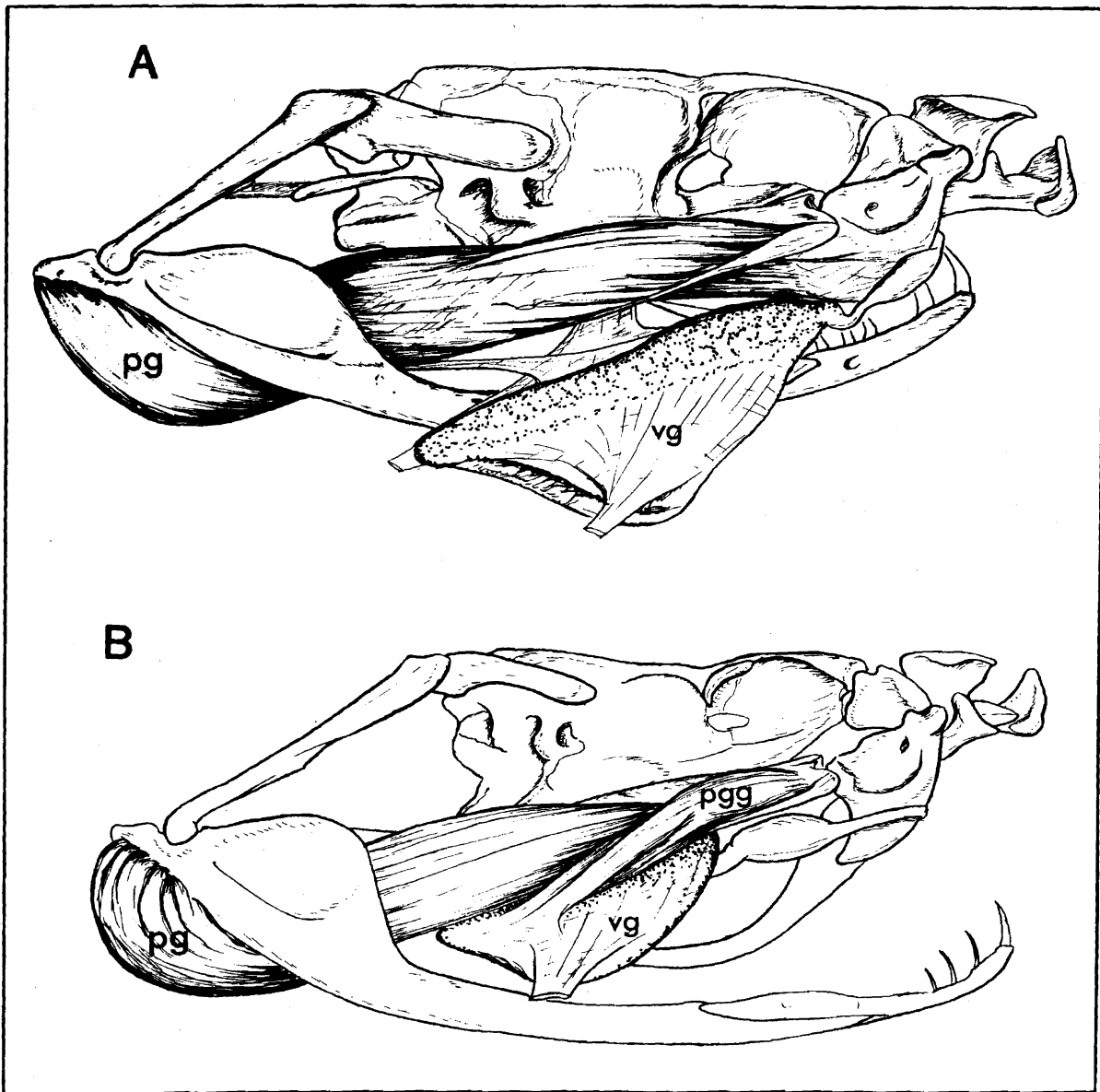When parts of this complex muscle seemed promising in anatomical, functional, or taxonomic

FIGURE 3. Character 8—Lateral view of M. pterygoideus (pg). The apex of the venom gland (vg) has been pulled away from the skull and downward to better expose the pterygoid muscle. A. Character state 1 as illustrated by A. contortrix (KVK 392). B. Character state 3 as illustrated by C. rhodostoma (KVK 393), showing the M. pterygoideus glandulae (pgg); main venom gland (vg).

research, appropriate names were given or emphasized. Generally, in agkistrodontines, the main body of this muscle originates by two heads, the lateral head from the maxillary process of the ectopterygoid, the medial head from the maxilla via a strong tendon. As fibers from both heads pass posteriorly, they soon merge into the main body of the *pterygoideus* and insert directly to the retroarticular process of the mandible. The main venom gland lies against the lateral wall of the pterygoid and is held in association with it via various attachments. Webbing and diffuse connective tissue loosely bind muscles, glands, and passing ligaments. However, four discrete structures were found variously among the agkistrodontines that held or linked the main venom gland and *pterygoideus* into association with each other. The first is the *Ligamentum transverso-glandulare* found in all agkistrodontine species. It runs from the base of the ectopterygoid to the venom gland thus holding the *pterygoideus* between both bone and venom gland. The second connection of *pterygoideus* to the main venom gland is via a short tendon arising from the epimysium of the *pterygoideus* and passing laterally to the medial wall of the venom gland. This short, unnamed fibrous tendon was variously present among the genera.

The other two links between *pterygoideus* and venom gland are formed by the muscle itself. One of these is the *M. retractor glandulae* present to some degree in all species of agkistrodontines examined. It is a gathering of muscle fibers along the ventral surface of the *pterygoideus* that passes forward becoming a tendon that in turn becomes incorporated (inserts) into the transverso-glandular ligament and usually onto the ventral edge of the venom gland.

The other muscular derivative of the *pterygoideus* is the *M. pterygoideus glandulae*, present in only several species of agkistrodontines. When present, it runs from the maxillary process of the ectopterygoid backward to insert on the medial wall of the main venom gland. The systematic importance of this muscle, especially among Old World pit vipers, has been introduced and stressed in previous research (Groombridge, 1986).

Other structural subtleties of *M. pterygoideus* can be found (Kardong, 1973). The functional significance of these described anatomical connections to the venom gland are not known. However, a few variations in its attachments fall into distinctive character states.

State 1. The *M. pterygoideus glandulae* is absent (State B of Groombridge, 1986). A slender fibrous tendon arising posteriorly from the belly of the *pterygoideus* inserts along the medial wall or base of the venom gland near the transverso-glandular ligament, but the *pterygoideus glandulae* is not present (Fig. 3A). This fibrous tendon, arising from the belly of the *pterygoideus*, is actually a specialization of the epimysium that wraps the belly of the muscle. Muscle

fibers of the *M. pterygoideus* do not terminate in this fibrous tendon, but instead run uninterrupted in an anteroposterior direction.

State 2. The second state exists in *D. acutus* (State C of Groombridge, 1986). The muscle fascicle of *pterygoideus* that forms the *pterygoideus glandulae* is evident, but it is still partially incorporated into the main body of the *pterygoideus*. Thus, the *pterygoideus glandulae* is not entirely anatomically independent. Muscle fibers that constitute this emerging *pterygoideus glandulae* converge into a strong cordlike tendon that attaches to the base of the venom gland. The nearby fibrous tendon arises from the epimysium of the belly of the *M. pterygoideus* and joins the strong cordlike tendon of the *M. pterygoideus glandulae*.

State 3. An anatomically discrete *M. pterygoideus glandulae* is present (State D of Groombridge, 1986). It arises directly from the lateral maxillary process of the ectopterygoid bone and inserts broadly over the posteromedial face of the venom gland (Fig. 3B). No fibrous tendon from the epimysium of the belly of the *pterygoideus* is evident.

(d) *Character 9—M. adductor mandibulae externus medialis*

The *M. adductor mandibulae externus medialis*, as its full name implies, belongs to the mandibular adductor group. It is a parallel-fibered muscle that runs from the braincase and often from the supratemporal to the lower jaw. In a few species, the *Ligamentum quadrato-glandulare* passed through the muscle near its origin. The *L. quadrato-glandulare* together with the *L. quadrato-maxillare* and *L. transverse-glandulare* are the three major ligaments that respectively secure the three corners of the triangular venom gland. Even though the origin of this muscle is near or straddles the quadrato-glandular ligament, the muscle probably exerts no significant action on the ligament and thus no significant direct effect on the venom gland. However, the association of muscle origin and course of the ligament exhibited two distinct character states.

State 1. Herein the muscle, arising by a single head from the temporal region, passes downward to the lower jaw. The *Ligamentum quadrato-glandulare* lies next to this muscle (Fig.4-A).

State 2. In this second condition, the *Ligamentum quadrato-glandulare* actually courses through the muscle so that two heads of the muscle do not join until they pass below this dividing ligament (Fig. 4B).

Evaluation of Characters

If the characters discussed herein are to aid in taxonomy, then their variations should fall within useful species boundaries. Yet, character variation can arise from more than just differences in species. Such nonspecific variation arises from several sources. First, artifacts can affect variation. For instance, speed or

completeness of preservation following death of a specimen can affect muscle and other soft tissue appearance. Second, some variation can arise from individual uniqueness, ontogenetic/allometric differences, functional differences, and from geographic/ ecological location. The impact of these (and other) sources of non-specific variation upon the characters cannot be completely assessed because form-function-environment (Bock, 1978) studies are lacking and because large numbers of specimens from representative habitats are lacking. However, with caution, a tentative assessment of characters can be made.

There is evidence that snake skull proportions within a species vary ontogenetically and that some changes are possibly related to jaw function (Cowan and Hick, 1951; Jansen, 1981). If skull proportions (e.g., Character 4) are to be used as taxonomic characters, then the proportion should hold throughout the size range of the species. Or at the very least, the ontogenetic change in proportion should be determined so it can be known at what body size the proportion becomes a reliable species indicator. However, most studies that include skull proportions use only "adult" skulls, thus diminishing the confidence in and weight given this skull character.

Judging from the work of others (Varkey, 1979) and from my own experience (Kardong, 1980), muscle attachment areas of sites vary within a species. This seems partially related to size, but also to indi-
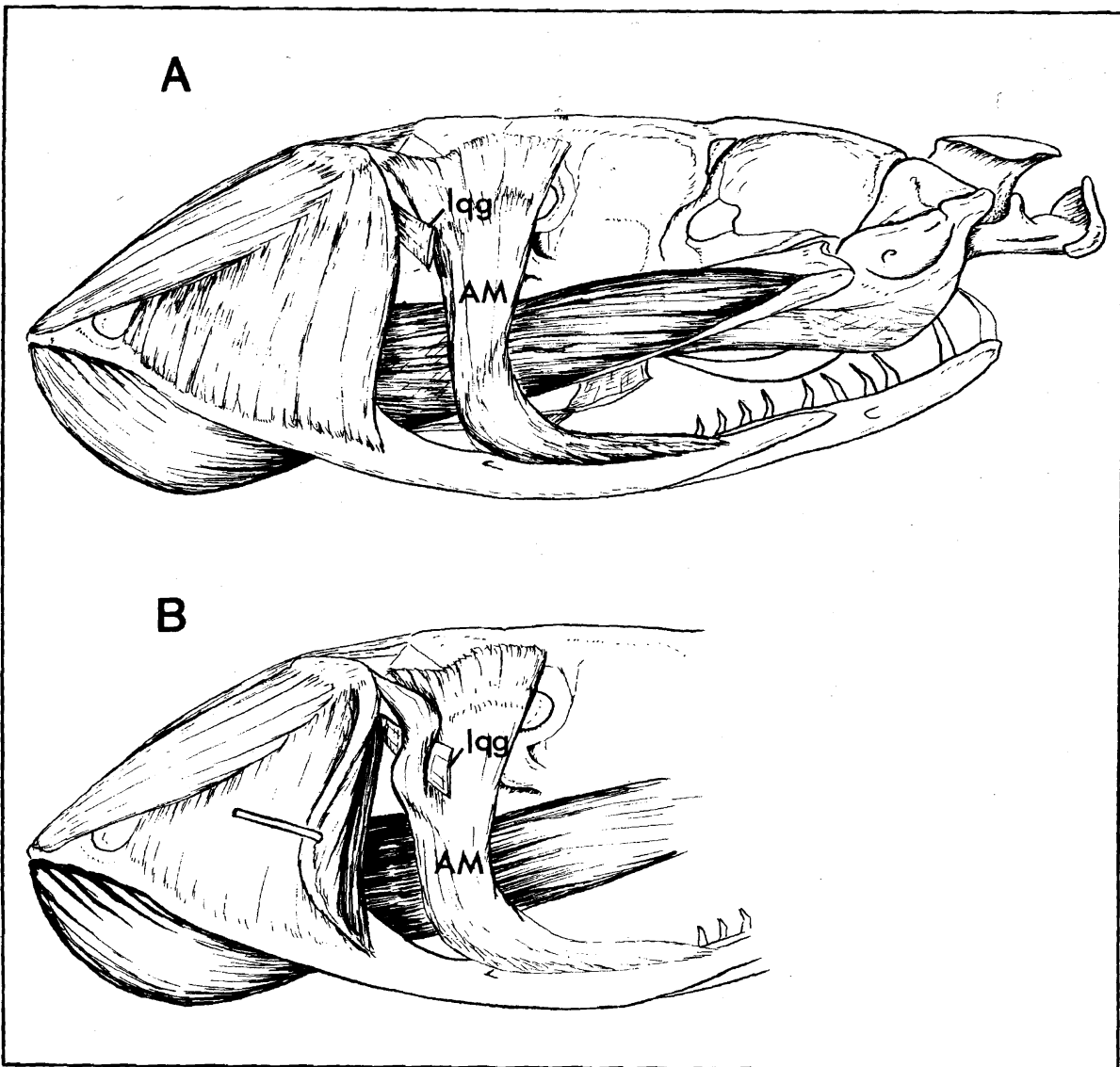

FIGURE 4. Character 9—Lateral view of M. adductor mandibulae externus medialis (AM) and L. quadrato-glandulare (lqg). A. Character state 1 as illustrated by A. contortrix (KVK 392). B. Character state 2 as illustrated by A. himalayanus (USNM 48473), showing quadrato-glandular ligament passing through the medialis.

vidual differences. However, internal muscle partitioning and division seems less susceptible to individual or size differences. Thus, Characters 6 and 7, having to do with variations in muscle attachments, carry less weight than Characters 8 and 9 that relate to muscle structure and subdivision.

DISCUSSION

(1) Deinagkistrodon

The distinctiveness of this genus is reflected in dental, osteological, and myological characters. The choanal process of the palatine bone is narrow and high although not so tall as that of Calloselasma. Its dentiferous bones generally bear more teeth than most Old World members of the genus Agkistrodon.

It is unlike all other related genera in two aspects of its myology. First, the origin of M. levator anguli oris lies posterior to that of the M. pseudotemporalis with no overlap of their origins. Second, only a partially distinct M. pterygoideus glandulae can be discovered. Attachment to the venom gland is quite distinctive. Rather than via an anatomically separate M. pterygoideus glandulae muscle, as in Calloselasma and Hypnale, in Deinagkistrodon the only partially delineated M. pterygoideus glandulae converges into a single strong tendon that passes laterally to attach to the venom gland. This is an intermediate, yet distinctive state between absence and discrete presence of a separate M. pterygoideus glandulae.

(2) Calloselasma

The tall, slender choanal process of the palatine sets this genus apart from all others (Chernov, 1957). Additionally the absence of direct attachment of the

M. retractor palatine to the palatine is also unusual, although as mentioned earlier, subtle differences in muscle attachments are especially susceptible to individual and to size variation. However, the presence of a distinct M. pterygoideus glandulae separates this genus from Deinagkistrodon and Agkistrodon. The presence of edentulous palatines in some specimens of Calloselasma set them apart from all other related genera.

(3) Hypnale

The choanal process of the palatine is low or absent and in this the genus Hypnale is distinct from all other related genera. Further, an anatomically distinct M. pterygoideus glandulae is present, a character shared only with Calloselasma, but not the other related genera.

(4) Agkistrodon

The choanal process of the palatine is broad and keel-like, unlike related genera. No M. pterygoideus glandulae is present in Agkistrodon, nor is there an intermediate state of the M. pterygoideus glandulae present as in Deinagkistrodon. Thus, the genus seems to exhibit, at least in these features, a condition that sets it taxonomically apart as Gloyd envisioned (Gloyd, 1979).

Skull proportions have been introduced as a characteristic to divide the genus Agkistrodon into two genera (Hoge and Romano-Hoge, 1981). One is the proposed genus Gloydius, wherein the skull tends to be long and narrow, and the supratemporals do not extend backwards beyond the braincase. Agkistrodon is retained for species wherein the skull is stout, and

TABLE 4. Summary of character states within the species.

Character Species	6 retractor pterygoidei	7 levator anguli oris	8 pterygoideus glandulae	9 adductor medialis
Deinagkistrodon acutus	1	3	2	1
Calloselasma rhodostoma	2	2	3	1
Hypnale hypnale	1	1	3	1
H. nepa	1	2	3	1
Agkistrodon halys	1	2	1	2
A. intermedius	1	2	1	2
A. strauchi	1	2	1	2
A. himalayanus	1	2	1	2
A. saxatilis	1	2	1	2
A. shedaoensis	1	2	1	2
A. caliginosus	1	2	1	1
A. blomhoffii	1	2	1	1
A. bilineatus	1	2	1	1
A. contortrix	1	2	1	1
A. piscivorus	1	2	1	1

the supratemporals do extend beyond the back of the braincase (Fig. 1).

However, at present, there are two reasons to be reluctant to adopt such a division of the genus *Agkistrodon*. First, the use of skull proportions only from "adults" presents a concern. As mentioned earlier, skull proportions may change with snake size. The Old World *Agkistrodon* such as *A. blomhoffii* and *A. himalayanus* tend to be small. The New World *A. piscivorus, A. bilineatus*, and even *A. contortrix* can reach much larger adult sizes. The gracile skull of Old World and robust skull of New World *Agkistrodon* may be related to size and not to species differences. If skull proportions are to be introduced into the taxonomic discussion, then ontogenetic effects must be examined.

Second, the distribution of states of Character 9 (route of quadrato-glandular ligament) among currently recognized species of *Agkistrodon* does not support such a division of the genus. In two Old World species, *caliginosus* and *blomhoffii*, this ligament passes around the muscle. But in six Old World *Agkistrodon* species examined (Table 4), the quadrato-glandular ligament passed through the *M. medalis*. Thus, these six species are likely to be more closely related to each other than to other Old World *Agkistrodon*. Consequently, it seems at present inadvisable to lump these six with other Old World *Agkistrodon* into a new, and separate genus.

SUMMARY

Analysis of the dental, osteological, and myological characteristics of the skulls of the genus *Agkistrodon* and related genera tend to confirm the taxonomic distinctiveness of the four genera. *Deinagkistrodon* is unique among the four in the presence of a posterior origin for the *M. levator anguli oris* and intermediate method of attachment of the *M. pterygoideus glandulae* to the venom gland. *Calloselasma* possesses a slender choanal process on the palatine bone. *Hypnale* lacks or exhibits only a low choanal process. *Agkistrodon* stands apart from other related genera in its possession of a broad, keel-like choanal process taken together with the absence of a *M. pterygoideus glandulae*.

Old World adult members of the genus *Agkistrodon* tend to have slender skulls with non-projecting supratemporal bones; New World members tend to have robust skulls with projecting supratemporal bones. However, Character 9 used here does not fall into an Old and New World grouping. Thus, the division of the genus *Agkistrodon* into Old World (*Gloydius*) and New World (*Agkistrodon*) taxonomic groups along these lines does not yet seem warranted, at least in terms of the skull characters examined herein.

LITERATURE CITED

BOCK, WALTER
1978. Toward an ecological morphology. Vogelwarte, 29: 128-135.

BRATTSTROM, BAYARD HOLMES
1964. Evolution of the pit vipers. Trans. San Diego Soc. Nat. Hist., 13: 185-268.

CHEN, YUAN-CHUNG, XIANG-FU WU, and ER-MI ZHAO
1984. Classification of *Agkistrodon* species in China. Toxicon, 22: 53-61.

CHERNOV, SERGIUS ALEXANDROVICH
1957. Systematic position of the poisonous snake *Ancistrodon rhodostoma* (Boie) (Serpentes, Crotalidae) in connection with its craniology. Zool. Zhur., Moscow, 36: 79-792.

COPE, EDWARD DRINKER
1860. Catalogue of the venomous serpents in the museum of the Academy of Natural Sciences of Philadelphia with notes on the families, genera, and species. Proc. Acad. Nat. Sci. Philadelphia, 11: 332-347.

COWAN, IAN MCTAGGART and W. B. M. HICK
1951. A comparative study of the head region in three species of *Thamnophis* (Reptilia, Ophidia). Trans. Royal Soc. Canada, 45: 19-60.

CUNDALL, DAVID
1983. Activity of head muscles during feeding by snakes: A comparative study. Amer. Zool., 23: 383-396.

CUNDALL, DAVID and CARL GANS
1979. Feeding in water snakes: An electromyographic study. Jour. Exp. Zool., 209: 189-208.

GLOYD, HOWARD KAY
1979. A new generic name for the hundred-pace viper. Proc. Biol. Soc. Washington, 91: 963-964.

GROOMBRIDGE, BRIAN
1986. Comments on the *M. pterygoideus glandulae* of crotaline snakes (Reptilia: Viperidae). Herpetologica, 42: 449-457.

HAAS, GEORG
1973. Muscles of the jaws and associated structures in the Rhynchocephalia and Squamata. *In* Carl

Gans and Thomas Parsons (eds.), Biology of the Reptilia, volume 4: 285-490. London, Academic Press.

HOGE, ALPHONSE RICHARD and SYLVIA ALMA R. W. L. ROMANO-HOGE
1981. Poisonous snakes of the world. Part I. Check list of the pit vipers Viperoidea, Viperidae, Crotalinae. Mem. Inst. Butantan, 42/43: 179-310.

JANSEN, DAVID
1981. Allometric growth of the skull of Thamnophis elegans vagrans: Adaptive potentials. Amer. Zool., 21: 958. (Abstr.)

JIANG, YAU-MING and ER-MI ZHAO
1980. Ecological data of snake-island pit-viper and Pallas' pit-viper. Acta Herpetol. Sinica, 1(5): 1-5.

KARDONG, KENNETH V.
1973. Lateral jaw and throat musculature of the cottonmouth snake Agkistrodon piscivorus. Morph. Jahrb., 119: 316-335.
1974. Kinesis of the jaw apparatus during the strike in the cottonmouth snake Agkistrodon piscivorus. Forma et Functio, 7: 327-354.
1980. Jaw musculature of the West Indian snake Alsophis cantherigerus brooksi (Colubridae, Reptilia). Breviora, 463: 1-26.

KARDONG, KENNETH V., PIET DULLEMEIJER, and J. A. M. FRANSEN
1986. The feeding mechanism in rattlesnakes. Amphib.-Rept., 7: 271-302.

KOCHVA, ELAZAR
1962. On the lateral jaw musculature of the Solenoglypha with remarks on some other snakes. Jour. Morphol., 110: 227-284.

MA, JI-FAN
1982. Skeletal system of Dienagkistrodon [sic] acutus. [In Chinese.] In Zhao Ermi (ed.), Dienagkistrodon [sic] acutus: Its morphology, ecology, toxicology and applications. Acta Herpetol. Sinica, 6: 19-24.

MAO, SHOU-HSIAN, FON Y. YIN, and YAW W. GUO
1986. A comparative study of the heads of the Taiwanese common venomous snakes. Snake, 18: 6-15.

NILSON, GÖRAN
1983. A new subspecies of the Asiatic pit viper Agkistrodon halys Pallas, 1776 (Serpentes, Viperidae) from Afghanistan. Bonn. Zool. Beitr., 34: 469-476.

SAWAI, YOSHIO and YOSHIHARU KAWAMURA
1980. Study on immunological relationships among venoms of the Asiatic Agkistrodon. In D. Eaker and T. Wadström (eds.), Natural Toxins. London, Pergamon Press: 85-90.

VARKEY, ALEXANDER
1979. Comparative cranial myology of North American Natricine snakes. Milwaukee Pub. Mus., Publ. Biol. Geol., 4: 1-70.

WALL, FRANK
1921. Ophidia taprobanica or the snakes of Ceylon. Colombo, H. R. Cottle, i- xxii, 1-581.

YOSIDA, TOSIHIDE H. and MICHIHISA TORIBA
1986a. Chromosome evolution and speciation of reptiles. I. Karyotype of the Japanese mamushi, Agkistrodon blomhoffii blomhoffii (Viperidae, Crotalinae) with special regard to the sex chromosomes. Proc. Japan Acad., ser. B, 62: 13-16.
1986b. Chromosome evolution and speciation of reptiles. II. A comparative study on karyotypes of the Chinese mamushi (Agkistrodon blomhoffii brevicaudus) and the Ussuri mamushi (A. ussuriensis) (Viperidae, Crotalinae). Proc. Japan Acad., ser. B, 62: 17-20.

ZHAO, ER-MI
1979. A new Agkistrodon from Shedao (Snake Island), Liaoning. Acta Herpetol. Sinica, 1(1): 4-7.
1980. Taxonomic study of pit viper of Shedao (Snake Island), by morphological and experimental methods and a preliminary discussion on the origin of snake-island pit-viper on Shedao. Acta Herpetol. Sinica, 1(4): 1- 24.

ZHAO, ER-MI (editor)
1982. Dienagkistrodon [sic] acutus: Its morphology, ecology, toxicology, and applications. [In Chinese.] Acta Herpetol. Sinica, 6: i-x, 1-124.

ZHAO, ER-MI, YAO-MING JIANG, and QING-YUN HUANG
1979. On infraspecific categories of Pallas' pit viper in China. Acta Herpetol. Sinica, 1(2): 1-12.

ZHAO, ER-MI, GUAN-FU WU, and WEN-MING YANG
1979. Comparisons of toxicity and neutralization test among Pallas' pit-viper, snake-island pit-viper, and black eye-brow pit-viper. Acta Herpetol. Sinica 1(3): 1-6.