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A Re-Evaluation of the Pleistocene Hellbender, *Cryptobranchus guildayi,* and an Overview of *Cryptobranchus* Remains from Appalachian Caves.

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A Re-Evaluation of the Pleistocene Hellbender, *Cryptobranchus guildayi*, and an
Overview of *Cryptobranchus* Remains from Caves in the Potomac River Region

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A thesis

presented to

the faculty of the Department of Biological Sciences

East Tennessee State University

In partial fulfillment

of the requirements for the degree

Master of Science in Biology

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by

Keila E. Bredehoeft

May 2010

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Keywords: *Cryptobranchus*, hellbender, salamander, paleontology, Pleistocene

ABSTRACT

A Re-Evaluation of the Pleistocene Hellbender, *Cryptobranchus guildayi*, and an
Overview of *Cryptobranchus* Remains from Appalachian Caves

by

Keila E. Bredehoeft

Cryptobranchus guildayi is described as an extinct species of large salamander that is
closely related to the hellbender, *Cryptobranchus alleganiensis.* The validity of this
extinct taxon has been questioned, so an expanded osteological sample of modern
hellbenders was used for comparative purposes with the *C. guildayi* fossil material.
Based on this analysis, all supposed distinguishing morphological characteristics used to
define *C. guildayi* can be observed in specimens of *C. alleganiensis*, or are based on
misidentifications. Therefore, *Cryptobranchus guildayi* is considered to be conspecific
with *C. alleganiensis* and taxonomically should be considered a junior synonym of the
latter. The reassignment of the *C. guildayi* specimens to *C. alleganiensis* and
examination of undescribed fossil specimens from the same region expands the
prehistoric range of the species to the Potomac River and its tributaries and also extends
the age of the species to the Irvingtonian North American land mammal age.

Keila E. Bredehoeft

ACKNOWLEDGEMENTS

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and infinite patience. I am honored to have been his student. This work was supported in

part by the ETSU School of Graduate Studies Research Grant program.

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CHAPTER 1

INTRODUCTION

Hellbenders (*Cryptobranchus alleganiensis*, Cryptobranchidae; Caudata) are the largest of the North American salamanders. Compared to other salamanders they are rarely seen due in part to their secretive habits and aquatic habitat. Rarity of sightings and a shrinking range unfortunately results in a relative scarcity of comparative osteological specimens in research collections. This scarcity may be the reason that few were used when assigning species-level identifications to fossil cryptobranchid material in the past. Accurate species-level identifications are crucial for making larger interpretations from fossil localities such as paleoecology, biogeography, and evolutionary relationships. The use of only a few comparative specimens introduces the danger of identification inaccuracies due to underestimation of intraspecific variation.

Chapter 2 of this thesis presents the comparison of an expanded sample of extant *C. alleganiensis* skeletons with a Pleistocene cryptobranchid (*C. guildayi*) known from 2 sites and named on the basis of comparison with only as many as 4 (and possibly as few as one) extant skeletons. The expanded number of modern skeletons was examined in order to estimate the variation present in extant populations for use in a re-evaluation of the taxonomic validity of the extinct *C. guildayi* and to describe and diagnose new *Cryptobranchus* fossil material from the same region (Chapter 3). Variation present in the modern comparative specimens has important implications for paleontological research and in particular underlines the importance of examining a greater number of comparative specimens when working with fossil material. Skeletal variations observed

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in modern hellbenders are presented as a note in Chapter 4. The introductory section below provides a review of the life history, phylogeny, and classification of the genus *Cryptobranchus* in order to create the context for later discussion. The fossil history of cryptobranchids is also reviewed with an emphasis on those in North America.

<u>Hellbender Life History</u>

Hellbenders, *Cryptobranchus alleganiensis*, are the largest of all the living North American salamanders. They are capable of attaining 740 mm in total length, though most measure between 290-510 mm (Meszoely 1966). Today these salamanders are surpassed in size only by their Asiatic relatives, the 2 species of *Andrias.* All living cryptobranchids (*Andrias* and *Cryptobranchus*) are obligate paedomorphs (i.e., every member of the population retains juvenile characteristics into maturity). This means that adults forego the full metamorphic process typical of amphibians, undergoing instead a partial metamorphosis that leaves them with an assortment of typical adult and juvenile characteristics (Petranka 1998).

Obligate paedomorphs such as hellbenders always undergo the same type of incomplete metamorphosis resulting in a standard fully aquatic adult form. In contrast facultative paedomorphs such as some ambystomatid salamanders (Ambystomatidae) are induced by environmental factors to undergo different metamorphic pathways, resulting in adults that are terrestrial or aquatic depending on which degree of metamorphosis is attained. For hellbenders there is no terrestrial phase. They are fully aquatic throughout their lives.

A number of morphological changes take place during salamander metamorphosis. A typical larval salamander has numerous characteristics that facilitate their aquatic lifestyle: external gills, tail fins, a sensory lateral line, and no eyelids (Duellman and Trueb 1994). Their hyoid apparatus is set up so that it can be depressed ventrally and to the posterior as the animal opens its jaw creating a vacuum that sweeps food and water into the mouth. This style of feeding is called 'gape and suck' and is common among aquatic vertebrates.

Salamanders that undergo full metamorphosis to become terrestrial adults reabsorb their fins and gills, close the gill opening, develop eyelids, and lose their lateral line in favor of developing the components of the ear. Metamorphosing hellbenders reabsorb their gills, but though the gill openings are reduced in size, they remain open into adulthood. This small and often hidden opening forms the basis of the genus name *Cryptobranchus* (hidden branchial, or gill) and is one of the character differences that distinguishes this group from its sister taxon, *Andrias*, in which the gill slits, or spiracles, completely close (Duellman and Trueb 1994). Adult hellbenders lack eyelids, retain their lateral line system, and possess a jaw and hyoid arrangement that allows suction feeding, all features typical of larval caudates. Their skulls also lack some elements found in completely metamorphosed species such as postparietals, supratemporals, lacrimals, and septomaxillary bones are absent. Lungs develop but they mainly function as buoyancy control (Nickerson and Mays 1973).

<u>Range and Distribution</u>

The hellbender was described by Daudin (1803), and originally classified in the genus *Salamandra*. It gained its specific name from the Allegheny Mountains, its type locality (Nickerson and Mays 1973). The genus is monotypic, with only a single living species, *C. alleganiensis*, which is separated into 2 subspecies, the eastern hellbender *C. a. alleganiensis*, and the Ozark hellbender *C. a. bishopi*. The eastern hellbender occupies a larger range that extends from the Tennessee Valley and northern Alabama, to southern New York with a smaller disjunct population in central Missouri. It is helpful to frame the range of these creatures in terms of watersheds. As with other aquatic organisms, their distribution is tied to tributary capture and flooding events that allow dispersal. Historically eastern hellbenders have occupied the Susquehanna system of New York and bordering states, tributaries of the Savannah River in South Carolina and Georgia, and the extensive Tennessee and Ohio systems (Fig. 1).

The Ozark hellbender occupies a much smaller range: portions of the Missouri drainage in south-central Missouri; the Meramec (Mississippi drainage) in eastern Missouri; and the White system in southern Missouri and north-central Arkansas (Fig. 1) (Lannoo 2005). It is possible that the historic range of the hellbender included Iowa (Hay, 1892; McMullen and Roudabush 1936), but these reports are questioned (Firschein 1951), and certainly none live there now. Notably, hellbenders are known only anecdotally from the Potomac River and its tributaries (Gates et al. 1985). It is on this river system that the type locality of *Cryptobranchus guildayi,* the questionable Pleistocene species discussed in Chapter 2, is situated.

Figure 1. Range of extant *Cryptobranchus alleganiensis*. Modified from Petranka 1998.

Ecology and Reproduction

Unlike most salamanders, fertilization in *Cryptobranchus* and *Andrias* is external.

Males of *Cryptobranchus* and *Andrias* guard nesting sites in burrows or under rocks.

Females lay long strands of eggs, and the male exudes sperm to fertilize them.

Males continue to guard the nesting sites after eggs are laid, driving away any other

hellbenders (Lannoo 2005). This is the only form of parental care provided, but it is

important because both males and females will consume eggs (Nussbaum 2005).

Incubation of the eggs of the Ozark hellbender, *C. a. alleganiensis,* is reported to range

between 68 and 84 days (Nickerson and Mays 1973). Loss of the gills takes place after

one and a half to 2 years, and estimations of the time needed to reach sexual maturity

range from between 3 to 6 years (Smith 1907; Dundee and Dundee 1965; Nickerson and

Mays 1973).

Preferred habitat of the hellbender is a clear, fast-flowing, rocky-bottomed stream

or river in a forested area. Oak and hickory forests are prominent in hellbender habitat

areas. Rocks are important because they provide interstitial space that serves as nesting

sites and shelter. Dorsal coloration and mottled patterning provide camouflage when the

hellbender is viewed from above. Hellbenders appear to be territorial about their rock

shelters as well as their nests. They display a remarkable affinity for a small home range

and exclude other hellbenders. A variety of aquatic invertebrates make up the diet of the

hellbender, crayfish being an important component (Nickerson and Mays 1973).

One *C. alleghaniensis* has lived for at least 55 years in captivity (Nickerson and

Mays 1973). Though little is known about longevity in the wild, recapture studies

indicate a long life span, around 25 years (Taber et al. 1975; Tilley 1980; Peterson et al.

1983). Long-lived and slow to mature species like the hellbender are susceptible to

population loss. Because they employ an ecological scheme that requires a stable

population structure, recovery of numbers after perturbation occurs very slowly. Loss of

range, changing population demographics (trend of skew toward juveniles), and lower

estimates of body condition in hellbender populations indicate population decline

(Wheeler et al. 2003). Like many other amphibians, hellbenders are an indicator of good

water quality, as they are sensitive to pollutants. Habitat is also destroyed by damming

rivers or simply degrading stream water quality (Nickerson and Mays 1973). Harvesting,

both legal and illegal, also contributes to the decline of populations (Nickerson and

Briggler 2007). For these reasons hellbenders were not collected from the wild for the purposes of this study.

Phylogeny

Caudata is the amphibian group that includes all living salamanders, sirens, and newts. Together with Anura (frogs) and Gymnophiona (caecilians), they make up the Lissamphibia, or modern amphibians. Caudata is recognized as a monophyletic grouping on the basis of molecular work as well as morphological features (Larson 1991; Larson and Dimmick 1993; Milner 2000). It is traditionally split into three suborders: 1) Cryptobranchoidea that contains only the families Cryptobranchidae and Hynobiidae, 2) Sirenoidea that is comprised only of the Sirenidae and is considered the most basal, and 3) Salamandroidea. Salamandroidea is a much larger grouping, consisting of every other salamander family including the diverse group Plethodontidae (Wake 2003). Though the phylogenetic placement of many other salamander groups within the Caudata is disputed (Hay et al. 1995) , the association of Cryptobranchidae and Hynobiidae (Cryptobranchoidea) and their placement near the base of the clade is well accepted (Gao and Shubin 2001; Larson et al. 2005; Carroll 2009; Zhang and Wake 2009).

Because hynobiids completely metamorphose, superficially there is little resemblance between them and their sister taxa, the neotenic cryptobranchids. They are, however, linked together by several plesiomorphic characteristics including the internal fertilization mentioned previously. Derived characteristics linking the 2 groups include several soft tissue features that are of little use in the fossil record, including the fusion of

lower leg muscles (Nickerson 2003) and egg deposition in paired sacs (Duellman and Trueb 1994)

More important from the perspective of a vertebrate paleontologist, are the skeletal features that distinguish hellbenders and their kin from other groups. Cryptobranchoids possess a separate angular in the jaw. This bone is present only in cryptobranchoids and Paleozoic amphibians, making it a plesiomorphic trait (Wake 2003). Cryptobranchoids also possess distinctive vertebrae that are very useful in fossil identification. A typical salamander trunk vertebra (i.e., one that lies posterior to the atlas but anterior to the sacrum) bears a pair of transverse processes on each of the lateral sides of the centrum. Each paired process articulates with the bifurcated head of a single rib (Holman 2006). Cryptobranchoids have secondarily combined the 2 transverse processes into a single rib-bearer, but the original configuration is still recognizable in the lateral shape of the structure as there are 2 swellings in the articular surface (Fig. 3) (Milner 2000).
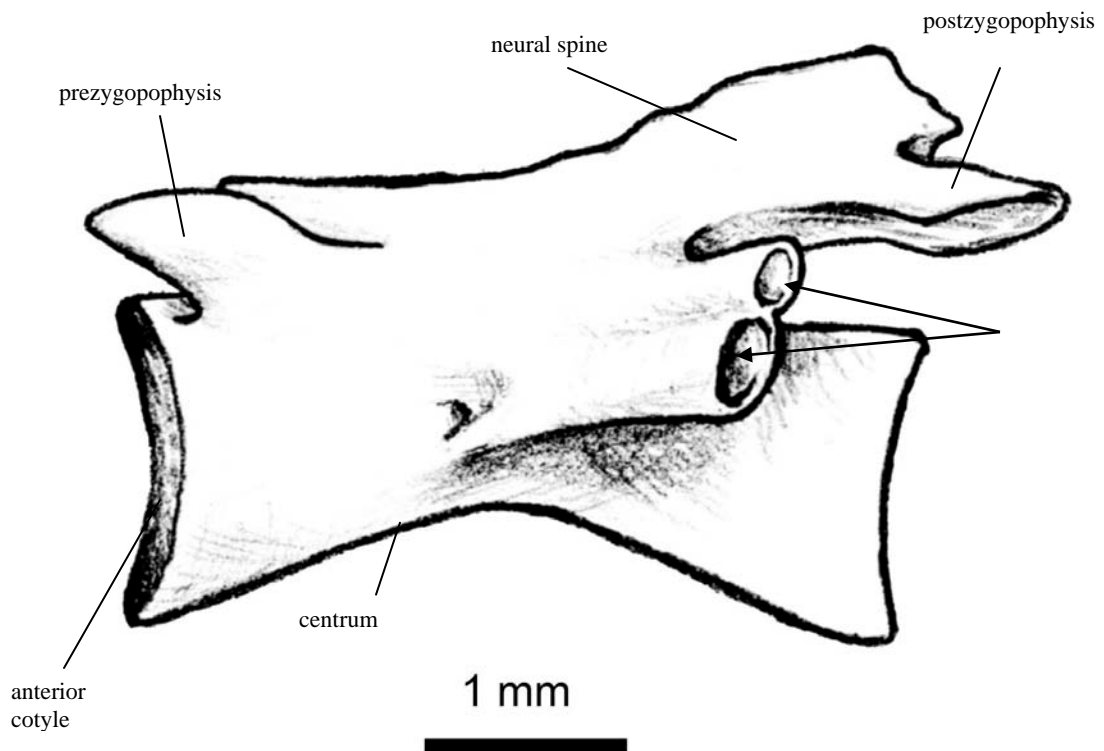
Figure 2. Trunk vertebra of a spotted salamander, *Ambystoma maculatum,* in lateral

view. Arrows indicate bifurcated articular surfaces of the transverse processes. Anterior

is to the left. Illustration by the author.

1 cm
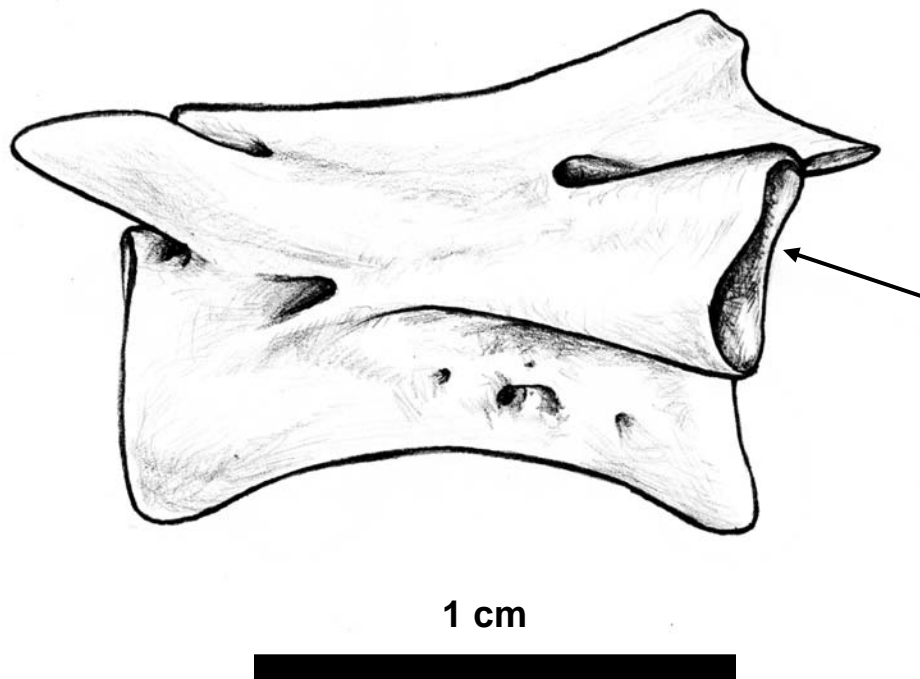
Figure 3. Lateral view of *Cryptobranchus alleganiensis* trunk vertebra. Arrow indicates the fused articular surface of the transverse processes. Anterior is to the left. Illustration by the author.

Extant Cryptobranchids

Skeletal elements of cryptobranchids are typically very large, making them easy to distinguish from other typically smaller North American salamanders. Osteologically, species of *Cryptobranchus* are separated from *Andrias* by having ossification present in the hyoid arch and the second and third visceral arches (Estes 1981), a frontal that contributes to the structure of the naris, and a greater separation between the maxilla and

pterygoid (Holman 2006). In the vertebrae of *Cryptobranchus* the angle between the neural spine and centrum is 15-20 degrees. This angle is smaller in *Andrias* (Meszoely 1966).

Perhaps most important from the standpoint of the paleontologist, the vertebrae of cryptobranchids are particularly distinctive; they are amphicoelous (the centrum or body of the vertebra is concave on the anterior and posterior side) and possess single-headed transverse rib processes. This single process, mentioned earlier, is formed by fusion of the 2 rib processes found in other salamanders, and is unique to cryptobranchoids (Holman 2006). Though the 2 separate processes are fused, they are still evident in the form of a 'bi-lobed' profile on the articular surfaces of the transverse processes of the vertebrae and the proximal ends of the ribs.

Cryptobranchus alleganiensis Subspecies

The hellbender is separated into 2 subspecies: the Eastern hellbender, *Cryptobranchus alleganiensis alleganiensis*, and the Ozark hellbender, *C. a. bishopi* (Grobman 1943). Differences between these 2 subspecies are that the Ozark hellbender is more blotched in coloration, tends to be smaller, and has a smaller spiracle (Grobman 1943). Populations of the eastern hellbender *C. a. alleganiensis* with the Ozark coloration have been reported in eastern Tennessee and northern Alabama (Nickerson and Mays 1973). Because *Andrias* species have a closed spiracle, the smaller spiracle of the Ozark hellbender has been interpreted as an intermediate condition between *Andrias* and the increased neoteny of the eastern hellbender. However, because this opening closes as the result of a metamorphic process, it may be difficult to determine whether

this difference represents a genetic shift affecting ontogeny as described above, or, as with many other ontogenetic shifts, the result of environmental factors. In any case no known quantifiable osteological differences exist between the 2 subspecies, so for the purposes of this study they will be treated as a single group.

Fossil Record

Caudate fossils are known from the Jurassic, so it is thought that early diversification of the major lineages is correlated with the breakup of Pangaea that was occurring at this time. The monophyly of Caudata is strongly supported, but there is disagreement about the phylogeny within Caudata, and there are differing versions of the sequence of divergence (Milner 2000; Duellman and Trueb 1994). *Karaurus* from the Late Jurassic of Central Asia and *Sinerpeton* from the Late Jurassic of northern China are both unmistakably salamanders. Interestingly, paedomorphosis had already developed; *Karaurus* was terrestrial, and *Sinerpeton* was aquatic and exhibited gills as an adult (Gao and Shubin 2001).

Cryptobranchids are relatively well represented in the fossil records of Europe and Asia, possibly due to a taphonomic bias because of size or habitat (Milner 2000). The cryptobranchid fossil genera *Aviturus* and *Ulanurus* appear in the Paleocene of Mongolia, and *Zaissanurus*, which may be *Andrias*, appears in the Eocene-Oligocene of Mongolia and Russia. *Andrias* makes its appearance in Europe in the Upper Oligocene, becomes abundant in the Miocene, and disappears in the Pliocene (Estes 1981). The first discovery of a fossil salamander is one of these European *Andrias* that is famously identified in 1726 as a human drowned in the biblical flood: *Homo diluvii testis*

(Meszoely 1966). Westphal (1958) noted that the variability present in extant

salamanders overlapped the supposed differences present between 2 groups and merged

Megalobatrachus, then the generic name of the extant Asian giants, with *Andrias*, which

previously had referred only to European fossils.

The mid-Oligocene was a time of Asian and American interchange, and it is

reasonable to suggest that cryptobranchids arrived in North America during this time

(Milner 2000; Duellman and Trueb 1994). In North America the cryptobranchid fossil

record extends back to the middle Miocene, and contrasts with Europe's Tertiary record

in that it is quite sparse despite the taphonomic advantage generally enjoyed by larger

animals. Meszoely (1966) noted the similarity of several North American taxa and

revised the taxonomy of the entire cryptobranchid clade. Material originally described as

Plicagnathus matthewi from the upper Miocene aged lower Snake Creek beds in Sinclair

Draw, Nebraska, was renamed *Andrias matthewi* in light of the similarities to the

European and Asian *Andrias*. It was distinct enough from these to retain a separate

species designation, and on the basis of morphological similarity and close geographical

and temporal distribution *Cryptobranchus mccalli* and several other undescribed North

American fossil cryptobranchids were placed in this species. Meszoely (1967) later

described a cryptobranchid from the lower Eocene of Wyoming, *Piceoerpeton*

willwoodensis, known only from a single trunk vertebra. This fossil is characterized as

resembling *Andrias* but with distinctions greater than those between the 2 recent genera

of cryptobranchids, and only distantly related to the 2 groups. No biogeographical

discussion was provided. Because of the conservatism of the recent Cryptobranchidae,

Naylor (1981) suggested that *Andrias* be considered a junior synonym of

Cryptobranchus. However, this recommendation has not been adopted by other authors (Duellman and Trueb 1994; Pough et al. 2004; Holman 2006; Carroll 2009).

Naylor (1981) also offered a tentative alternative to the Oligocene Asian dispersal of cryptobranchids to North America based on a species of *Cryptobranchus* he describes from the upper Paleocene of Saskatchewan: that Cryptobranchidae originated in North America. This species, *C. saskatchewanensis*, was notable for its stratigraphic position, which was older than any other previously known cryptobranchid but is known from only a single vertebra. However, a recently described and well-preserved basal cryptobranchid, *Chunerpeton tianyiensis*, from the Middle Jurassic of China reveals that cryptobranchids and hynobiids had diverged in Asia prior to this time (Gao and Shubin 2001, 2003). Also, because Naylor was also suggesting that *Andrias* should be included with *Cryptobranchus* at the time he described *C. saskatchewanensis*, it is possible that, as with the Miocene *C. mccalli,* this taxon should be referred to *Andrias* instead.

The North American cryptobranchid fossil record is sparse indeed: no record of North American cryptobranchids exists for the Eocene, Oligocene, or Pliocene. Upper Miocene *Andrias mccalli,* the doubtful *Piceoerpeton*, and lower Paleocene *Cryptobranchus saskatchewanensis* are the only non-Pleistocene/Holocene North American cryptobranchid taxa known. According to Holman (2006) *Cryptobranchus alleganiensis* is known from several localities, mostly cave sites, and all Pleistocene (Rancholabrean): Baker Bluff Cave (Guilday et al. 1978; Van Dam 1978) and Guy Wilson Cave (Holman 1995), Sullivan County, Tennessee; Cheek Bend Cave, Maury County, Tennessee (Miller 1992); Saltville Valley, Virginia (Holman and McDonald 1986); and Bell Cave, Colbert County, Alabama (Holman et al. 1990). *Cryptobranchus*

sp. material has been recorded from the following Rancholabrean localities: New Trout Cave, Pendleton County, West Virginia (Grady and Garton 1982; Holman and Grady 1987); Zoo Cave, Taney County, Missouri (Holman 1974); and the Irvingtonian site Hamilton Cave, Pendleton County, West Virginia (Holman and Grady 1989). These localities are shown in Figure 4.

Cave deposits provide a vital component of the fossil record wherever they are found. Typically, this is in a karst landscape, one that is dominated by carbonate-bearing rock beds such as dolomite or limestone. The carbonate content of the stone makes it susceptible to dissolution by acids contained in rain and groundwater, and systems of fissures develop into caves, sinkholes, pit traps, and other features. In eastern North America, especially in the Appalachian region, the near constant exposure of cave systems to water causes them to constantly but slowly change. This slow change limits the lifespan of a cave. Eventually they are filled completely by sediments or collapse. This, in addition to destruction by surface erosion, means that caves not only preserve a finite window of time, but those that are still open and able to be explored by humans usually preserve a younger assemblage of fossils. Though there are caves in North America that preserve terrestrial fossils from the Paleozoic (Schubert et al. 2003), the majority of cave fossils are from the Pleistocene or the Holocene and are no more than 100,000 years old (Guilday 1971).

Because caves typically preserve species that are geologically speaking very young, many cave fossils represent still-living, or extant, species. By evaluating the ecological requirements of the extant fossil species, especially small vertebrates,
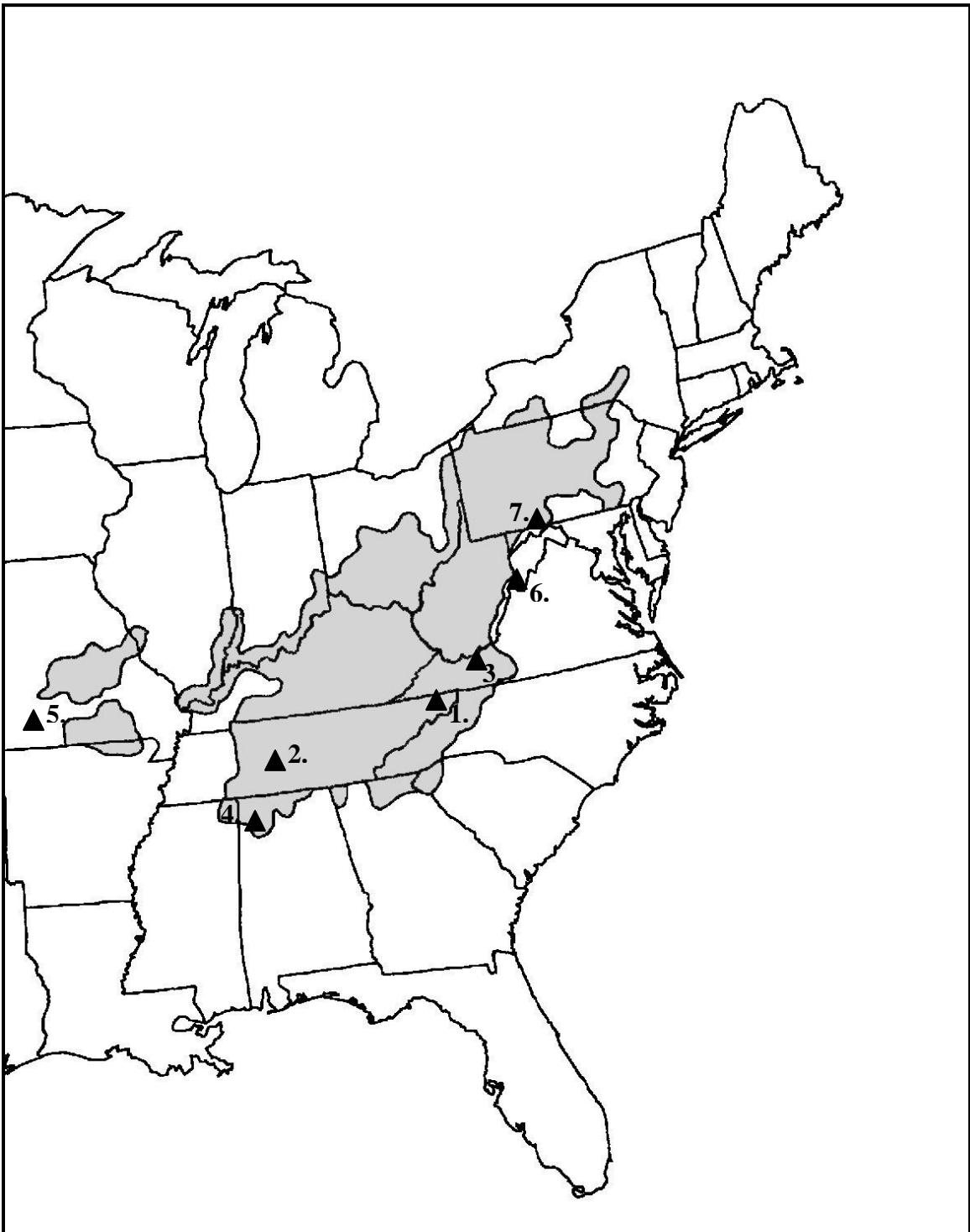
Figure 4. Map of Pleistocene *Cryptobranchus* fossil localities. Includes *C. alleganiensis, Cryptobranchus* sp, and *C. guildayi*. Gray areas represent known historic hellbender range. 1. Baker Bluff Cave and Guy Wilson Cave; 2. Cheek Bend Cave; 3. Saltville Valley; 4. Bell Cave; 5. Zoo Cave; 6. Hamilton, Trout, and New Trout Caves; 7. Cumberland Cave. Modified from Petranka 1998.

inferences can be made about the climate in the past. In order to make these inferences, it is important to be able to make proper fossil identifications as far down taxonomically as possible, preferably to species.

Interpretation of a cave fossil assemblage also necessitates an understanding of taphonomic forces that may influence what is to be found in a cave. Andrews (1990) identifies 4 ways in which animal bones may come to rest inside a cave. The first is by the animals living in caves, which is not the case for the hellbender. The second is by the animals falling in by accident. This may be possible in areas where the river or creek inhabited by the hellbender enters a 'sink', a place where the flowing water enters an underground cave system. The third is by the animal being brought into the cave by a predator. Water snakes, *Nerodia sipedon*, are known to eat hellbenders (Nickerson and Mays 1973) and may deposit their payloads in a cave, but snakes typically digest bones. Raptors, especially owls, thanks to their habits of roosting and regurgitating pellets containing the indigestible remnants of their victims, are major depositors of small bones in caves (Andrews 1990). Whether these birds feed on hellbenders is not known, but they do capture and consume hellbender predators, so it is also possible that the undigested remains of their prey would contain hellbender material. The fourth way is water transport into the cave. Andrews (1990) considers this the least likely means of bone accumulation as water tends to be dispersive. None of these methods except predation would seem to be terribly common events, which may account for the relative scarcity of hellbender fossil material. Otherwise, because of the larger size of the skeletal elements of a hellbender skeleton relative to other microfossil material, one would expect a positive bias in the fossil record.

CHAPTER 2

THE PLEISTOCENE HELLBENDER *CRYPTOBRANCHUS*

GUILDAYI (HOLMAN, 1977)

<u>Introduction</u>

Cryptobranchus guildayi is described as an extinct species of hellbender known from only 2 Pleistocene-age sites. This study provides a re-examination of the fossil material from this species with an emphasis on determining its taxonomic and systematic validity.

In 1977 J.A. Holman described a new species of *Cryptobranchus* from fossils recovered from Cumberland Cave in Allegany County, Maryland (Holman 1977). Based on the mammalian fauna present, this cave deposit was attributed to the Pleistocene. Holman describes the age as Kansan, but these glacial-interglacial based Pleistocene ages are no longer used because glaciation events are now known to have been much more frequent and more complex than originally assumed. The holotype material consists of only a single left dentary with a portion of the anterior missing (CM 20470). Further material attributed to this species has been recovered from only one other location, Trout Cave in Pendleton County, West Virginia. These fossils were also described by Holman (1982) and consisted of 2 right dentaries, one right epihyal, one atlas, one nearly complete and one fragmentary trunk vertebra, 3 fragmentary caudal vertebrae, 2 right femora, and one right scapula (CM 40416). The fauna of this deposit in Trout Cave

shares similar arvicolid rodent components with Cumberland Cave, which suggests the 2 are contemporaneous (Zakrzewski 1975). Originally assigned to the Wisconsinan glacial period, the age was later revised to the Irvingtonian land mammal age (Holman 2006) reflecting the increasing disuse of the glacial/interglacial method of describing the Pleistocene.

Cumberland Cave

Cumberland Cave, the type locality of *Cryptobranchus guildayi*, has a long history of fossil research. It is located in Allegany County just south of Corriganville, Maryland and 4 miles northwest of Cumberland at about latitude 39º41´ N and longitude 78º74´ W (Gidley and Gazin 1938). Originally discovered in 1912 as a result of railroad construction, fossil bone and sediment were removed by machine; no record of the position of the fossils exists. Devonian age limestone surrounds the cave, and because it is part of a deeply dipping anticline, the strata are nearly vertical. The original opening is a sinkhole near the top of the limestone ridge that is thought to have acted as a natural trap (Nicholas 1954). Cave sediments are composed of unstratified cave clays and breccias interspersed with stalactitic material. No sand or gravel is present to indicate the presence of moving water, and the fossils are broken but not water-worn (Gidley 1913). Wills Creek flows at the bottom of the ridge, and it is likely that aquatic taxa present in the cave would have come from there, probably as the result of predation. Wills Creek is a tributary of the North Fork of the Potomac River (GNIS 2009).

Cryptobranchus guildayi

Following Holman (1982), the characteristics distinguishing *C. guildayi* from *C. alleganiensis* are: 1) the dentary has a longer labial, or Meckelian, groove than in *C. alleganiensis*, and is more weakly curved; 2) the epihyal has a strongly developed posterior process not found in *C. alleganiensis*, possibly indicating a novel feeding mechanism; 3) the single complete vertebra from Trout Cave is shorter and wider than that of *C. alleganiensis*; 4) the distal ridge of the femur is better developed and extends farther down the shaft than *C. alleganiensis;* 5) the scapula of *C. guildayi* has a more rounded dorsal surface and the posterior process makes a greater angle with the shaft.

Because Holman apparently had only a single comparative specimen of *C. alleganiensis* available at the time of the original diagnosis (MSU 13216) (Holman 2006), no assessment of intraspecies osteological variation could have been made. In addition, only one of the distinguishing characteristics of the new species, the posterior process on the epihyal, exists as a discrete character state. Discrete characters are preferred in fossil identification, as other more subjective, less quantifiable characteristics are at risk of being interpreted differently by researchers especially when remains are fragmentary, as is almost always the case with smaller vertebrates (Bever 2005). All of *C. guildayi*'s other distinguishing characteristics are of this type, existing as differences of degrees. Not only is this type of difference difficult to quantify, but because of the low number (no more than 6 for the amended diagnosis) of comparative specimens used, it is possible that these characters may be attributed to intraspecific variation. Indeed, other authors have noted the variability present in some of these elements and questioned the validity of the taxon (Estes 1981; Nickerson 2003). Holman admitted that *C. guildayi*

may be shown to be conspecific with *C. alleganiensis* (Holman 2006). However, no re-evaluation of the fossil material had yet taken place. Consequently, this study provides a re-examination of *C. guildayi* with an emphasis on determining its systematic validity.

Methods

In order to assess the validity of *C. guildayi* as a species separate from *C. alleganiensis* the fossil material attributed to *C. guildayi* from the Carnegie Museum was compared with a number of modern *C. alleganiensis* skeletal specimens. Twenty-six modern individuals in all were examined. Juvenile or larval specimens were excluded, and several (DCP 661, DCP 705, ASU 12311, CM 37478, CM 92273, CM 37479, CM 37476) were of equivalent size to the individuals represented by the fossil material. Excluding larva and the very young reduces the risk of observing differences that are the result of ontogenetic changes. All recent comparative material used appears below (Table 1). Each character state described by Holman (1982) was examined on both the fossil material and the modern skeletons and discussed below. Notable variation observed in modern *C. alleganiensis* skeletons is discussed in Chapter 4.

Table 1: Comparative specimens of *Cryptobranchus alleganiensis* used in the analysis. Institutional abbreviations appear in Appendix 1.

ASU 12311	CM 92273	NVPL 6917
CM 6262	DCP 661	UF 21844
CM 5885-A	DCP 705	UF 34990
CM 5885-B	DCP 3252	UF 38233
CM 37477	DCP 3253	UF 52537
CM 37478	DCP 3254	UF 55786
CM 37479	DCP 3255	UF 57153
CM 92271	DCP 3256	UF 99064
CM 92272	DCP 3257	

Results

(1) Dentary – The holotype (CM 20470) of *C. guildayi* is a left dentary missing a portion of the anterior (Fig. 5). Holman (1977, 1982) describes this dentary as more weakly curved than that of *C. alleganiensis*. However, the posterior portion of the jaw of a hellbender is essentially straight with the anterior half possessing a nearly hemispherical curve (Elwood and Cundall 1994). Making an estimate of curvature in a dentary lacking a portion of the anterior is therefore not possible. The *C. guildayi* material from Trout Cave (CM 40416) includes 2 right dentaries, one of which is complete. The curvature of this dentary is indistinguishable from that of *C. alleganiensis* (DCP 661) (Fig. 6). No other distinguishing features were observed in the dentaries attributed to *C. guildayi.*

Holman (1977) estimated the length of the Meckelian groove by counting the number of teeth and alveoli along the groove. The holotype is cited as having a Meckelian groove that extends for a total of 41 teeth and alveolar spaces (Holman, 2006), with the teeth represented only by their bases as all crowns have been broken off. Upon

examining this dentary, only 29 teeth and alveolar spaces were present along the

Meckelian groove. In fact, for the entire length of this dentary only an estimated 39 teeth

are present, so it is possible that Holman counted the teeth along the entire length. There

were fewer teeth actually present than described in the Trout Cave dentaries as well.

(2) 'Epihyal' – The epihyal of *C. guildayi* was described as having a strongly developed

posterior process not present in the epihyal of the modern specimen (Holman 1982);

however, this skeletal element was misidentified. The element from Trout Cave
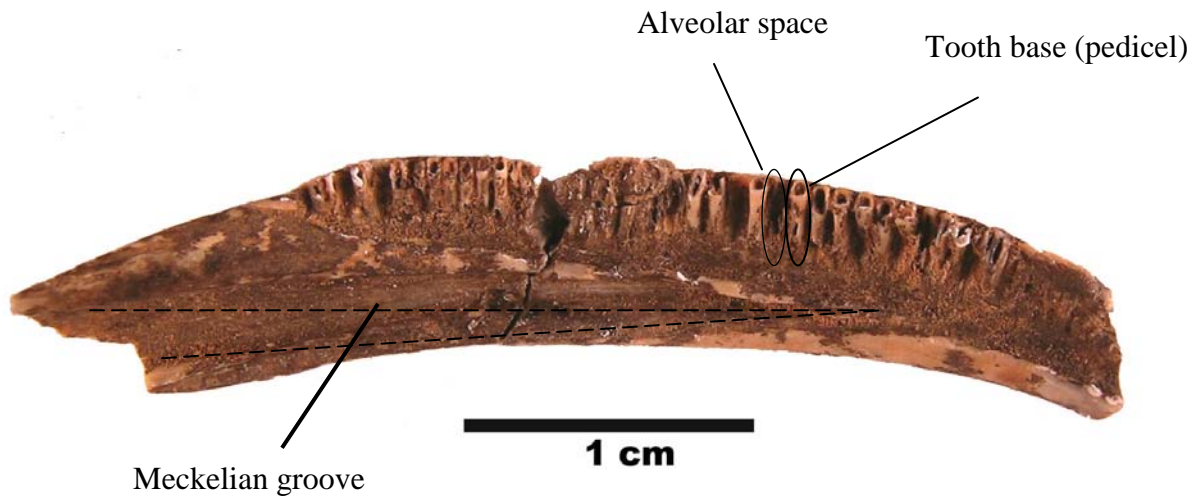
Figure 5. Lingual surface of *C. guildayi* holotype dentary CM 20470. Anterior is to the

right. Slashed line indicates approximate location and extent of the Meckelian groove.

described as the epihyal, a component of the hyoid apparatus, is actually a sacral rib. A salamander's sacrum is a single vertebra that has expanded transverse processes to which the sacral rib attaches (Figs. 7, 8). Sacral ribs differ from the ribs of the trunk vertebrae in that they are heavier and longer and have a downward curve that terminates in an articular surface for the attachment of the ilium (Fig. 7). The proximal articular surface of the sacral rib has the bilobed shape characteristic of Cryptobranchoidea (Fig. 9). The posterior articular process, supposedly unique to *C. guildayi,* is found on the lateral side of the sacral ribs of modern *C. alleganiensis* (Fig. 10), though in the fossil there is damage to this region (Fig. 9).

The 2 right dentaries from Trout Cave (CM 40415) are similar in size to the modern *C. alleganiensis* specimen (DCP 661). The epihyal of this modern hellbender is pictured to scale with the misidentified 'epihyal' of *C. guildayi* (Fig. 11). Assuming the fossil 'epihyal' is from one of the 2 fossil individuals from this cave (both dentaries are rights), there is an extreme size difference between the 2 elements. If the fossil element is from a different individual of greater or smaller size than the 2 dentaries, there are still shape discrepancies that preclude the identification of the fossil element as an epihyal.

Last, a note on hyoid nomenclature: The term epihyal is used by Holman for describing the ossified portion of the ceratohyal. Other authors (Özeti and Wake 1969; Duellman and Trueb 1993) use the term ceratohyal for the entire structure regardless of ossification, and this is the term that I will use for the remainder of this work. (For further clarification of hyoid terms, see Figure 16).

Figure 6. Dentary attributed to *C. guildayi* (CM 40416) from Trout Cave, top and a similarly sized modern *C. alleganiensis* (DCP 661) bottom in dorsal view. Note the overall similarity in curvature.
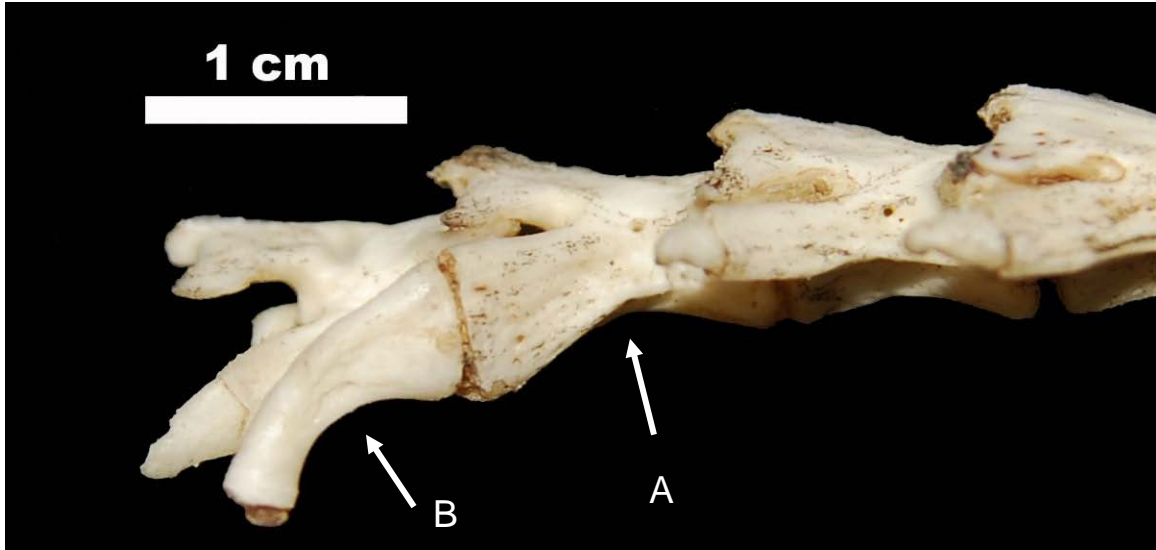
Figure 7. Articulated trunk vertebrae, sacrum, and first caudal vertebra with attached ribs of modern *C. alleganiensis* (NVPL 6917) in lateral view. A - sacral vertebra; B - sacral rib. Anterior is to the right.
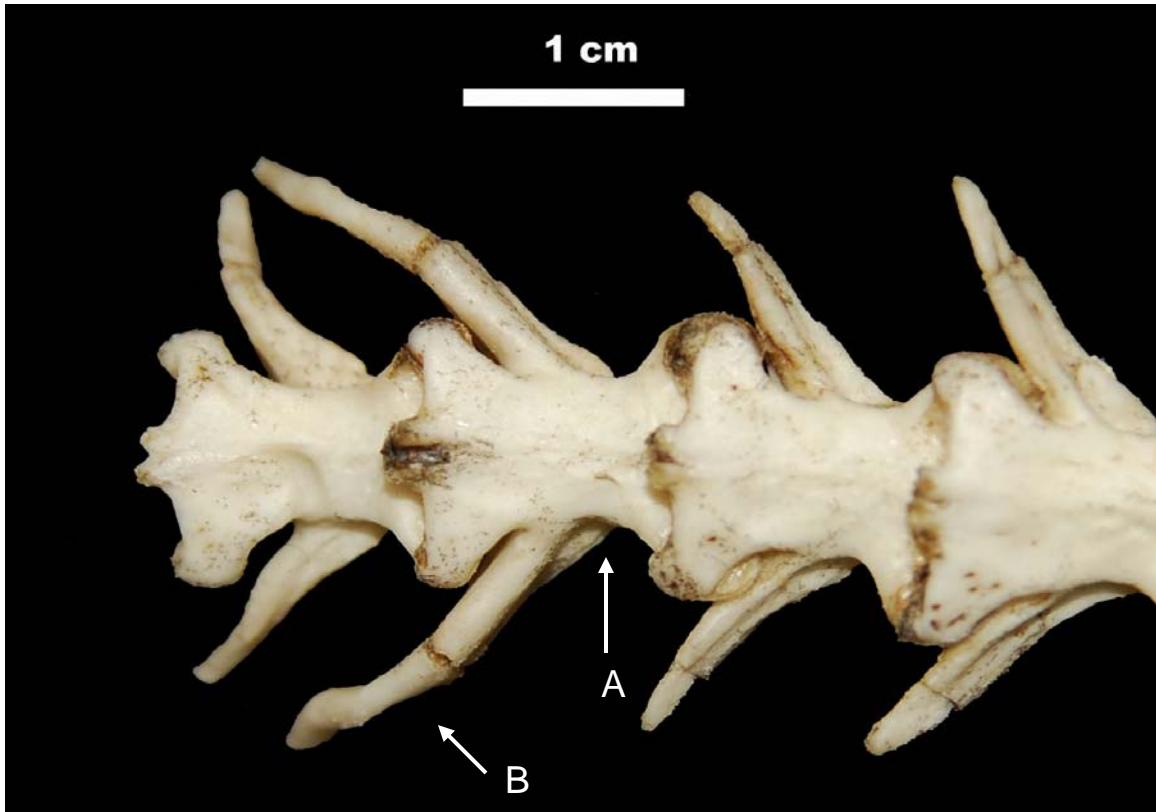
Figure 8. Dorsal view of the articulated vertebral column of *Cryptobranchus alleganiensis* (NVPL 6917). A - sacral vertebra; B - sacral rib. Anterior is to the right.

Figure 9. View of the articular surfaces of the sacral rib (CM 40416)(left) previously assigned to *C. guildayi* , left, and a sacral rib of *C. alleganiensis*. Note the characteristic bilobed shape.
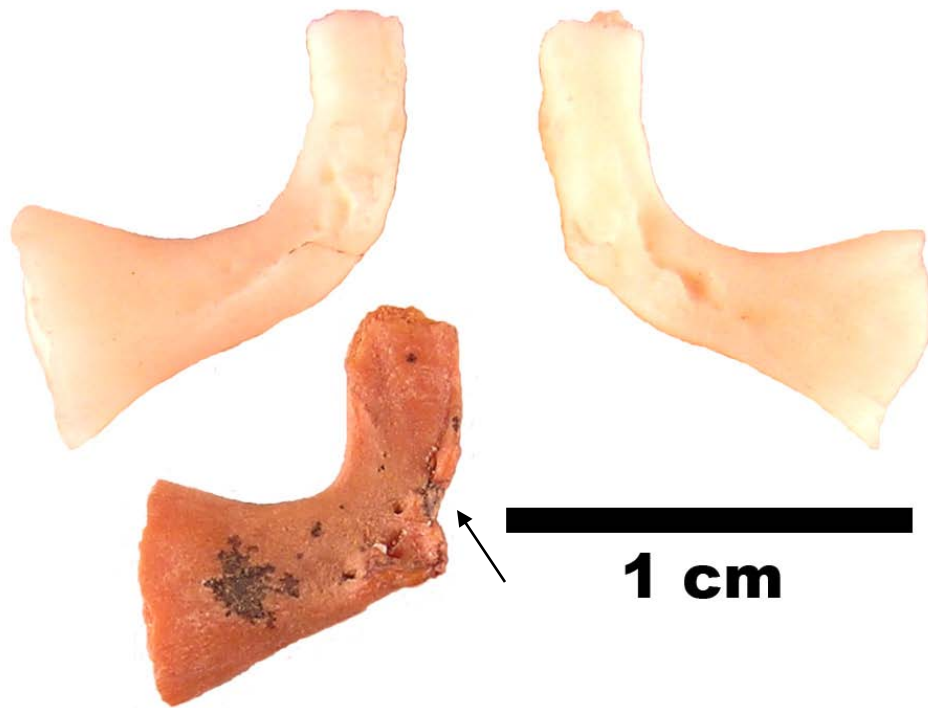
Figure 10. Comparison of the sacral ribs of a modern *C. alleganiensis* (DCP 661), top, and the misidentified sacral rib previously assigned to *C. guildayi* (CM 40416), in lateral view. The wider ends articulate with the sacrum; the narrower articulate with the ilium. Arrow indicates broken region with a small amount of missing material. Also note the variation in this region of the 2 modern sacral ribs; these are from the same individual.

Figure 11. Ceratohyal, or "epihyal", of *C. alleganiensis* (DCP 661), left, with the misidentified sacral rib previously identified as the "epihyal" of *C. guildayi* (CM 40416).

(3) Trunk Vertebrae – the single complete trunk vertebra attributed to *C. guildayi* is from the collection of additional material from Trout Cave (CM 40416). Holman (1982) estimates this vertebra was shorter and wider than the trunk vertebrae of *C. alleganiensis* by using a ratio of the greatest width by the greatest length of the zygapophyses (Fig. 12). The ratio of these measurements of the *Cryptobranchus guildayi* vertebra was cited as (0.69), greater than the range and mean of a sample of 18 trunk vertebrae of modern *C. alleganiensis,* which was reported as 0.56-0.65, ($x = 0.602 \pm 0.021$). However, a repeat of the measurements of the zygapophyses of the *C. guildayi* trunk vertebra (CM 40416)

yielded a result of (0.65) that falls within the reported range of modern *C. alleganiensis* by Holman (1982).

Further measurements of 101 trunk vertebrae from 6 individual modern hellbenders gives a broader view of variation in trunk vertebra dimensions. Following Holman (1982), trunk vertebra proportions were estimated by measuring the zygopophyses. Both sets of zygopophyses were measured for each dimension, and the larger of the 2 measurements was used (Appendix B). The range and mean of the ratios of this set of measurements is 0.61- 0.94, (x = 0.70 ± 0.053). The vertebra attributed to *C. guildayi* falls within the range of sizes exhibited by modern *C. alleganiensis* vertebrae (Fig. 13), and therefore it is clear that the specimens previously assigned to *C. guildayi* are not proportionally different than the extant species.
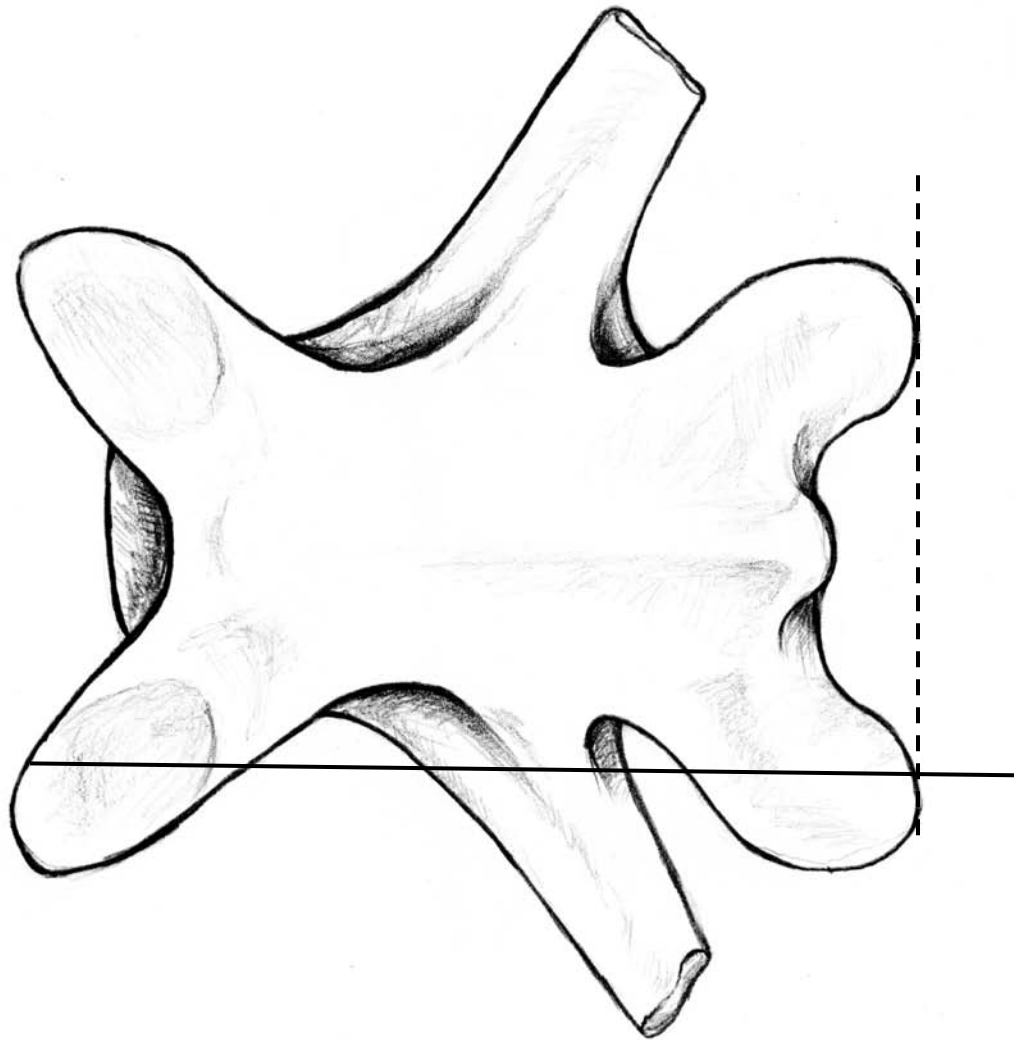
Figure 12. Dorsal view of a *Cryptobranchus* trunk vertebra. Lines indicate linear measurement scheme used for diagnostic ratio. The solid line represents the greatest length through the zygapophyses, GLZ; the dotted line the greatest width through the zygapophyses (GWZ). Anterior is to the left. Illustration by the author.
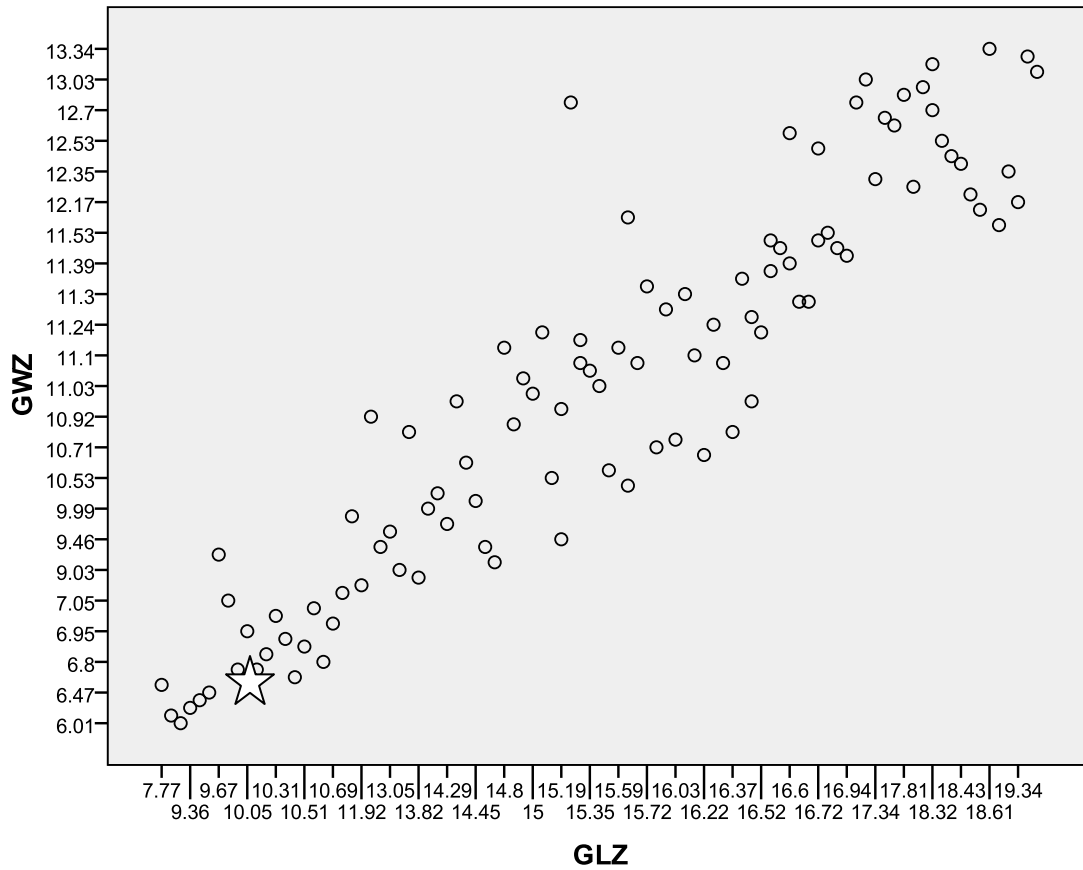
Figure 13. Bivariate plot of *Cryptobranchus alleganiensis* trunk vertebra dimensions. GWZ - the greatest width through the zygopophyses; GLZ – the greatest length through the zygopophyses. Star indicates fossil vertebra attributed to *C. guildayi*.

(4) Femora – The distal muscular ridge of the femur was described as being better developed and extending further down the shaft in *C. guildayi*. This character was used by Holman (1982) to distinguish the femur of *C. guildayi* from that of *C. alleganiensis*, but no definition of the 'distal muscular ridge' was found in any of the literature cited. This is unfortunate because the distal muscular ridge could not be located on either of the

2 partial right femora attributed to *C. guildayi* or on any referred specimen of modern *C. alleganiensis.* Most confusing is that Holman (1982) describes the 'distal muscular line' as extending two-thirds down the length of the shaft in *C. guildayi,* because the shorter of the 2 incomplete fossil femora found in Trout Cave at most has only half of the femur present. Whether some of the proximal portion of this femur has been lost in the intervening years can not be absolutely determined because it is only described in Holman's work, not illustrated. However, the break did not appear to be a 'fresh' one, i.e., the edges appeared rounded instead of angular and there was sediment infilling in the hollow trebecular bone. The other partial femur is less damaged but is missing both the proximal and distal ends. No difference between it and a modern *C. alleganiensis* femur could be discerned (Fig. 14).

(5) Scapula – The diagnostic characters of the scapula of *C. guildayi* are described as having a more rounded dorsal surface and the posterior process making a greater angle with the shaft than in the modern species (Holman, 1982). The scapulae of *C. alleganiensis* exhibit much variation in both of these characters. The dorsal surfaces of different *C. alleganiensis* individuals exhibit a range of 'roundnesses'. Some *C. alleganiensis* individuals have differing angles of the posterior process with the shaft on left and right scapulae. This is not surprising, given the cartilaginous nature of much of the pectoral girdle.

Figure 14. Dorsal view of a modern *C. alleganiensis* femur, left; and the shorter distal

portion of the *C. guildayi* femur from Trout Cave (CM 40416), right.

Figure 15. Scapula of *Cryptobranchus guildayi*.

<u>Discussion</u>

Because the characters that were used to define *Cryptobranchus. guildayi* can either be found in modern specimens of *C. alleganiensis* or are based on descriptive errors, it is recommended that the 2 species be considered conspecific. Because the fossil material previously attributed to *C. guildayi* is known from localities representing the Irvingtonian North American land mammal age (NALMA) of the Pleistocene, this material now represents the earliest record of *C. alleganiensis*, which was previously known only from the subsequent age, the Rancholabrean. In addition, because the fossil species are conspecific with modern *C. alleganiensis,* the fossil localities attributed to *C. guildayi* also conclusively extend the prehistoric range of *C. alleganiensis* to include the Potomac River drainage. Hellbenders currently do not occupy this river system, but they are found in nearby rivers. This represents an example of loss of geographical range for this species, but the reasons why this has occurred are not clear.

The morphological findings described here highlight the importance of using a large comparative collection when identifying fossil remains. Because Holman used only a few comparative specimens in conjunction with a limited amount of fossil material, skeletal variation present in modern hellbenders was underestimated, and the ability to use slight differences observed in the fossil material to differentiate taxa was overestimated. It is also possible that Holman may have been influenced by the fact that these fossils were recovered from outside the historic range of modern hellbenders. Indeed, there has recently been a shift in the way fossil identifications are made in microfossil assemblages, away from suites of diagnostic characters that may be difficult

to interpret or may not be present on fragmentary remains, to a more quantitative or apomorphic approach (Bever 2005; Bell et al. 2009).

If in fact *Cryptobranchus saskatchewanensis* does belong in the genus *Andrias,* the taxonomic loss of *C. guildayi* makes the genus *Cryptobranchus* monotypic. This is a problem for apomorphy-based approaches to identification. This identification scheme requires the use of adapted, shared, and mutually exclusive characteristics to separate groups. Its strengths are that it allows an evolutionary approach to fossil species identification and avoids the circularity introduced by selecting a group of modern comparative species based on current geographic distribution, then using the fossil identifications in a biogeographical study. In the case of *Cryptobranchus* because there is only a single modern species, geographic circularity is easily avoided. However, all of the morphological characteristics that identify *C. alleganiensis* as a species are also the same characteristics that identify the genus. Given a purely apomorphic basis of identification, all North American fossil localities since the Paleocene would be referred to *Cryptobranchus* sp. because with a monotypic genus there are no distinguishing species characteristics as there is only one species. However, because the fossil cryptobranchid material examined so far is identical to the modern species, designating these Pleistocene fossil records as *Cryptobranchus* sp. seems to be an unnecessary level of caution.

Conclusions

- *Cryptobranchus guildayi* fossils display no morphological characteristic not seen in the modern hellbender, *C. alleganiensis,* so the 2 are considered conspecific

- The fossils from Trout Cave and Cumberland Cave previously attributed to *C. guildayi* represent the first record of *C. alleganiensis* from the Irvingtonian and the earliest record for the species

- Cumberland and Trout caves are situated on tributaries of the Potomac River, so *C. alleganiensis* did prehistorically inhabit the Potomac River drainage

- With the loss of *C. guildayi*, the genus *Cryptobranchus* is now possibly monotypic

CHAPTER 3

NEW *CRYPTOBRANCHUS* FOSSILS FROM NORTH FORK POTOMAC RIVER

REGION CAVES

Included in this chapter is the description of additional *Cryptobranchus* fossil

material from 3 Appalachian caves: Trout Cave, New Trout Cave, and Hamilton Cave, all

in Pendleton County, West Virginia and thought to represent the Irvingtonian Land

Mammal Age of the Pleistocene. Each cave has produced prior fossil *Cryptobranchus*

material; however, these records are notable for coming from different localities within

the caves and for the general scarcity of hellbender remains in the fossil record. Because

these caves are from the same age and from the same region as the fossil material

previously described as *C. guildayi,* the *Cryptobranchus* material from these sites

presumably may have been referable to this now defunct taxon. Each cave site is

discussed separately below.

Trout Cave

This site, like the other caves discussed in this chapter, is located in Pendleton

County, West Virginia. All 3 caves are formed in Devonian limestone and situated in the

same ridgeline above the South Fork of the Potomac River, about 5 kilometers from

Franklin, West Virginia (Kurtén and Anderson 1980). Hellbenders are not currently

known to inhabit this waterway, though they are found in nearby western counties

(Lannoo 2005). The age dating of the localities from Trout Cave discussed here are derived based on the mammalian faunal components present (arvicolid, geomyid, and ochotonid) (Holman 1982) that indicate a similarity to the assemblage in Cumberland Cave and a place within the later part of the Irvingtonian land mammal age (Zakrzewski, 1975).

Initially a stratified sequence separated by a layer of flowstone was excavated by the Carnegie Museum of Natural History (Kurtén and Anderson 1980). Later collection efforts yielded a collection of fossil material that included the *Cryptobranchus* fossils discussed in Chapter 2 that Holman referred to *C. guildayi* and used to produce his amended diagnosis of the species (Holman 1982). Further collection in this area, since dubbed Locality 2, yielded additional material among which were 3 *Cryptobranchus* vertebrae (USNM 537781), one of which is pictured in Figure 16. Two of the 3 vertebrae had intact zygopophyses complete enough for linear measurement, which was performed in the same way as the vertebral measurements illustrated and described in Chapter 2. These measurements are shown in comparison with the measurements from the range of vertebrae from modern *Cryptobranchus alleganiensis* (Fig. 18), and all lie within the dimensions observed in the modern vertebrae.

Another site within the cave (Locality 3) lay closer to the entrance, near a ledge. The microtine rodents of this locality are similar to those of Locality 2, suggesting a similar age (Fred Grady, personal communication). Included in the Locality 3 material is a single *Cryptobranchus* vertebra (USNM 537780), illustrated in Figure 17. This vertebra too is within the range of measurements taken from modern *C. alleganiensis.*

Figure 16. Vertebra representative of Trout Cave Locality 2 material. Bar = 1 cm.

Figure 17. Vertebra from Trout Cave Locality 3 material. Bar = 1 cm.
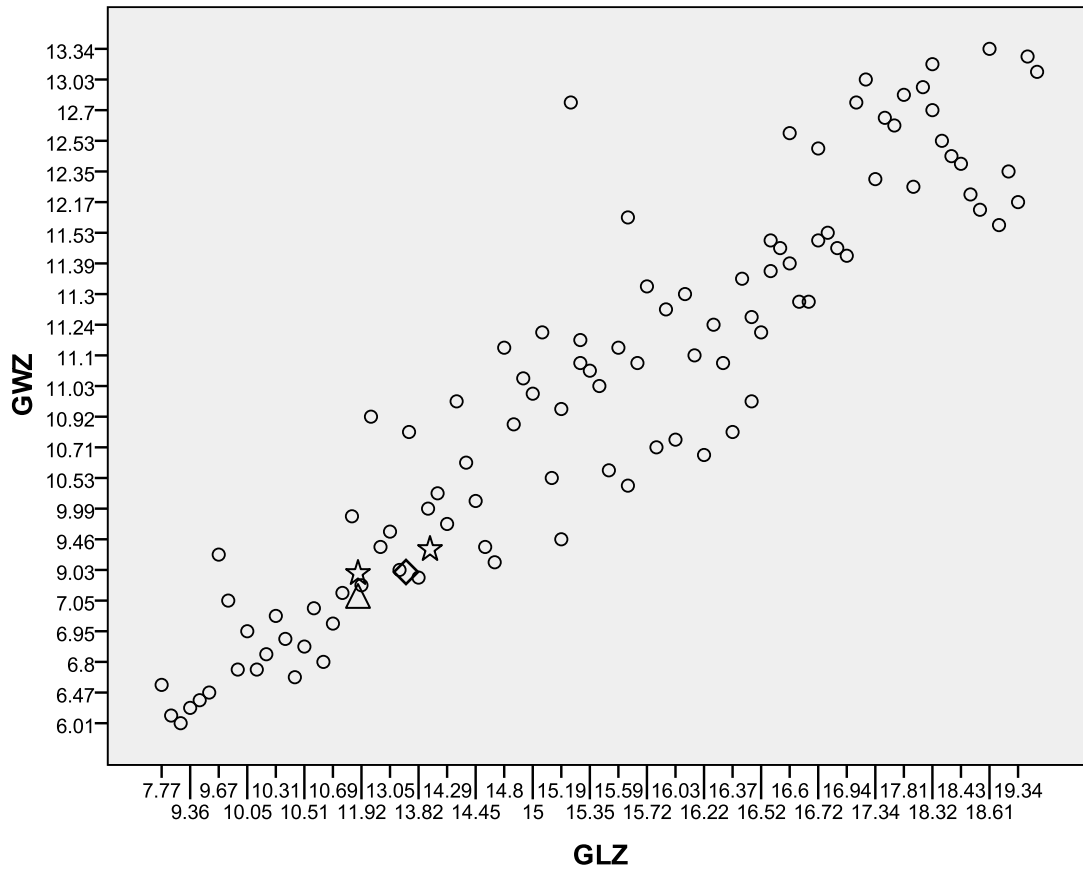
Figure 18. Linear measurements of the new fossil *Cryptobranchus* vertebrae compared to the measurements of modern *C. alleganiensis*. Stars - Trout Cave Locality 2 vertebrae; Triangle – Trout Cave Locality 3 vertebra; Diamond - Hamilton Cave vertebra.

<u>New Trout Cave</u>

This cave, located near Franklin, West Virginia in Pendleton County and insinuated in Devonian age limestone, has 2 bone-yielding localities within it, a larger area dubbed Main Site and a smaller area located a few meters closer to the entrance, New Site (Holman and Grady 1987). Main Site is notable for having had good

stratigraphic control (Holman and Grady 1987) as well as radiocarbon dating (Mead and

Grady 1996). *Cryptobranchus* fossils were previously reported in lower levels of Main

Site and New Site that date to greater than 30,000 year bp (Holman and Grady 1987).

This material is referred to *Cryptobranchus* sp. by Holman and Grady, but among this

material is another likely misidentified sacral rib that is described as being an epihyal

intermediate between *C. guildayi* and *C. alleganiensis*. Though this specimen (USNM

410611) was not viewed for the current study, the illustration of this element from

Holman and Grady's 1987 publication is very similar to that of the sacral rib identified as

an epihyal in Holman's 1982 treatment of the herpetofauna of Trout Cave discussed in

Chapter 2. If this is the case, then no intermediate condition exists as the sacral rib of

modern hellbenders exhibits the characteristics needed to separate the two.

Further excavations in New Site have yielded additional *Cryptobranchus*

vertebral elements, one vertebra, a partial centrum, and a partial vertebral transverse

process (USNM 537778). All are highly fragmentary and therefore are not discussed in

more detail here.

Hamilton Cave

Hamilton Cave is probably best known for producing fossils of large carnivorans,

including a nearly complete skeleton of the American cheetah, *Miracinonyx inexpectatus*

(Van Valkenburgh et al. 1990). Two sites in the eastern part of the cave, 'Cheetah' and

'Smilodon 2', have produced previously reported *Cryptobranchus* fossils (Holman and

Grady 1989). According to this report, the skeletal elements of the large carnivorans

were well preserved, but the herpetological material was quite fragmentary and possibly

coprolitic. Whether this difference in preservation was due to collection method was not discussed, but the herpetological material was collected like most microfossils are, via screened bulk matrix. This material, which included over 40 vertebrae, a scapula, 2 dentaries, and 2 'epihyals', was referred to *Cryptobranchus* sp. owing to the similarity of the epihyals (ceratohyals) to those of *Cryptobranchus guildayi*. In contrast the rest of the material resembled modern *Cryptobranchus alleganiensis*. Although this material was not analyzed for the current study, the identification of the ceratohyals is suspect based on previous identifications of this element. It seems, therefore, likely that this material is referable to *C. alleganiensis*.

Further excavations in the Cheetah Room site have yielded additional fossil material. Like that of Holman and Grady's 1989 report, the material is quite fragmented. *Cryptobranchus* remains are represented by 2 atlases, several fragmentary and one complete vertebra, and 4 dentary fragments. The similarity of these fossil elements to those of *C. alleganiensis* is notable.

The age of this site, like the others, is based on similarities of the mammalian fauna to each other and to that of Cumberland Cave, Maryland. It is important to note that although these faunas are generally accepted to have been Irvingtonian, external age control is lacking for all and actual age estimates vary (Bell et al. 2004).

CHAPTER 4

A NOTE ON SKELETAL VARIATION IN *CRYPTOBRANCHUS*

ALLEGANIENSIS

During the course of examining modern skeletons of *C. alleganiensis*, some specimens were found that exhibited unusual skeletal morphologies. In particular, one individual (NVPL 6917) exhibited an ossified element of the hyoid that had previously been disagreed upon by other researchers. Elwood and Cundall (1994) conducted a radiograph examination of the jaw and hyoid apparatus of *Cryptobranchus* that showed the first of the 4 branchial arches, ceratobranchial I, to be entirely cartilaginous (Fig. 19), contradicting earlier reports of ossification in this element (Jollie 1962; Parker 1882). Both positions are correct; in some individuals the ceratobranchial is entirely cartilaginous (Figs. 20, 21), and in others the posterior portion is calcified or ossified (Fig. 22).

Another hellbender, DCP 705, exhibited an unusually short tooth row on the left dentary but not the right (Fig. 23). Roughly one-third of the posterior tooth row is not present; it appears that the lateral surface of the dentary has folded inward to meet the medial portion of the coronoid. This feature was undoubtedly pathological in origin, as the atlas of the same individual exhibited a stunted left zygopophysis and an asymmetry-producing tilt to the neural tube, but the dentary itself appears quite normal, with none of the spongy texture characteristic of infection or lumps that indicate healed breakage.

Figure 19. Diagram of *Cryptobranchus alleganiensis* hyoid elements. Ventral view.

Modified from Duellman and Trueb 1994. Gray – cartilaginous elements, White –

ossified, bony elements
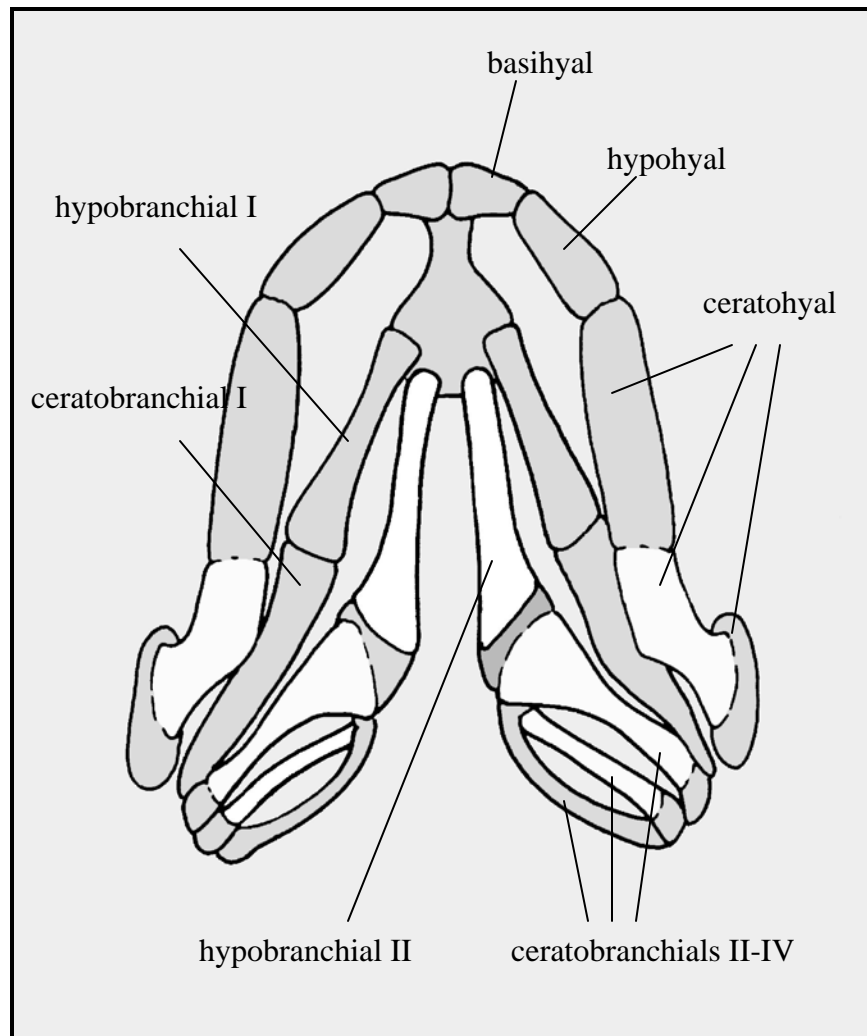
Figure 20. Articulated hyoid region of *C. alleganiensis* (UF 99064) in ventral view.

Arrows indicate ceratobranchial I. Note that this element is entirely cartilaginous.

Figure 21. Articulated hyoid region of UF 21844, in ventral view. Arrows indicate ceratobranchial I. As with UF 99064, this element is entirely cartilaginous.

Figure 22. Ventral view of *C. alleganiensis* (NVPL 6917). Arrows indicate

ceratobranchial I. Note that this element is ossified in this specimen.

Figure 23. Left and right dentaries of a modern *C. alleganiensis* (DCP 705) showing asymmetry. Bar = 1 cm.

Morphological peculiarities extend to the vertebrae as well. Meszoely (1966) describes a specimen of *Cryptobranchus alleganiensis* with an unusual sacrum. The enlarged transverse processes for articulation with pelvic elements were present on 2 different adjacent vertebrae, a condition confirmed by the observations of this study. Other vertebral variations include what are apparently fused vertebrae, with multiple sets of transverse processes present on what appears to be a single vertebra, some with 2 present on one side and only one on the other (Fig. 24). Because salamander vertebrae do not have sutures, it can be difficult with these fused elements to distinguish where one begins and another ends. One can imagine that if a vertebra such as these were to be

found as an isolated element in the fossil record that the possibility of misdiagnosis would exist.

The unusual morphologies observed in these modern specimens have some implications for the vertebrate paleontologist. Small vertebrates are seldom found in articulation. Frequently, work is done on isolated elements. In the case of the stunted dentary (Fig. 23), had the left dentary been found out of association with the right, which is very frequently the case with smaller vertebrates recovered from fossil localities using microfossil techniques, there would be a risk of misinterpreting this kind of aberrant morphology as a phylogenetic novelty.

The ossified hyoid element is problematic as well. Whether this calcification is the result of ontogenetic changes is unknown. The salamanders exhibiting these different conditions were not unlike in size, but the hellbender with the ossified ceratobranchial is reported to have been advanced in age, possibly as old as 30 years (Kelly Irwin, personal communication). Though calcification would undoubtedly cause greater rigidity of this

Figure 21. Fused vertebrae of a modern hellbender (CM 37476). Dorsal view. Bar = 1 cm.

element, it is not definitely known whether function would be impaired or affected. The role of the ceratobranchial is to swing down, ventrally and posteriorly with the hyoid to produce the 'gape' of gape-and-suck feeding (Elwood and Cundall 1994). The stiffened ceratobranchial appears to have still been able to have performed this movement, as there are articular surfaces on the posterior ends, so it is possible that despite the osteological change there could be little effect on the feeding mechanism.

Because fossil sample sizes can be very small, estimation of osteological variation present in fossil populations is frequently not possible. When working with fossils of an extant species or one that has close living relatives, the importance of using many modern comparative specimens cannot be overemphasized because these can help illustrate intraspecific variation that may or may not be seen in the fossil samples available. This brief chapter serves as an illustration of examples of modern intraspecific variation present in a modern species that may be misinterpreted in the fossil record.

CHAPTER 5

SUMMARY

In 1977 an extinct species of hellbender (*Cryptobranchus guildayi*) from

Cumberland Cave, Maryland was described. An amended diagnosis of this species

followed with additional material from Trout Cave, West Virginia. Since the original and

amended diagnoses, some researchers have questioned the validity of this taxon, but the

material has not been reanalyzed. Here the *C. guildayi* fossil material is compared to

modern hellbenders (*C. alleganiensis*) to test the validity of the described extinct form.

Becausee a limited number of modern comparative specimens were used in naming *C.

guildayi,* it is hypothesized that intraspecific variation of the modern hellbender was

underestimated. Indeed, the results presented here show that each of the characters

thought to be diagnostic to *C. guildayi* can be observed in modern *C. alleganiensis*

specimens or were based on misidentification. For these reasons the Pleistocene

salamander *C. guildayi* should be considered conspecific with the modern hellbender, *C.

alleganiensis*.

Originally this project began as an evaluation of the validity of the questionable

species *C. guildayi*. Because this was found to be an invalid taxon, subsequently other

hellbender material potentially referable to *C. guildayi* from the surrounding region was

evaluated. Because the genus *Cryptobranchus* is now possibly monotypic (certainly

since the Paleocene), it is probable that the Pleistocene fossil hellbender material

previously referred to *Cryptobranchus* sp. may be identified as *C. alleganiensis.* Also, the presence of *C. alleganiensis* in caves along the North Fork of the Potomac River conclusively extends the prehistoric range of hellbenders to this river system. Why hellbenders are found in the counties west of this area but are no longer present in the Potomac drainage is not known.

In the course of inspection of the modern hellbender skeletal material required for this project, interesting anomalies were observed and reported. The implications of these anomalies are important for the paleontological researcher, who must frequently use a small sample size when evaluating fossil vertebrates. Without an understanding or estimate of the variation that may be present in the whole population of organisms studied, the risk of misinterpreting variation as a morphological novelty develops. Indeed, the characters defining *C. guildayi* were mainly of slight differences, which were observed in the modern species given a large enough modern sample.

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APPENDICES

APPENDIX A: List of Institutional Abbreviations

ASU – Appalachian State University

CM – Carnegie Museum of Natural History

DCP – Dennis Parmley's collection at Georgia State

UF – University of Florida Museum of Natural History, Gainesville

NVPL – Neogene Vertebrate Paleontology Lab, East Tennessee State University

USNM – Department of Paleobiology of the National Museum of Natural History

APPENDIX B: Linear Measurements of the Vertebrae of 6 Modern Hellbenders

Specimen	GWZ	GLZ
DCP 661	11.25	16.40
	11.24	16.23
	10.28	15.61
	10.71	15.91
	9.07	14.63
	11.50	16.72
	11.09	16.29
	10.97	16.40
	10.55	15.54
	11.53	16.86
	10.81	16.37
	11.45	16.56
	10.65	16.22
	9.46	15.19
	11.42	16.94
	9.60	13.05
	9.43	14.59
	11.10	16.21
DCP 705	9.17	9.67
	9.43	12.30

	9.70	11.75
	11.03	15.39
	11.26	15.98
	11.23	16.52
	10.08	14.45
	11.29	16.71
	10.59	14.37
	11.29	16.69
	10.81	13.72
	11.50	16.54
	11.39	16.60
	11.37	16.54
	11.34	16.38
	11.45	16.92
	11.30	16.08
	11.09	15.32
CM 37476	12.17	19.34
	12.53	18.37
	12.42	18.42
	12.24	18.45
	13.20	19.48
	12.00	18.82

	12.05	18.60
	12.41	18.43
	12.35	19.45
	13.30	19.35
ASA 12311	11.01	15.00
	9.66	14.29
	11.04	14.96
	11.08	15.35
	11.15	14.80
	10.75	16.03
	9.03	13.08
	10.84	14.82
	10.53	15.15
	8.83	13.82
	11.33	15.72
	10.93	15.19
	11.09	15.67
	11.20	15.32
	11.15	15.59
	10.24	14.25
	9.99	14.07

	8.79	11..92
DCP 3257	7.04	10.54
	6.84	10.51
	6.74	10.06
	6.19	9.56
	6.71	10.43
	6.80	10.63
	6.83	10.22
	7.12	10.70
	6.74	9.89
	6.95	10.05
	6.18	9.36
	7.01	10.31
	6.85	10.37
	6.96	10.69
	6.13	8.66
	6.01	8.96
	7.05	9.76
	6.47	9.62
	6.62	7.77
NVPL 6917	10.92	12.04
	10.97	14.36

11.23	15.10
12.03	16.52
12.54	16.60
12.71	17.18
13.03	17.30
13.29	18.32
13.34	18.61
12.96	18.14
12.86	17.81
12.70	18.32
12.64	17.58
12.60	17.67
12.31	18.05
12.33	17.34
12.43	16.72
12.71	15.27

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2008   **Bredehoeft**, K.E. and B.W. Schubert. Revised Species Status of the Extinct Hellbender, *Cryptobranchus guildayi*. Society of Vertebrate Paleontology Meeting, Cleveland, Ohio. *Journal of Vertebrate Paleontology* 28:54.

2008   Wallace, S., and K. **Bredehoeft**. Using Morphometrics for the Designation of Enigmatic Holotypes: an Isolated Tooth as a Test Case. Society of Vertebrate Paleontology Meeting, Cleveland, Ohio. *Journal of Vertebrate Paleontology* 28:157.

2008   **Bredehoeft**, K.E. and B.W. Schubert. On the status of *Cryptobranchus guildayi. Southeastern Association of Vertebrate Paleontologyn Proceedings* 1:15.

Awards: GPSA travel grant award

                                    ETSU Graduate Student Research award