

AN ILLUSTRATED GUIDE TO TRUNK VERTEBRAE OF COTTONMOUTH (*Agkistrodon piscivorus*) AND DIAMONDBACK RATTLESNAKE (*Crotalus adamanteus*) IN FLORIDA

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The cottonmouth, or water moccasin (*Agkistrodon piscivorus*), and the diamondback rattlesnake (*Crotalus adamanteus*) are distributed throughout Florida and their skeletal remains, usually vertebrae, are often present in zooarchaeological assemblages. Although the two viperid snakes exhibit different habitat preferences—one a semi-aquatic snake, the other terrestrial—their vertebrae are very similar. This illustrated guide helps to distinguish between the vertebrae of the two taxa. A strategy of limiting species identifications to the middle trunk series of mature adults and employing multiple characteristics is recommended to overcome the intracolumnar and individual variability that occurs in the vertebrae of these snakes.

Key words: *Agkistrodon piscivorus*, *Crotalus adamanteus*, Florida snakes, vertebrae, viperid

In varying degrees of abundance and diversity, the skeletal remains of snakes are a component of many zooarchaeological assemblages collected from Florida's pre-Columbian archaeological sites (Fradkin 1978). Their presence in these assemblages can be attributed to incidental inclusion (i.e., a snake was attracted to the human habitation site and died there either naturally or by human hands) and the snake may or may not have been eaten by humans. Their presence also may be due to purposeful hunting of snakes for human consumption. If one or two individuals are identified in an assemblage, often the snakes are considered by zooarchaeologists to be incidental inclusions. Size may be another factor in determining whether or not the snakes were targeted for food with the reasoning that the meat provided by smaller species and juvenile forms may not have been worth the effort. If several or many individuals are represented by the remains, then snakes are considered to have been a food resource. Archaeological sites in the southern third of the state in particular produce significant quantities of snake skeletal material. There is no doubt that snakes were an important food for American Indians who inhabited such areas as the Big Cypress Swamp and the Everglades (Danielson 1991; Fradkin 1978; Griffin 1988; Hale 1984; Wing 1984).

While an impressive taxonomic array of snake taxa has been identified in Florida's zooarchaeological assemblages, this paper focuses on two taxa, both

members of the Viperidae family and Crotalinae subfamily. Within this pit-viper family, there are eleven species and subspecies known for the southeastern U.S. (Conant and Collins 1998). Of this total, six occur in Florida (Ashton and Ashton 1988; Conant and Collins 1998; Tennant 1997). Of these six, one copperhead subspecies, *Agkistrodon contortrix contortrix*, one cottonmouth subspecies, *Agkistrodon piscivorus piscivorus*, and one rattlesnake, *Crotalus horridus*, are limited to localized areas within the state: north-central northwest panhandle, extreme northwest panhandle, and northeast Florida, respectively.

Only three vipers are distributed throughout the entire state. These are the Florida cottonmouth, *Agkistrodon piscivorus conanti*, often called the water moccasin, the eastern diamondback rattlesnake, *Crotalus adamanteus*, and the dusky pigmy rattlesnake, *Sistrurus miliarius barbouri*. For the majority of Florida archaeofaunal assemblages then, zooarchaeologists have only these three viperid taxa with which to concern themselves. Osteologically, no differences are known among the three southeastern cottonmouth subspecies or the three pigmy rattlesnake subspecies, so Florida zooarchaeologists need not be concerned with the subspecies names *conanti* or *barbouri*. Even in the small areas of Florida and elsewhere in the southeast where copperheads (*A. contortrix*) and cottonmouths (*A. piscivorus*) co-occur and the diamondback (*C. adamanteus*) and timber rattlesnakes (*C. horridus*) co-occur, these species sometimes can be separated osteologically (Auffenberg 1963:200; Meylan 1982:57-59).

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PURPOSE

With the keen observation skills that normally are required of the zooarchaeologist, one can readily distinguish between most of the primary cranial and mandibular elements of *Agkistrodon piscivorus* and *Crotalus adamanteus*. However, the majority of skeletal elements that are preserved and found in archaeological sites are not from the fragile skull. Rather, the curved rib and the compact but complex vertebrae are the most frequently recovered elements. Ribs are diagnostic of only the Class level, Serpentes. Vertebrae, however, can often be assigned to family and genus levels, and sometimes to species levels, if fragmentation is absent or minimal. Thus, I have arrived at the purpose of this paper, which is to provide an illustrated guide for distinguishing between the vertebrae of *A. piscivorus* and *C. adamanteus* from Florida's zooarchaeological assemblages. It is critical, however, that the guide be used in concert with multiple modern comparative specimens so that the researcher can appreciate the existing intracolumnar and individual variation.

Much of what is described and illustrated here is based on the work of Auffenberg (1963) and Meylan (1982) who studied Florida assemblages of snake bones representing many taxa from deposits dating to the Miocene, Pliocene, and Pleistocene epochs. The present paper combines their observations with the present author's into a more usable form, including a table and a correlating series of five illustrations presenting the vertebral diagnostic characteristics for each species side-by-side by osteological view. It further recommends, through the use of the table and figures, a strategy of limiting identification to the middle precaudal, or trunk, vertebrae of mature individuals and using multiple characteristics to achieve an identification.

SIGNIFICANCE

Zooarchaeologists and paleontologists alike generally strive for a species-level identification of a given skeletal specimen when that specimen is a diagnostic element, either complete or fragmented, but still exhibiting major structural characteristics. Clearly, for the zooarchaeologist, a species-level identification maximizes the amount of information that can be inferred about the specimen, the source animal, and the relationship between it and the human residents of the site from which its remains came. From a natural history perspective, biodiversity and biogeographic databases benefit from archaeological identifications made to species level. These are also issues of interest to zooarchaeologists.

Specific-animal habitat preferences can allow inferences about environmental conditions during the times of site occupation. Depending on the extent of the zooarchaeological dataset being used in a given study, inferences can be made at multiple scales, spatially and temporally. Concerning *Agkistrodon piscivorus* and *Crotalus adamanteus*, zooarchaeologists studying Florida archaeofaunal assemblages especially want to distinguish between these two taxa because the first is a semi-aquatic (freshwater) snake and the second almost exclusively terrestrial. Combined with other lines of evidence, past fluctuating water levels might be inferred from varying abundances of water snakes through time based on present-day correlations between intra-annual snake abundance and wet seasons (e.g., Dalrymple et al. 1991).

MATERIALS AND METHODS

VERTEBRAL OSTEOLOGY

The snake vertebral column can be divided, more or less, into four sections. The anterior, or cervical, vertebrae, including the atlas, are located in the "neck" region. These exhibit hypapophyses (median ventral processes, also called haemal processes) even in taxa whose trunk vertebrae have no hypapophyses, such as many of the colubrid genera. In taxa whose trunk vertebrae do have hypapophyses, the anterior vertebrae often exhibit hypapophyses that are longer than those of the trunk vertebrae. In the anterior region, an elongated hypapophysis functions in concert with the muscles of this area to facilitate the snake's lifting of the head and neck region. The sacral vertebrae, located in what might be thought of as a pelvic region, have multiple gracile projections, both ventrally and dorsally, and thus, if not completely broken and eroded, are easily recognized. The caudal vertebrae do not have these projections, but they are easily recognized by the presence of paired median processes called lymphapophyses. Both sacral and caudal vertebrae have these. Even in poorly preserved archaeological specimens, one can almost always recognize caudal vertebrae based on the presence of lymphapophyses.

The last and most important category of vertebrae is the trunk vertebrae (already mentioned above), all those found between the anterior and sacral/caudal vertebrae. All trunk vertebrae exhibit rib attachment structures, called paradiapophyses, one on each side of the centrum, adjacent to the cotyle. Auffenberg (1963:154) and others agree that the trunk vertebrae in adult individuals are the most consistent vertebrae in terms of intracolumnar and individual morphological

variation and therefore are the most useful for identification purposes. Even so, all researchers observe that subtle variations do occur in these vertebrae, for example, the more anterior of the trunk vertebrae versus the middle trunk vertebrae versus the more posterior trunk vertebrae. This is to be expected since the morphological change from one end of the vertebral column to the other end is gradual. Nonetheless, with considerable comparative study and thus familiarity with snake vertebrae, one can with some confidence determine that an isolated vertebra is a middle trunk specimen of an adult individual, the most diagnostic of all the trunk vertebrae even though these too exhibit some variation. If one cannot determine that a vertebra is a middle trunk one, identification should be made only at the family or subfamily level. Auffenberg (1963:154) states that he used the relative large size of the neural canal as a guide to assigning a middle trunk position to an isolated vertebra. Additional characteristics are an overall large size and a high neural spine. Thus, in following the tested lead of Auffenberg and others, this guide is focused on only these diagnostic vertebrae for zooarchaeological genus and species identification.

Structural vertebral terminology, most abbreviations, and vertebral measurements used in this paper follow Auffenberg (1963:151-155), who outlined these in detail, with the goal of future consistency among researchers. Directional terms (anterior, posterior, lateral, dorsal, and ventral views) also follow Auffenberg (1963), although others may prefer "cephalad" and caudad" over "anterior" and "posterior." Although Auffenberg's (1963) and Meylan's (1982) foci were on pre-Holocene faunal assemblages, these studies are highly useful to zooarchaeologists and should be consulted for complete osteological terminology and study of a variety of snake taxa, certainly ones common to zooarchaeological assemblages. In addition, Holman's (1963, 1979, 2000) work should be consulted. The illustrations presented here (figs. 1 through 5) are the original work of artist Sue Ellen Hunter, executed in the Florida Museum of Natural History's (FLMNH) Environmental Archaeology Laboratory in consultation with the author. They represent the most complete set of vertebrae illustrations known for these taxa, providing five views essential to the guide's purpose. With few exceptions, these illustrations are not stylized, so that illustrated differences in a morphological feature, even between one half of a vertebra and the other, are realistic and thus are not artistic error. As indicated in the figure legends, FLMNH modern specimens from the Herpetology

and Zooarchaeology comparative collections were used for illustration. In addition, other skeletons were used for comparative study. These include: *Agkistrodon piscivorus* (Zooarchaeology: Z62, Z1703, Z2381, UF27539-S, UF27540-S; Herpetology: UF893, UF8950, UF14435, UF676335, UF14107, UF99084, UF115019, UF9828, UF99027, UF11834, UF11928, UF14330, UF37020; *Crotalus adamanteus* (Zooarchaeology: Z1252, Z1260, Z2183, Z3092, Z3668, Z3671, Z3686, Z3795, Z7726; Herpetology: UF9705, UF14444, UF18396, UF32545, UF32557, UF35130, UF37513, UF41510, UF53428, UF56113, UF99060); and *Sistrurus miliarius* (Zooarchaeology: Z1301, Z1780; Herpetology: UF19078, UF19092, UF40610).

IDENTIFICATION OF *AGKISTRODON PISCIVORUS* AND *CROTALUS ADAMANTEUS* MIDDLE TRUNK VERTEBRAE

ELIMINATION OF NATRICINE VERTEBRAE

In addition to the viperids, archaeofaunal assemblages from sites in fresh-water environments often contain skeletal remains of the aquatic natricines. Like the viperids and unlike most other colubrids, the natricines have hypapophyses along the entire vertebral column. Depending on condition and place in the column, archaeological natricine and viperid vertebrae can sometimes be confused, as some of the natricine genera have high neural spines similar to the middle trunk vertebrae of the viperids. In particular, some of the anterior natricine vertebrae with their elongated hypapophyses can be similar to viperid vertebrae. But even if the hypapophysis is broken, its cross-section shape can help to distinguish the natricine vertebra from a viperid one. The natricine trunk hypapophysis is thin and bladelike with a distinctive shape in the lateral view and, if unbroken, is still relatively short. The viperid hypapophysis, on the other hand, is more rodlike, more rounded in cross section, and, if unbroken, relatively long. In addition, natricine centra are somewhat longer than those of the viperids and natricine accessory processes are well developed (but not in some anterior vertebrae), unlike those of the viperids. In those anterior natricine vertebrae that are so similar to viperids, the neural spines are directed more posteriorly, while in the viperids the neural spine is more erect.

VIPERID VERTEBRAE

As observed by Auffenberg (1963), Holman (1963, 1979), Meylan (1982), and this author, viperid middle trunk vertebrae generally exhibit the characteristics discussed

below organized by osteological view. Many of the structural characteristics are described in relation to snakes of other families, especially those of Colubridae. The vertebrae of *Agkistrodon piscivorus* and *Crotalus adamanteus* serve to illustrate these general viperid descriptions.

Lateral view (Fig. 1). The centrum (c) is short, giving each vertebra a compact quality. The condyle (co) is slightly to moderately oblique, on a short neck, and directed posteriorly. The hypapophysis (h) is long and appears narrow, and exists on all vertebrae within the column. The neural spine (ns) is much higher than long, either straight at the anterior edge or overhanging and usually overhanging at the posterior edge. The parapophyseal processes (pp) project ventrally and anteriorly well beyond the lower lip of the cotyle (ct). The paradiapophyseal articular surfaces (pas) are separated and distinct from one another.

Ventral view (Fig. 2). The centrum has well developed subcentral ridges (sr), extending from the base of the diapophysis (d, the upper articular surface of the paradiapophysis) posteriorly to near the bottom of the

condyle. Accessory processes (ap) are short and not well developed; sometimes they barely project beyond the margins of the prezygapophysial articular surfaces (pras).

Dorsal view (Fig. 3). The prezygapophysial articular surfaces are variably oval in shape. Accessory processes are short. From above, the zygosphenes (z) is variable in shape.

Anterior view (Fig. 4). The paradiapophyseal articular surfaces are separated. The hypapophysis is not compressed laterally, is almost rodlike, and is sometimes thickened distally. The cotyle shape is oval to sometimes rounded. The zygosphenes is variable in thickness.

Posterior view (Fig. 5). Also seen in this view is that the hypapophysis is not compressed laterally, is almost rodlike, and is sometimes thickened distally. The condyle is large and round. The neural arch (na) is wide, short, and depressed. Auffenberg (1963:200) states that the neural arch sometimes exhibits an epizygapophysial spine (es) and, based on my observations, this seems to be the case in older individuals of *Agkistrodon piscivorus*.

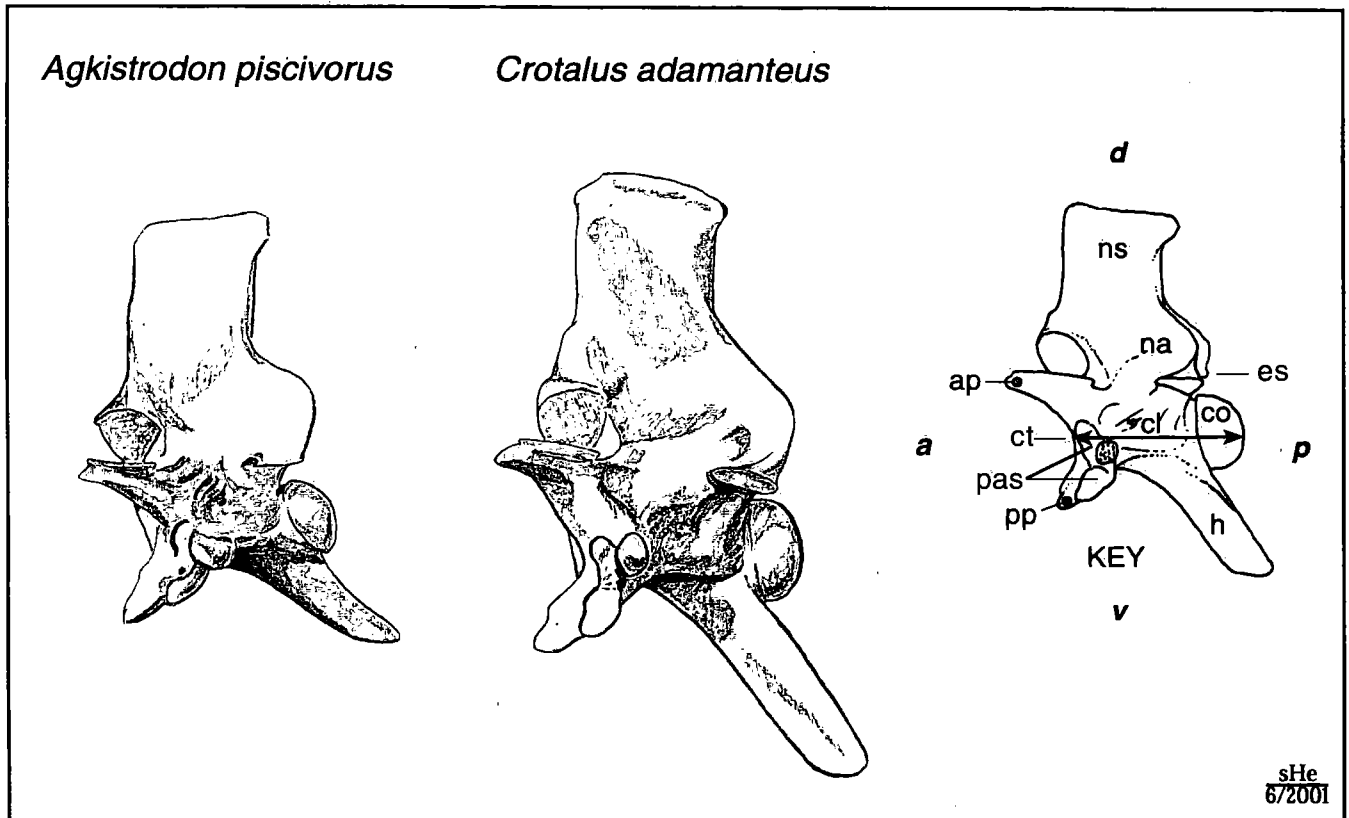


Figure 1. Comparative lateral view of typical mature *Agkistrodon piscivorus* (Herpetology: UF893) and *Crotalus adamanteus* (Zooarchaeology: Z1252) trunk vertebrae: anterior (a); posterior (p); dorsal (d); ventral (v); neural spine (ns); neural arch (na); epizygapophysial spine (es); condyle (co); centrum length (cl); hypapophysis (h); parapophyseal process (pp); paradiapophyseal articular surfaces (pas); cotyle (ct); accessory process (ap).

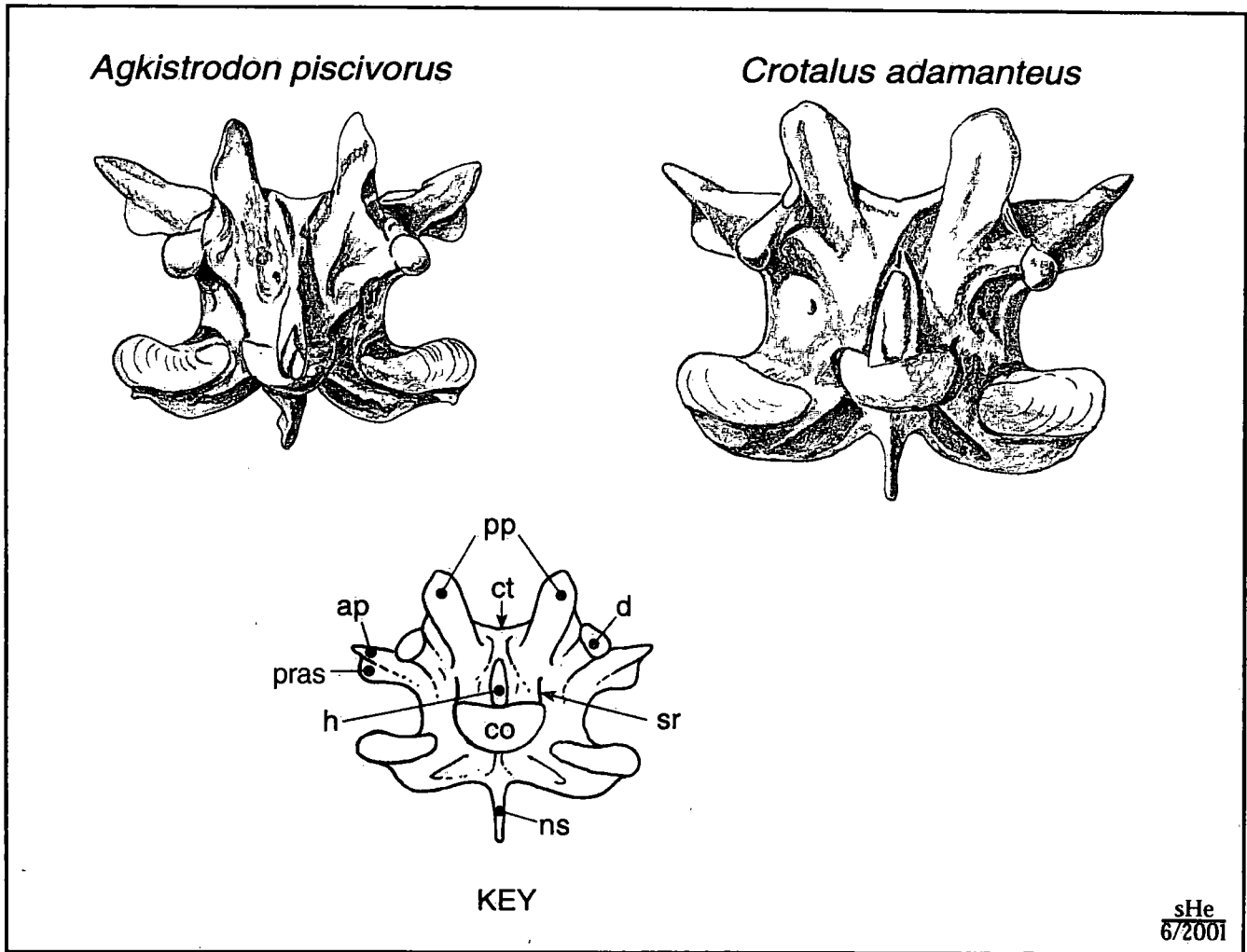


Figure 2. Comparative ventral view of typical mature *Agkistrodon piscivorus* (Herpetology: UF893) and *Crotalus adamanteus* (Zooarchaeology: Z1252) trunk vertebrae (anterior is up): parapophysial processes (pp); cotyle (ct); diapophysis (d); subcentrum ridge (sr); condyle (co); neural spine (ns); hypapophysis (h); prezygapophysial articular surface (pras); accessory process (ap).

VERTEBRAE OF *SISTRURUS MILIARIUS*

Zooarchaeologists must always consider the possibility of the presence of *S. miliarius* vertebrae in Florida's archaeofaunal assemblages. Adult vertebrae are small (unlike those of adult *Agkistrodon piscivorus* and *Crotalus adamanteus*), as *S. miliarius* in life averages only 20" (51 cm), according to Ashton and Ashton (1988:165). Auffenberg (1963:201) used the following combination of vertebral characteristics to distinguish *S. miliarius* specimens from young *A. piscivorus* and *C. adamanteus* specimens: round cotyle; absence of epizygapophysial spine; wide zygosphenes, convex in anterior view; longer and narrower centrum. Meylan (1982:61) separated out fossil *S. miliarius* vertebrae from young *A. piscivorus* and *C. adamanteus*

based on the proportionally smaller, round cotyles of *S. miliarius*. Of all these characteristics, while the rounded cotyle is the clearest and most consistent one, my observations include some small, round cotyles within the columns of both *A. piscivorus* and *C. adamanteus* specimens, away from the middle trunk vertebrae. This author's recommendation is to leave small viperid vertebrae exhibiting round cotyles at the family/subfamily level.

AGKISTRODON PISCIVORUS OR CROTALUS ADAMANTEUS?

Once natricines and *Sistrurus miliarius* are eliminated as possible identifications for an isolated adult trunk vertebra, the final challenge is to determine whether or not a vertebra can be assigned an *Agkistrodon piscivorus* or *Crotalus adamanteus* identification or

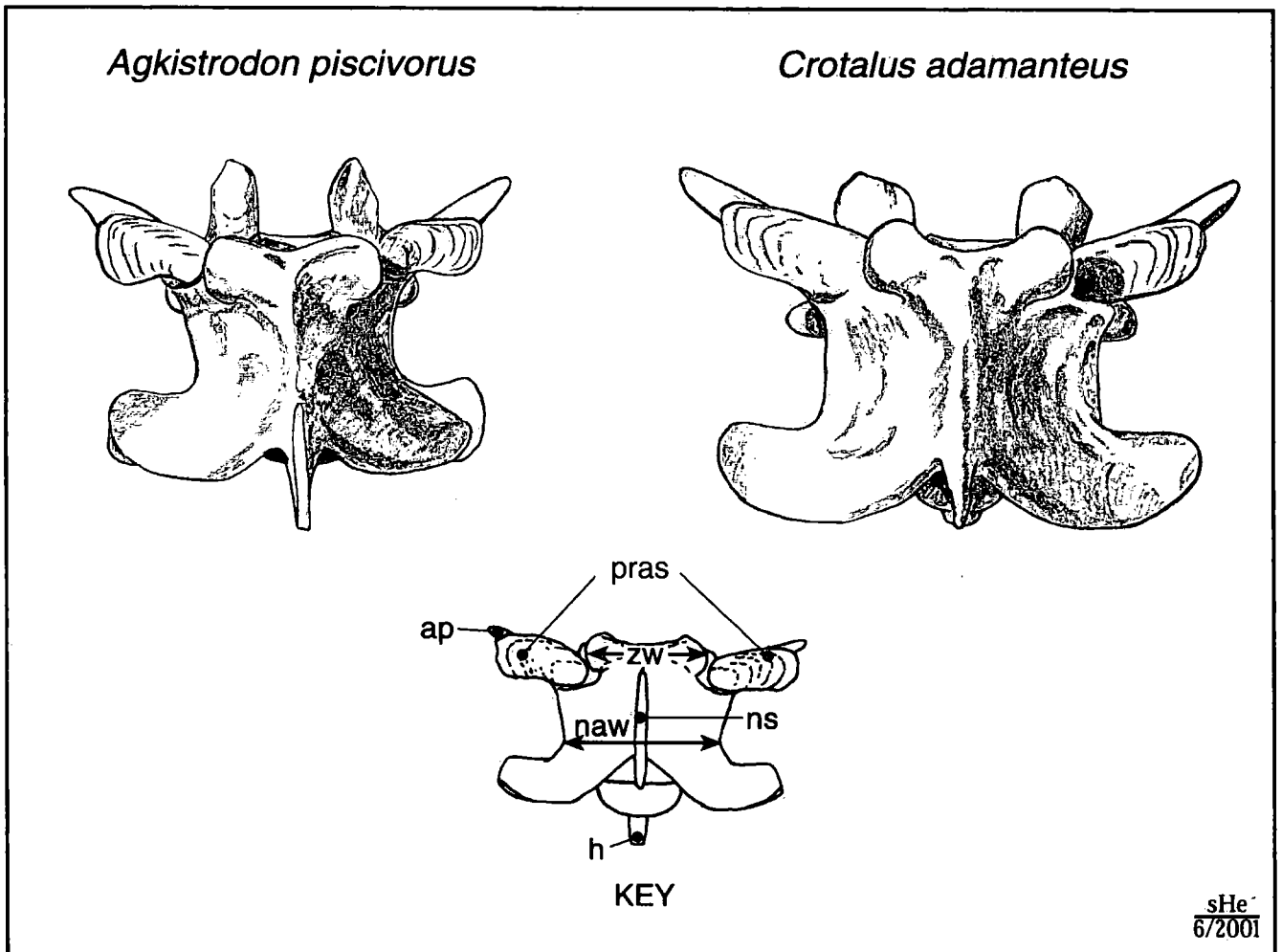


Figure 3. Comparative dorsal view of typical mature *Agkistrodon piscivorus* (left, Herpetology: UF893) and *Crotalus adamanteus* (right, Zooarchaeology: Z1252) trunk vertebrae (anterior is up): prezygapophysial articular surfaces (pras); zygosphene width (zw); neural spine (ns); neural arch width (naw); hypapophysis (h); accessory process (ap).

whether it is best left at family/subfamily level. Those structural characteristics observed to be the most constant within the middle trunk vertebrae series of these two taxa are presented in Table 1 and described below. Nonetheless, as pointed out above, some variation within the middle trunk series does occur and for this reason, no one characteristic can be relied upon for separating *A. piscivorus* and *C. adamanteus*. A multicharacter approach is required. There must be enough of a vertebra present in order to discern a combination of two or more primary diagnostic characteristics (those with an asterisk in Table 1) for a confident identification. The variation is such that some of the primary characteristics may be evident and some not. If observed, secondary characteristics may be helpful, but should not be relied upon. Even if the vertebra is complete,

uneroded, and clean of encrusting sediment, the characteristics in Table 1 may not clearly point to one taxon or the other, in which case the vertebra should be identified to family or subfamily only.

Lateral view (Fig. 1). Several primary characteristics can be seen in the lateral view. The hypapophysis of *Agkistrodon piscivorus* is slightly shorter, more gracile, and projects slightly more posteriorly than that of *Crotalus adamanteus*. Related to the projection, the angle between the anterior edge of the *A. piscivorus* hypapophysis and a vertical line drawn through the center of the centrum is greater than that of *C. adamanteus*. The parapophysial processes project more anteriorly in *A. piscivorus*. Auffenberg (1963) noted that the neural spine of *A. piscivorus* has a "tendency" to be lower than the neural spine of *C.*

adamanteus. Illustrator Hunter and this author observed a less than 50% occurrence of higher *C. adamanteus* spines and for this reason consider this characteristic to be of secondary importance. (The neural spines are not drawn to illustrate the difference.) Another secondary characteristic is that the neural spine of *A. piscivorus* is usually thinner and shows no thickening on the upper anterior edge. The *A. piscivorus* condyle is usually more oblique and gracile. Meylan (1982:59) experimented with several vertebral-measurement ratios in an attempt to separate *A. piscivorus* and *C. adamanteus*. One is centrum length (cl, Fig. 1) divided by neural arch width

(naw, Fig. 3). Whereas Meylan's means for the two taxa were similar, 1.25 mm and 1.24 mm, respectively, results from a small sample combining two small (Zooarchaeology Z3092, UF27539-S) and two large (Herpetology UF893; Zooarchaeology UF32540) individuals produced means of 1.10 mm for *A. piscivorus* and 0.85 mm for *C. adamanteus*. The very different results suggest that too much variability may exist for this ratio to be diagnostically useful.

Ventral view (Fig. 2). Three primary characteristics are exhibited in the ventral view. The parapophysial processes of *Agkistrodon piscivorus* appear narrower

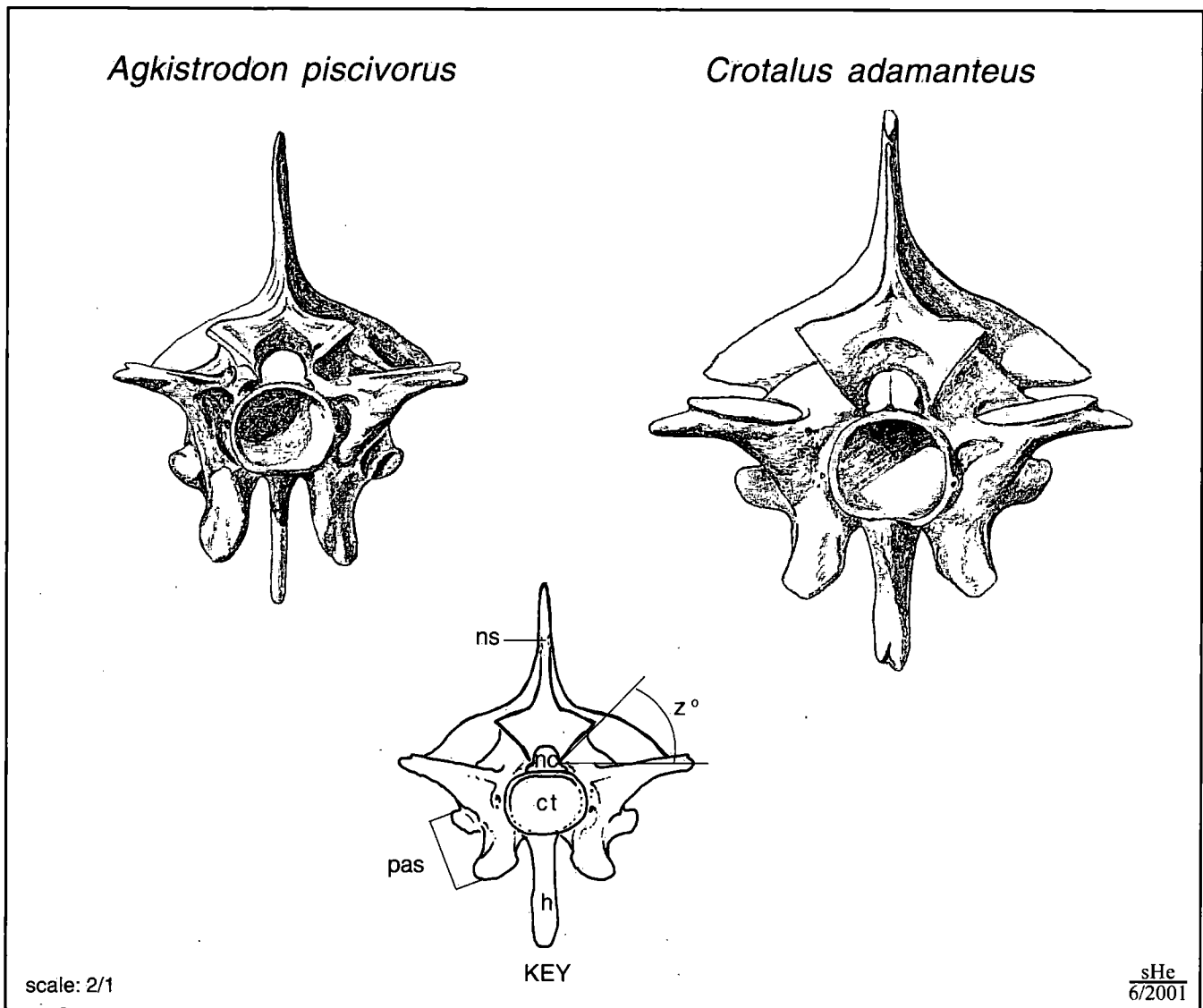


Figure 4. Comparative anterior view of typical mature *Agkistrodon piscivorus* (Herpetology UF893) and *Crotalus adamanteus* (Zooarchaeology Z1252) trunk vertebrae: neural spine (ns); zygosphene angle (z°); neural canal (nc); cotyle (ct); hypapophysis (h); parapophysial articular surfaces (pas).

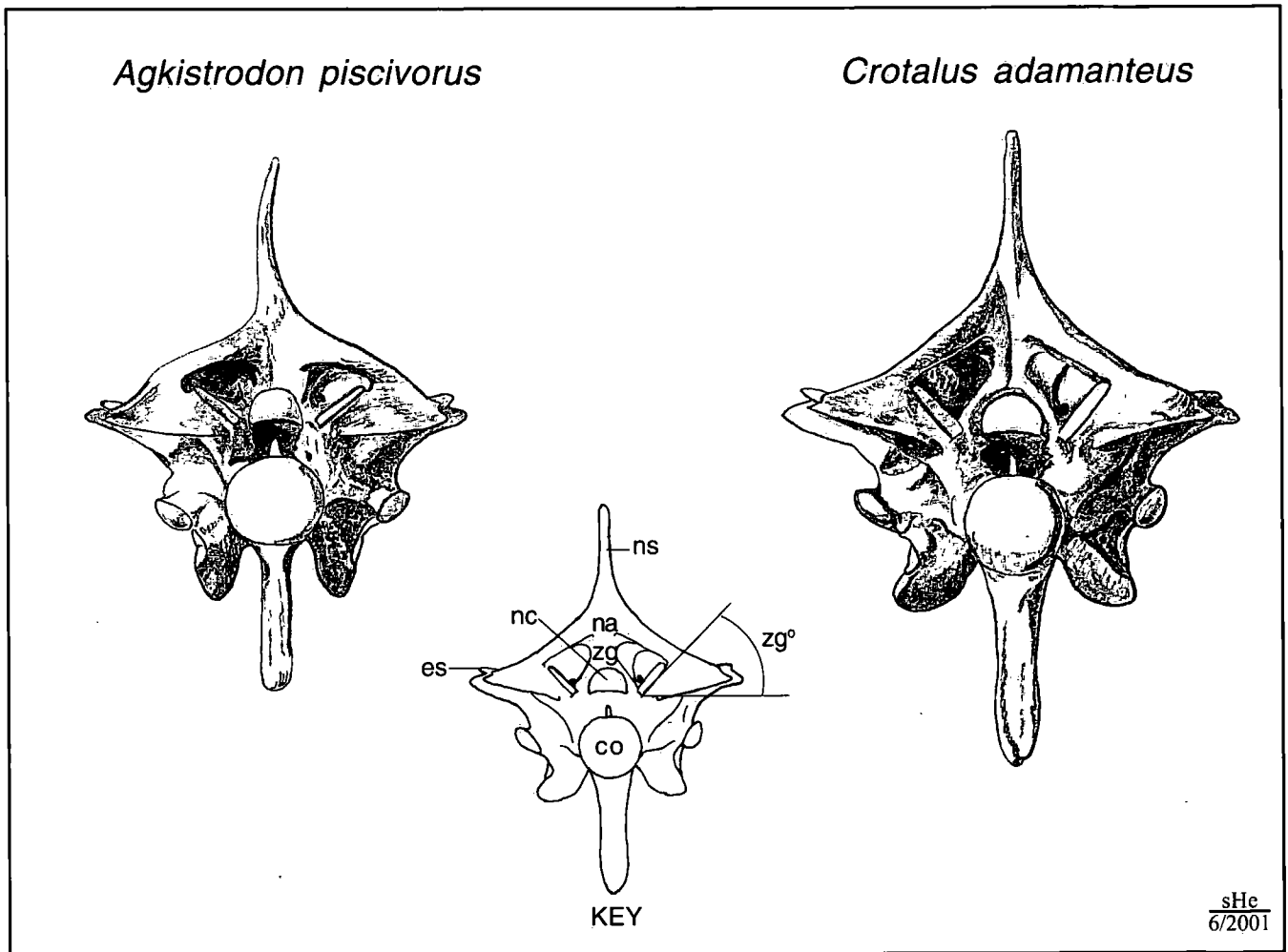


Figure 5. Comparative posterior view of typical mature *Agkistrodon piscivorus* (left, Herpetology: UF893) and *Crotalus adamanteus* (right, Zooarchaeology: UF1252) trunk vertebrae: neural spine (ns); neural arch (na); zygantrum (zg); condyle (co); hypapophysis (h); epizygapophysial spine (es); neural canal (nc).

and more parallel to each other, while the *Crotalus adamanteus* processes are wider and more diverging or V-shaped. The third primary feature is that often at the base of the *C. adamanteus* cotyle is a well developed ridge, usually absent in *A. piscivorus*. A secondary feature is that the condyle of *C. adamanteus* often is more bulbous.

Dorsal view (Fig. 3). The shapes of both the accessory processes and the prezygapophysial articular surfaces can be variable even between left and right sides of a single vertebra. But a fairly constant and therefore primary characteristic is that both are directed more laterally in the *Agkistrodon piscivorus* and slightly more anteriorly the *Crotalus adamanteus*. Secondary characteristics are also seen in the dorsal view. The neural spine of *A. piscivorus* is usually thinner. The distal end of the *C. adamanteus* hypapophysis is more robust and

roughly grooved. The zygosphenoid is often more concave in *A. piscivorus* and more crenate in *C. adamanteus*. Meylan's (1982:59) results of calculating the zygosphenoid width to neural arch width ratio (zw/naw) were the most promising for separating the two taxa because they resulted in a difference in the means of *A. piscivorus* (0.88 mm) and *C. adamanteus* (0.82 mm). However, a test of the *A. piscivorus* ratio mean, measuring vertebrae ($n = 25$) of four recent individuals (Zooarchaeology Z62, Z2381, UF27539-S, UF27540-S), produced a mean of 0.78 mm with a range of 0.74 to 0.80 mm. Based on this author's admittedly limited measurements, the ratio might be an unreliable characteristic for identifying isolated archaeological vertebrae.

Anterior view (Fig. 4). Observed in the anterior view, a primary characteristic is the flattened top edge

Table 1. A comparison of structural characteristics of the middle trunk vertebrae of mature *Agkistrodon piscivorus* and *Crotalus adamanteus*. Asterisks indicate primary characteristic; figure citations are for the present paper. "A" indicates Auffenberg 1963 as primary reference; "H/M" as Holman 1963 in Meylan 1982; "H" as Holman 1979; "M" as Meylan 1982; "W" as Walker, this paper.

Vertebral structure	<i>A. piscivorus</i> characteristic	<i>C. adamanteus</i> characteristic
*hypapophysis (Fig. 1)	A: shorter	A: longer
*angle between anterior edge of hypapophysis & line drawn perpendicular to center of centrum (Fig. 1)	W: greater	W: less
*parapophysial processes (Fig. 1)	A: more projected anteriorly	A: less projected anteriorly
epizygapophysial spines (Fig. 1)	A: faint when present	A: usually absent
neural spine (Fig. 1)	A: lower	A: higher
neural spine (Figs. 1, 3, 4)	A: thinner with no thickening on upper anterior edge	A: thicker, usually with a tubercle on anterior, upper edge
condyle (Fig. 1)	W: more oblique	W: less oblique
cl/naw (centrum length/neural arch width) (Figs. 1, 3)	M: (n = 31) mean of 1.25 mm W: (n = 6) mean of 1.10 mm	M: (n = 31) mean of 1.24 mm W: (n = 6) mean of 0.85 mm
*parapophysial processes (Fig. 2)	W: narrower	W: wider
*parapophysial processes (Fig. 2)	A: more parallel	A: more diverging
*base of cotyle (Fig. 2)	W: area is smooth	W: well developed ridge
condyle (Fig. 2)	W: more gracile	W: more robust
*accessory processes (Fig. 3)	W: more laterally directed	W: more anteriorly directed
*prezygapophysial articular surfaces (Figs. 3, 4)	A: more laterally directed	A: more anteriorly directed
*distal end of hypapophysis (Fig. 3)	W: more gracile and smooth	W: more robust and grooved
zygosphene shape (Fig. 3)	W: more concave	W: more crenate
zw/naw (zygosphene width/neural arch width) (Fig. 3)	M: (n = 32) mean of 0.88 mm W: (n = 25) mean of 0.78 mm	M: (n = 31) mean of 0.82 mm
*cotyle (Fig. 4)	W: dorsal edge usually rounded	W: dorsal edge is flattened
*indentations or pits on either side of cotyle (Fig. 4)	A: more deeply indented	A: less indented
*indentations or pits on either side of cotyle (Fig. 4)	H/M: pits are distinct and each contains one large foramen	H/M and H: one or more small foramina in indistinct pits when present
*position of zygantrum within neural arch (Fig. 5)	W: lower	W: higher

of the *Crotalus adamanteus* cotyle compared to the more rounded *Agkistrodon piscivorus* cotyle. Meylan (1982:59) noted that Holman (1963) observed one large foramen in each of the pits or indentations that occur on either side of the cotyle in *A. piscivorus* and one or more small foramina in *C. adamanteus*, thus the *A. piscivorus* pits themselves are larger than those of *C. adamanteus* (see also Holman 1979). Meylan concluded that the pitting and foramina adjacent to the cotyle held true for the "majority of midbody vertebrae."

Posterior view (Fig. 5). The zygantum within the neural arch is positioned lower in *Agkistrodon piscivorus* and higher in *Crotalus adamanteus*.

CONCLUSIONS

There is general agreement among researchers that certain structural characteristics of snake vertebrae tend to be more constant than others within the adult middle trunk series of varying taxa, as in the case of the viperids *Agkistrodon piscivorus* and *Crotalus adamanteus*. All stress that, nonetheless, subtle intracolumnar and individual variation does occur, even within the middle trunk series. For this reason, it is risky to rely on any one characteristic for an identification of *A. piscivorus* or *C. adamanteus*. Rather, a multicharacter approach in which two or more primary characteristics should be recognizable for a confident identification is recommended. It is also emphasized that more often than not, archaeological viperid vertebrae may be better left at the family or subfamily level. However, a species-level identification for these two widespread Florida vipers is preferable whenever possible due to the contrasting ecological factors associated with them.

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