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Taxonomy and Nomenclature of the *Pantherophis obsoletus* Complex

In 1836, John Holbrook (1836) described and distinguished *Coluber alleghaniensis* and *Coluber quadrivittatus* of the eastern United States, both of which he considered distinct from the previously described *Coluber obsoletus* found to the west. Holbrook noted many differences between the two forms he described, and especially noted the differences in color pattern (*alleghaniensis* was solid black; *quadrivittatus* was yellowish with brown stripes), their distribution (*quadrivittatus* was found on the coastal plain, from at least North Carolina to Florida, whereas *alleghaniensis* was found "throughout the Alleghanies," which at the time referred to the entire Appalachian Mountain range), and habits (Holbrook considered *quadrivittatus* to be more arboreal than *alleghaniensis*). Despite these differences, however, in the second edition of his *North American Herpetology*, Holbrook (1842:91) followed his description of *C. quadrivittatus* with this comment:

> "Schlegel thinks this snake may prove identical with Coluber Alleghaniensis, to which, indeed, it bears considerable resemblance in form; but its colours are entirely different and are constant; its habitats and geographical distribution are not the same; the Coluber Alleghaniensis lives constantly on the ground, but the Coluber quadrivittatus I have met with on trees; one belongs to the mountains, the other lives on the plains." [lack of italics and capitalization as in the original]

Recently, Burbrink et al. (2020) published an analysis of the taxonomy and biogeography of these snakes, now placed in the genus *Pantherophis*. They supported the recognition of the same three taxa delimited by Holbrook (in addition to *P. bairdi* of west Texas, which was unknown to Holbrook), although Burbrink et al. (2020) found that there are very wide zones of admixture between all the pairs of taxa recognized by Holbrook, wherever they come into contact. For example, Burbrink et al. (2020) found the "zone of admixture" to be approximately 500 km wide in the case of the montane and coastal plain forms that Holbrook (1842) noted "may prove identical." In their Supporting Information, Burbrink et al. (2020: p. 9 of SI) noted that "We acknowledge difficulties recognizing the eastern lineages as distinct and could argue for recognizing them as a single taxon, *P. alleghaniensis*."

The broad zones of intergradation among these taxa, and the lack of any reproductive isolation or barriers to gene flow, mean that they fit the criteria that are usually used to distinguish subspecies, rather than species (Hillis 2020). The point of the present article, however, is not to argue whether these taxa should be recognized as subspecies or as species. In either case, the three earliest names for the three taxa recognized by Burbrink et al. (2020) are clearly *obsoletus* (for the earliest named, western lineage), *alleghaniensis* (for the blotched and solid-colored snakes found between the Mississippi River and the fall line of the eastern seaboard, including the Appalachian/Alleghany Mountains), and *quadrivittatus* (for the striped snakes found on coastal plain of the southern United States). Oddly, Burbrink et al. (2020) applied the names *obsoletus*, *spiloides*, and *alleghaniensis* to these three taxa, respectively. In other words, the taxon Holbrook named *alleghaniensis*, Burbrink et al. (2020) called *spiloides*, and the taxon Holbrook named *quadrivittatus*, Burbrink et al. (2020) called *alleghaniensis*.

The reason for this switch in appropriate names appears to be the continuation of an earlier mistaken association by Burbrink (2001). In that paper, Burbrink delimited similar taxa based on differences in their mitochondrial DNA. However, the boundaries of the taxa delimited by Burbrink (2001), and those delimited by Burbrink et al. (2020), are considerably different, as the mitochondrial lineages identified by Burbrink (2001) do not closely correspond to the taxa delimited by Burbrink et al. (2020). The new boundaries of taxa delimited by Burbrink et al. (2020) match the original distinction made by Holbrook (1836), and also fit the morphological descriptions by Holbrook (1836). The earlier delimitation by Burbrink (2001) suggested a "zone of uncertainty" (a region poorly sampled at the molecular level, and in which populations assigned to his concepts of *P. alleghaniensis* and *P. spiloides* could not be distinguished on the basis of morphology) that included most of the Appalachians/Alleghanies. In contrast, Burbrink et al. (2020) emphasized that the two species of the eastern United States are divided primarily along the fall line of the eastern coastal plain, as first noted by Holbrook (1836), and that the central lineage is clearly the taxon that is present in the Appalachians/Alleghanies (the type locality for Holbrook's *Coluber alleghaniensis*).

Holbrook (1836) did not designate a specific holotype for either *Coluber alleghaniensis* or *Coluber quadrivittatus*, but he illustrated and described both taxa. In both his illustrations and descriptions, he made clear that the striped coastal plain form is *quadrivittatus*, and that the solid black montane form is *alleghaniensis*, which corresponds with the two taxa recognized by Burbrink et al. (2020) in the eastern United States. Holbrook (1836) noted in his description of *Coluber alleghaniensis*:

> "This serpent was first observed on the summit of the Blue Ridge, in Virginia, by Mr. George Robbins, of Philadelphia. Dr. Wickens, of New York, has also favored me with a specimen from the Highlands of the Hudson; and I have received many from the mountains of Carolina, so it is probable its range extends throughout the Alleghanies."

Given that Holbrook specifically mentioned the specimen furnished to him by Dr. Wickens, from the "Highlands of the

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Hudson" in New York, this is likely the specimen that was illustrated by Holbrook. That specimen (now ANSP 16792) was considered the only known syntype of the species by Malnate (1971). In any case, all the specimens examined by Holbrook came from montane regions that are clearly far above the fall line, as well as above the zone of admixture on the Piedmont identified by Burbrink et al. (2020). Despite this, Burbrink et al. (2020: p. 8 of SI) argue that the specimens of *alleghaniensis* described by Holbrook

> "…are likely composed of admixed individuals, though obtaining genomic sequences from the type specimen, if possible, or samples from the type locality would clarify the degree of admixture. Importantly, the International Code of Zoological Nomenclature (ICZN) forbids naming species based on hybrids (Article 1.3.3; ICZN, 1999), however, the intention of this ICZN article likely refers to F1 hybrids and clearly does not consider proportions of admixture."

The maps and analyses provided by Burbrink et al. (2020) do not support that the areas from which Holbrook obtained specimens of *alleghaniensis* are from regions of significant admixture, and they are certainly not "hybrids." Burbrink et al.'s (2020) figure 5 clearly shows these regions to be inhabited by the same taxon that Burbrink et al. called *P. spiloides*. Although the earlier paper by Burbrink (2001) suggested this was a "region of uncertainty," the analyses by Burbrink et al. (2020) show that the Appalachians/Alleghanies are well outside the primary region of admixture. Of the type localities of the various relevant taxa, only the type locality for *Elaphis spiloides* of Duméril et al. (1854) is near a zone of intergradation among the taxa delimited by Burbrink et al. (2020). This locality is on the Mississippi River, which is the proposed center of the zone of admixture between the western and central forms. In any case, the species described by Holbrook as *C. alleghaniensis* is clearly the same taxon called *P. spiloides* by Burbrink et al. (2020), based on both color pattern and distribution.

Burbrink et al. (2020: p. 8 of SI) also argued that the "type [of *Coluber quadrivittatus*] from South Carolina may be admixed as well." However, Burbrink et al. (2020) presented no evidence that specimens of *quadrivittatus* (which Burbrink et al. called *P. alleghaniensis*) from the coastal plain of South Carolina are admixed, and again, they are clearly not hybrids in the sense used by the International Code of Zoological Nomenclature. This is the region where Holbrook was familiar with the species, although again, he designated no type specimen. A specimen deposited by Holbrook (ANSP 3773) and thought to be from South Carolina was considered the type specimen by Malnate (1971); Schmidt (1953) restricted the type locality to Charleston, South Carolina, where Holbrook lived. Furthermore, Holbrook (1836) made it clear that the taxon he named *quadrivittatus* was the one found on the coastal plain of the Carolinas and Florida. Therefore, there can be no confusion that the coastal plain taxon is *quadrivittatus* (whether recognized as a subspecies of *P. obsoletus*, or as a distinct species), and that the taxon called *Pantherophis spiloides* by Burbrink et al. (2020) should actually be *alleghaniensis*. Holbrook (1836) described *Coluber alleghaniensis* 18 years before Duméril et al. (1854) described *Elaphis spiloides*, so there is no question that the former has priority as a subjective senior synonym.

In summary, the three taxa recognized by Burbrink et al. (2020) should be called *P. obsoletus* (primarily west of the Mississippi River), *P. alleghaniensis* (the central taxon), and *P. quadrivittatus* (on the southeastern coastal plain), if they are recognized as distinct species. If they are considered subspecies, given the broad areas of intergradation among all the forms where they come into contact, then they should be called *P. o. obsoletus*, *P. o. alleghaniensis*, and *P. o. quadrivittatus*, respectively.

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