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A Re-Evaluation of the Pleistocene Hellbender, *Cryptobranchus guildayi*

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ABSTRACT.—*Cryptobranchus guildayi* has been described as an extinct species of large salamander that is related closely to the modern Hellbender, *Cryptobranchus alleganiensis*. The validity of this extinct taxon has been questioned; thus, an expanded osteological sample of modern Hellbenders was compared to the *C. guildayi* fossil material. Based on our analysis of the fossil material, all morphological characters used to define *C. guildayi* can be observed in specimens of *C. alleganiensis*, or are based on misidentifications. Therefore, *C. 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* expands the prehistoric geographical range of the modern species to the Potomac River and its tributaries and also extends the age of the species into the Irvingtonian North American land mammal age.

The extant Hellbender (*Cryptobranchus alleganiensis*, Cryptobranchidae; Caudata) is the largest North American salamander. Historically, *C. alleganiensis* has inhabited eastern river systems: 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, with a smaller disjunct population in the Ozarks of Missouri and north-central Arkansas (Lannoo, 2005). The fossil record of *C. alleganiensis* includes Rancholabrean and younger localities from the eastern United States, all from within the known historic range (Holman, 2006).

In 1977, J. A. Holman described a new species of Hellbender (*Cryptobranchus guildayi*) from Pleistocene fossils recovered in Cumberland Cave, Allegany County, Maryland. The mammalian fauna from Cumberland Cave has been well studied (e.g., Gidley and Gazin, 1938; Guilday, 1971; Van der Muellen, 1978; Repenning, 1987; Mead and Grady, 1995) and is considered to represent the Irvingtonian North American land mammal age (NALMA, stage II, that dates to ~0.85–0.4 Ma (Bell et al., 2004). The *C. guildayi* holotype (CM 20470) consists of a partial left dentary that is missing the anterior-most portion (Fig. 1A). Additional material attributed to this species was later recovered and described from Trout Cave in Pendleton County, West Virginia (Holman, 1982). The Trout Cave fossils (CM 40416) consist of two right dentaries, a skeletal element identified as a right epiphyal, one atlas, one nearly complete and one fragmentary trunk vertebra, three fragmentary caudal vertebrae, two right femora, and one right scapula. The Trout Cave fauna is poorly known (Bell et al., 2004), but it shares similar arvicoline rodent components with Cumberland Cave; therefore, it has been suggested that the two are contemporaneous (Zakrzewski, 1975). Although the absolute degree of contemporaneity is unknown, the co-occurrence of *Ondatra annectens* and *Atopomys* suggests an Irvingtonian age for the fauna (after Bell et al., 2004).

Following Holman (1982), the characteristics distinguishing *C. guildayi* from the modern Hellbender *C. alleganiensis* (Daudin, 1801–03) are as follows: 1) the dentary has a longer labial, or Meckelian, groove than in *C. alleganiensis*, and is more weakly curved; 2) the epiphyal 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 in *C. alleganiensis*; and 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 had a limited number (four, Holman, 2006) of small comparative specimens of *C. alleganiensis* available at the time of the original 1977 diagnosis and only one (MSU 13216) at the time of the revised diagnosis (Holman, 1982), little or no assessment of intraspecific osteological variation could have been made. In addition, discrete character states are now preferred in fossil identification because more subjective, less quantifiable characteristics are subject to differing interpretation by researchers, especially when remains are fragmentary, as is almost always the case with small fossil vertebrates (Bever, 2005). The morphological variation of skeletal elements in the modern Hellbender species, *C. alleganiensis* has been noted and the systematic validity of the fossil taxon questioned (Estes, 1981; Holman, 2006), but no re-evaluation of the fossil material has been published. Accurate identifications of fossil taxa are crucial for making larger interpretations about paleoecology, biogeography, and evolutionary relationships. The use of a small number of comparative specimens introduces the danger of identification inaccuracies attributable to underestimation of intraspecific variation. Consequently, our study provides a re-examination of *C. guildayi* with an emphasis on scrutinizing its systematic validity.

MATERIALS AND METHODS

To assess the validity of the distinguishing characteristics of *C. guildayi* that purportedly separate it from *C. alleganiensis*, the fossil material attributed to *C. guildayi* (CM 20470, CM 40416) was compared with a larger sample of modern *C. alleganiensis* skeletons. Twenty-seven modern *C. alleganiensis* skeletal specimens were examined from the following collections: Appalachian State University (ASU); Carnegie Museum of Natural History (CM); Dennis Parmley Collection at Georgia College and State University (DCP); East Tennessee State University Vertebrate Paleontology (ETVP); Florida Museum of Natural History (UF); and Museum of Vertebrate Zoology, University of California, Berkeley (MVZ). Juvenile or larval specimens were excluded, and several (DCP 661, DCP 705, ASU 12311, CM 37478, CM 92273, CM 37479, CM 37477, ETVP 6917, MVZ 185226) were of similar size to those individuals represented by

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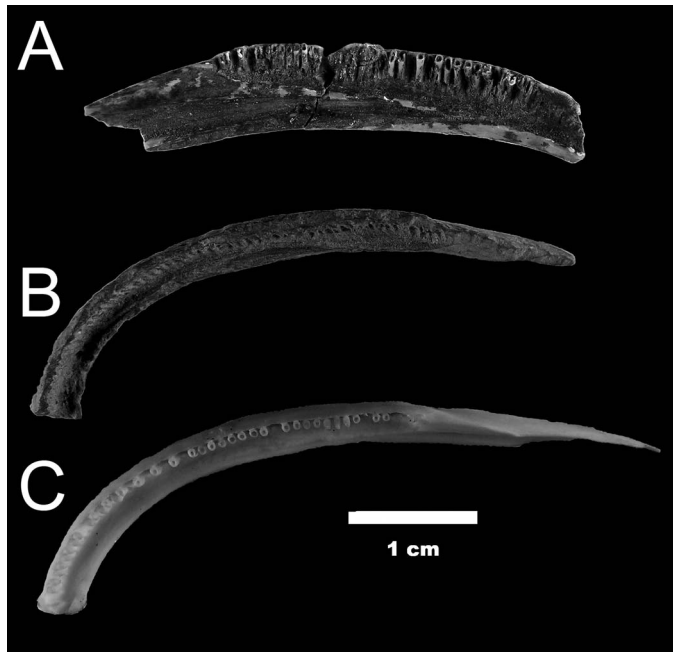


FIG. 1. A) *Cryptobranchus guildayi* fossil holotype used for original diagnosis of the species, a left partial dentary in lingual view (CM 20470); B) fossil dentary attributed to *C. guildayi* in the amended species diagnosis, in occlusal view (CM 40416); C) modern *Cryptobranchus alleganiensis* right dentary, in occlusal view (DCP 661).

the fossil material. The character states described in Holman's amended diagnosis (1982) that were used for distinguishing the fossil from the modern species were examined on both the fossil material and the modern skeletons and are discussed below. The remaining comparative material used is cataloged as follows: CM 6262; CM 5885-A; CM 5885-B; CM 92271; CM 92272; DCP 3252; DCP 3253; DCP 3254; DCP 3255; DCP 3256; DCP 3257; UF 21844; UF 34990; UF 38233; UF 52537; UF 55786; UF 57153; UF 99064.

In addition to morphological comparison of the fossil material to a modern sample, a ratio of linear measurements of an expanded number of modern vertebrae was taken. Following Holman (1982), trunk vertebra proportions were estimated using a ratio of linear measurements of the vertebral zygapophyses. The greatest length through the zygapophyses (GLZ) was taken by measuring the greatest extent anteroposteriorly through the pre- and post-zygapophyses on left and right sides of the vertebra, and the greatest width through the zygapophyses (GWZ) was taken by measuring the greatest extent laterally through the paired sets of pre-zygapophyses and post-zygapophyses. Both sets of zygapophyses were measured for each dimension, and the larger of the two measurements was used. Measurements were taken from the mostly complete Trout Cave trunk vertebra (CM 40416) and from 119 vertebrae from seven modern *C. alleganiensis* skeletons. All measurements were taken with Mitituyo Digimatic digital sliding calipers, with an accuracy of 0.01 mm.

RESULTS

Morphology of the Dentary.—The holotype (CM 20470) of *C. guildayi* is a left dentary missing the anterior-most portion (Fig. 1A). Holman (1977, 1982) describes this dentary as more weakly curved than that of *C. alleganiensis*. However, the posterior

portion of the jaw of *C. alleganiensis* is essentially straight with the anterior half possessing a nearly hemispherical curve (Elwood and Cundall, 1994). Making an estimate of curvature in the holotype dentary, which lacks the anterior region, therefore, is not possible. The *C. guildayi* material from Trout Cave (CM 40416) includes two right dentaries, one of which is complete (Fig. 1B). The curvature of this dentary is indistinguishable from that of *C. alleganiensis* (DCP 661) (Fig. 1 B,C).

Holman (1977) estimated the length of the Meckelian groove by counting the number of teeth and alveoli along the groove. The holotype (CM 20470) 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, all crowns having been broken off. Upon our examination of this dentary, we counted only 29 teeth and alveolar spaces along the Meckelian groove. We counted 39 teeth and alveolar spaces along the entire length of this dentary thus, consider it to be possible that the teeth were counted along the entire length of the dentary in the original description. The Trout Cave dentaries also presented fewer teeth than described in the amended diagnosis. Estimation of the length of the Meckelian groove cannot be established using tooth counts in these dentaries.

As noted by Estes (1981), the depth of the labial groove of the dentary is a highly variable characteristic in *C. alleganiensis*. In the dentary of the fossil holotype, the labial groove, indeed, is well developed and also includes within it a series of mental foramina but no deeper or longer than the groove found in modern Hellbenders, which also possess a varying number of foramina. The depth of the labial groove of the dentary may develop ontogenetically because smaller Hellbenders tend to have less developed grooves. No other distinguishing features were observed in the dentaries attributed to *C. guildayi*.

Morphology of the Epiphyal.—The epiphyal, a component of the hyoid apparatus, was described as having a strongly developed posterior process in *C. guildayi* that is not present in the modern species (Holman, 1982). The term "epiphyal" as used by Holman (1982), describes the ossified portion of the ceratohyal although others (Özeti and Wake, 1969; Duellman and Trueb, 1994) use the term "ceratohyal" for the entire structure regardless of regional ossification. Regardless of terminology, the element from Trout Cave that was described as an epiphyal is actually a *Cryptobranchus* sacral rib. A salamander's sacrum is a single vertebra that has expanded transverse processes to which the sacral rib attaches. Sacral ribs differ from the ribs of the trunk vertebrae in that they are both thicker and longer and have a downward curve that terminates in an articular surface for the attachment of the ilium. Because the transverse process of the vertebrae of cryptobranchids is fused, the proximal articular surface of the sacral ribs shows a characteristic bilobed shape (Fig. 2 B,D). Thus, the posterior process described as being unique to *C. guildayi* is actually the muscular process present on the lateral side of the sacral ribs of modern *C. alleganiensis* (Fig. 2 A,C). Note that, in the fossil sacral rib (CM 40416), there is damage to the muscular process and a small notch-shaped piece missing (Fig. 2A).

Morphology of the 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) estimated that this vertebra was shorter and wider than the trunk vertebrae of *C. alleganiensis* by using a ratio of the greatest width (GWZ) to the greatest length (GLZ) of the zygapophyses. The ratio of these measurements (GWL/GLZ) of the *C. guildayi* vertebra was cited as 0.69, greater than the range and mean of a sample of 18 trunk vertebrae of a modern

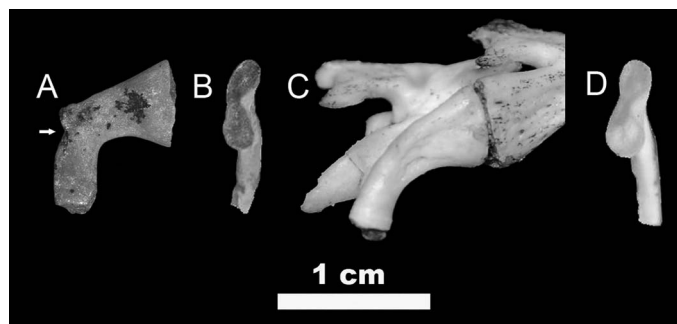


FIG. 2. Fossil sacral rib (CM 40416) attributed to *Cryptobranchus guildayi* and previously identified as a hyoid element in the species' amended diagnosis in A) lateral view (the arrow indicates the damaged region), and B) articular view; C) a modern *Cryptobranchus alleganiensis* sacral rib in lateral view in articulated life position (anterior is to the right; ETVP 6917); D) a modern *C. alleganiensis* sacral rib in articular view (DCP 661).

C. alleganiensis, which was reported as 0.56–0.65, (mean = 0.602 \pm 0.021). However, our repeat of the measurements of the zygapophyses of the *C. guildayi* trunk vertebra (CM 40416) yielded a result of (0.65), which falls within the range of modern *C. alleganiensis* reported by Holman (1982).

Our additional measurements of 119 trunk vertebrae from seven modern *C. alleganiensis* gave us a broader view of variation in trunk vertebral dimensions. The mean GWZ/GLZ ratio was 0.70 ± 0.053 and values ranged between 0.61 and 0.94. The vertebra attributed to *C. guildayi* falls within the range of size ratios exhibited by these modern *C. alleganiensis* vertebrae (Fig. 3); therefore, it is clear that the specimens previously assigned to *C. guildayi* are not proportionally different than the extant species.

Morphology of the Femur.—Holman (1982) described the distal muscular ridge of the femur as being better developed and extending further down the shaft in *C. guildayi* when compared with *C. alleganiensis*. The distal muscular ridge of the femur 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. Consequently, we were unable to locate a distal muscular ridge on either of the two 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*; however, the longer of the two incomplete fossil femora found in Trout Cave at most has only half of the femur present. Whether some of the proximal portion of the Cumberland Cave femur has been lost since Holman's original diagnosis is uncertain because it was described but not illustrated in Holman (1982). However, the broken edges of the femoral shaft appeared rounded instead of angular, and there was sediment filling the hollows of the trabecular bone, suggesting that the break in the femur occurred in the cave. The other Trout Cave partial femur has more of the shaft present but is missing both the proximal and distal ends. No other differences between the fossil femora and modern *C. alleganiensis* femora could be discerned.

Morphology of the Scapula.—The scapulae of extant cryptobranchids represent a rather general morphology among caudates. Holman (1982) indicates that scapulae of *C. guildayi* have a more rounded dorsal surface and that the posterior process makes a greater angle with the shaft than in the modern species (Holman, 1982). The scapulae of our sample of *C. alleganiensis* exhibit great

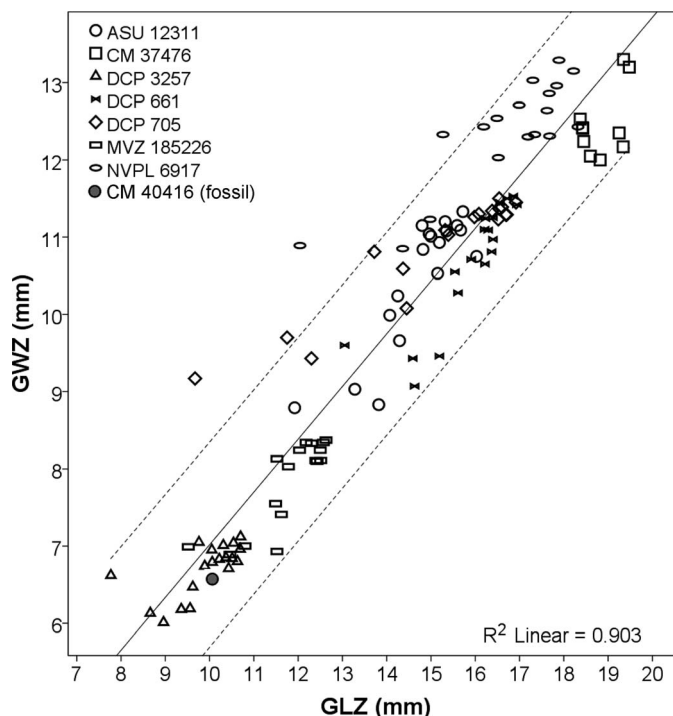


FIG. 3. Bivariate plot of *Cryptobranchus alleganiensis* trunk vertebrae dimensions, with best fit regression (solid line) and 95% confidence interval (dashed lines). GWZ = the greatest width through the zygopophyses; GLZ = the greatest length through the zygopophyses.

variation in both of these characters. The dorsal surfaces of the scapulae of different individual *C. alleganiensis* exhibit a range of “roundnesses.” Some scapulae from the same individual salamander have differing angles of the posterior process with the shaft on left and right scapulae. Variability in scapular morphology is not surprising, given the cartilaginous nature of much of the pectoral girdle; therefore, nondiscrete character states such as minor differences in shaft angle and roundness are not useful for distinguishing species.

DISCUSSION

Our re-evaluation found that the characters that were used to define *C. guildayi* can either be found in modern specimens of *C. alleganiensis* or are based on descriptive errors. The two putative species are morphologically indistinguishable; thus, it is recommended that they be considered conspecific. Because the fossil material attributed previously to *C. guildayi* is known from localities representing the Irvingtonian NALMA of the Pleistocene, these fossils now represent the earliest record of the modern species *C. alleganiensis*, which was known previously only back to the Rancholabrean NALMA. In addition, Cumberland and Trout Cave are both situated on tributaries of the Potomac River; therefore, these re-assigned fossils also extend the known prehistoric range of *C. alleganiensis* to include the Potomac River system. *Cryptobranchus alleganiensis* do not currently occupy the Potomac River system, indicating a reduction in the species' range since the Pleistocene. Our proposed range reduction is consistent with a Pleistocene refugium hypothesis that is supported by genetic evidence (Sabatino and Routman, 2009).

Despite large body size, cryptobranchids have a rather poor fossil record in North America. The only other fossil *Cryptobranchus* species that has been described is *Cryptobranchus*

saskatchewanensis, a species named based on fragmentary remains from the Upper Paleocene Ravenscrag Formation in southeastern Saskatchewan (Naylor, 1981). At the time, it was the earliest known cryptobranchid material, leading the author to suggest a North American origin for cryptobranchid salamanders that would require the inclusion of *Andrias* species in the genus *Cryptobranchus*. Subsequent discovery of basal cryptobranchids from the Middle Jurassic of China (Gao and Shubin, 2003) refutes this idea and reinforces the placement of the Paleocene species (Holman, 2006) in the genus *Andrias* rather than *Cryptobranchus*. If the living subspecies of *C. alleganiensis* are considered a single group, then with the loss of *C. guildayi*, the genus *Cryptobranchus* is now monotypic.

The morphological findings described here highlight the importance of using a large comparative collection when identifying fossil remains. Because Holman (1982) used a small number of comparative specimens in conjunction with a limited amount of fragmentary fossil material, skeletal variation present in modern *C. alleganiensis* 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. There has recently been a shift in the way fossil identifications are made in microfossil assemblages, away from suites of subjective characters to a more quantitative or apomorphic approach (Bever, 2005; Bell et al., 2010), and our study underscores the importance of using these new methods. Like the *Cryptobranchus* specimens examined here, other Pleistocene or even earlier microvertebrates likely warrant re-examination. A better understanding of the diversity and distributions of taxa would facilitate studies on the evolution of species and faunas through time and, in the case of extant taxa with a recent fossil record, would inform conservation efforts.

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