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Distribution of Native and Exotic Earthworms in the Eastern United States: Implications for the Ecology of Vermivorous Snakes

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Introduction

Earthworms are the primary prey documented for several North American snake species, including worm snakes (*Carphophis* spp.), earth snakes (*Virginia* spp.), swamp snake (*Seminatrix pygaea*), lined snake (*Tropidoclonion lineatum*), and short-headed garter snake (*Thamnophis brachystoma*) (Ernst and Ernst, 2003). However, more often than not, the earthworm species found to be preyed upon are not identified, and when they are, they represent European species introduced within the past 500 years (see Clark, 1970; Fitch, 1999; Pisani, 2009). The geographic distributions of the above-listed snake species occur mainly south of the boundary that represents the southernmost extension of the Wisconsinan glaciation. Furthermore, these snakes' distributions are sympatric with the majority of North America's native earthworms, and prior to the introduction of exotic earthworms, native earthworm species likely served as primary prey for these vermivorous (i.e., worm-eating) snakes. Vermivorous snake species are not restricted to unglaciated areas, however. In glaciated regions, Kirtland's snake (*Clonophis kirtlandii*), Butler's garter snake (*T. butleri*), and common garter snakes (*T. sirtalis*) include earthworms as a substantial component of their diets. The earthworm fauna in the glaciated north is almost exclusively exotic, suggesting that these snake species fed on something other than earthworms during recolonization of formerly glaciated regions (Reynolds, 1994a; Catling and Freedman, 1980). The ring-necked snake (*Diadophis punctatus*) and brown snake (*Storeria dekayi*) also have populations that feed primarily on earthworms. In this paper I discuss the relationships between vermivorous snakes and earthworms, and propose possible effects that exotic earthworms may have had, and may continue to have, on these snakes. I hope that the following discussion will encourage collaboration between herpetologists and oligochaetologists.

Glaciation and the distribution of worms and snakes

The last glacial event to affect North America was the Wisconsinan, which occurred during the Pleistocene Epoch and lasted approximately 100,000 years, beginning about 110,000 years before present (ybp) and ending around 10,000 ybp (Holman, 1995). During the Wisconsinan glacial event, massive ice sheets—the Cordilleran to the west and the Laurentide to the east—advanced and retreated, scouring the land beneath and creating the underlying topography seen in Canada and the northern United States. South of the ice sheets, a narrow 80–200 km belt of permafrost existed, where mean annual temperatures were likely less than −6°C (Dawson, 1992). After the final retreat of the ice sheets, ca. 15,000 ybp, bare ground consisting of sterile mud and unconsolidated sediments of gravel, sand and silt were left in their wake (Pielou, 1991; Holman, 1992, 1995). Such environments of bare rock and shallow soil are inhospitable for the development of biotic communities (Holman, 1992), and would have lacked adequate food (e.g., plant remains) for earthworms. According to the Post-Quaternary Introduction Theory of megadriles, earthworms occurred north of the southern limit of the Wisconsinan glaciation in North America prior to glaciation, but were extirpated during glaciation and have since been reintroduced by agents/vectors such as man (Reynolds, 1994a; Reynolds and Wetzel, 2004). Colonization of previously glaciated territory was probably slow, and it is likely that few native earthworms inhabited northern regions of North America at the time of European colonization about 500 years ago (Gates, 1967, cited in Hendrix and Bohlen, 2002). Furthermore, the ability of earthworms to migrate by their own means (0.5–1.0 km every 100 years; Marinissen and van den Bosch, 1992; Hale et al., 2006) is limited by their lack of limbs and eyes, their intolerance of ultraviolet radiation, and their dependence on moist habitats with sufficient dissolved oxygen for cutaneous respiration (James, 1984; Reynolds and Wetzel, 2004). During the Pleistocene, south of the ice sheets, summers may have been cooler and winters warmer, thus allowing northern and southern snake species to coexist (Harding and Holman, 1982; Holman, 1995).

As per Holman (1992), it is assumed that snakes (and earthworms) during the Pleistocene Epoch had the same ecological and physiological tolerances that they do today. It is also assumed that the presence of fossils of obligate vermivorous snake species, such as *Carphophis*, at a site implies that there were native earthworms there as well. Since earthworms do not fossilize well, their historic distributions prior to glaciation are not known (Proulx, 2003). Thus, using fossils to delineate the historic distributions of obligate vermivorous snakes may also serve as a baseline in the study of the historic distribution of native earthworms.

The worms and the snakes

Approximately 161 species (116 native, ca. 45 introduced) of earthworms have been described from North America north of Mexico (Reynolds and Wetzel, 2004). The native earthworms are found generally in the southeastern United States. Most of the earthworm species considered to be native to North America belong to the families Acanthodrilidae, Glossoscolecidae, Lutodrilidae, Komarekionidae and Sparganophilidae; however, several species in the genus *Bimastos* are in the family Lumbricidae. With the exception of the Pacific Northwest, where several native earthworms appear, Canada's earthworm fauna is primarily exotic (Fender, 1995; Hendrix and Bohlen, 2002). The exotic earthworms are primarily members of the families Lumbricidae and Megascolecidae; several species in the families Octochaetidae and Ocnerodrilidae have also been introduced (Reynolds and Wetzel, 2004). The introduced earthworm species are primarily of European origin, although members of the genera *Amynthas* and *Metaphire* are native to the Orient, mainly China and Japan (Reynolds, 1978). The introduction of exotic earthworms into North America is a relatively recent phenomenon, and most species were likely brought over in soil and plant roots by European settlers. Presently, discarded earthworms used as fishing bait and transport of earthworm cocoons via mud in tire treads are assumed to be important anthropogenic routes of dispersal of exotic earthworms into northern hardwood forests that previously lacked native earthworms (Cameron et al., 2007; Keller et al., 2007; Hale, 2008). It is also possible that earthworm cocoons (native and exotic) may be transported in mud on the feet of wading birds. Pisani (pers. com.) suggested that earthworm cocoons may also be dispersed in moist soil on the fur or hooves of large ungulates (e.g., deer, elk or bison). Today, some sites still lack earthworms; others may harbor earthworm species that are entirely native, a mixture of native and exotic species, or completely exotic (Hendrix and Bohlen, 2002).

Different species of earthworms utilize different microhabitats; for instance, epigeic species are litter- and surface-dwelling earthworms exemplified by some native *Diplocardia* spp. and the exotic *Lumbricus rubellus*. The endogeic earthworms are soil-dwelling; *Aporrectodea* spp. and *Octolasion tyrtaeum* are exotic examples. The anecic species are deep burrowers, such as the exotic nightcrawler, *Lumbricus terrestris*. Knowing the type of earthworm that a snake feeds upon may allow speculation about the snake's foraging habits—for instance, an observation that only endogeic species are utilized implies that the snake may burrow when feeding. Addison (2008) cautioned that the actual behavior of earthworms may not always conform to such classification. For example, endogeic *Aporrectodea turgida* feed below the soil surface, but cast on the soil surface. Furthermore, heavy rains may bring earthworms of all categories to the surface; it is therefore important to take previous precipitation into account when interpreting such data. Due to differences in habitat selection and/or behavior, not all species of earthworms may be available as prey to predators including snakes (Reynolds, 1977a). For instance, *Sparganophilus* spp. and *Lutodrilus multivasiculatus* are limicolous (mud-dwelling) species; most *Bimastos* and *Eisenoides* species are confined to forests; and some species of *Diplocardia* feed on surface litter, while others feed in the subsoil, consuming humus (Reynolds, 1980; James, 1995; Kalisz and Wood, 1995). Earthworms in the genus *Amynthas* are very active (Reynolds, 1978), and their erratic writhing and jumping may prevent small snakes such as *Carphophis amoenus* from successfully subduing them. I have personally observed this in captive *C. amoenus* and *T. brachystoma*. The snakes attempted to grasp the worms, but released them after only a few seconds; apparently because of the worms' erratic and animated behavior.

As with most dichotomies, the classification of obligate and facultative vermivorous snakes presented here has its weaknesses. In particular, juveniles of almost all the species discussed are obligate vermivores. Also, some populations of facultative vermivorous snakes may, in fact, be obligate vermivores (e.g., *Diadophis punctatus* in eastern Kansas [Pisani, 2009]). Furthermore, the distribution of native earthworms in some states is incomplete; therefore, the amount of overlap with the ranges of some vermivorous snakes is not fully known (see the discussion of *Tropidoclonion lineatum* below).

The following snake species are obligate vermivores, and each species shares a combination of at least four of the following characteristics: 1) earthworms are the only prey item documented from most populations; 2) their distributions are primarily restricted to unglaciated regions, with the majority (at least 75%) of their range sympatric with that of at least one native earthworm species; 3) they are usually found in damp or moist situations; 4) they are small species, usually less than 50 cm total length (TL); and 5) they have a limited gape that restricts them to feeding on elongate prey.

The eastern worm snake, *Carphophis amoenus*, is a small (to 35 cm TL [Ernst and Ernst, 2003]) snake with a tan to brownish dorsum and pinkish translucent ventral surface. It has a narrow, dorsoventrally flattened head; a cylindrical body; smooth scales; tiny eyes; and a short spine-tipped tail—all morphological features indicative of a burrowing life style (Gibbs et al., 2007).

The geographic distribution of *C. amoenus* is primarily south of the southernmost boundary of the Wisconsinan Glaciation. Ernst and Ernst (2003) give the distribution as extending from southern New England, southeastern New York, eastern Pennsylvania, southern Ohio, southern Indiana and southern Illinois, south to South Carolina, northern Georgia, Alabama, southeastern Louisiana, and eastern Arkansas. The eastern worm snake is

Table 1. The degree of overlap between the geographic distributions of vermivorous snakes and native earthworms. Obligate vermivores are listed in bold italics; facultative vermivores are listed in regular italics. Y indicates that significant (90–100%) overlap does occur. P indicates partial overlap occurs, with 25, 50, and 75 representing the approximate percentage of partial overlap. N indicates that there is very little (less than 10%) to no overlap in the ranges.

	Native earthworm genera				
Snake species	*Bimastos*	*Diplocardia*	*Eisenoides*	*Komarekiona*	*Sparganophilus*
Carphophis amoenus	Y	Y	Y	Y	Y
C. vermis	Y	Y	P50	N	Y
Clonophis kirtlandii	Y	Y	P25	P25	Y
Diadophis punctatus	Y	Y	Y	Y	Y
Seminatrix pygaea	Y	Y	Y	N	Y
Storeria dekayi	Y	Y	Y	P50	Y
Thamnophis brachystoma	Y	Y	P25	N	Y
T. butleri	Y	P75	N	N	Y
T. sirtalis	Y	Y	Y	Y	Y
Tropidoclonion lineatum	P50	P50	N	N	P25
Virginia pulchra	Y	Y	P50	P50	Y
V. striatula	Y	P75	P75	N	P75
V. valeriae	Y	Y	P75	P50	P75

most often found in ecotonal areas of open to thick woodlands, and the borders of wetlands. Such sites also need to have an abundance of cover in the form of rocks, logs, and leaf litter (Ernst and Ernst, 2003). Throughout this species' range, it is excluded from areas with particularly compact soils (Gibbs et al., 2007). In Connecticut, Klemens (1993) noted that "worm snakes may be excluded from higher elevations by poorly drained and rocky soils, which are not suitable for burrowing and by late spring and early autumn frosts." These situations are also unfavorable to earthworms. In Mississippi, Cook (1954) found worm snakes under rotten logs and leaves on wooded hillsides; the endemic earthworms in the genus *Bimastos* may be found in similar habitats.

Several references note that *C. amoenus* is primarily an earthworm predator, but do not specify whether or not the earthworm species consumed were native (e.g., Mount, 1975; Bush, 1959; Mitchell, 1994; Hulse et al., 2001). The range of *C. amoenus* is within the range(s), in part or whole, of native earthworms in the following genera: *Bimastos*, *Diplocardia, Eisenoides* and *Sparganophilus* (Table 1) (see James [1995] for maps). *Carphophis amoenus* was reported by Means (cited in Reynolds, 1980) in *Sparganophilus eiseni* habitat. All genera of exotic earthworms discussed in this paper have ranges that overlap with the range of *C. amoenus* (Table 2). In captivity, an eastern worm snake readily consumed the exotic earthworms *Aporrectodea tuberculata, Lumbricus rubellus*, and pieces of *L. terrestris*, but refused *Amynthas agrestis* (pers. obs.).

North of the glacial boundary in southeastern New York, Connecticut, Rhode Island and southern Massachusetts, workers may wish to focus on determining if native earthworms are found at sites with *C. amoenus*. Documented occurrences of endemic earthworms in New England are rare—for instance, *Bimastos parvus* in Massachusetts; *Eisenoides lonnbergi* in Connecticut, Massachusetts and Rhode Island (Reynolds, 2002; Reynolds and Wetzel, 2008); and *Sparganophilus eiseni* in Connecticut and Massachusetts (Reynolds, 1980). Also, the ranges of *Sparganophilus*, *Bimastos*, *Eisenoides* and *Diplocardia* extend into southern Georgia and Florida (Reynolds, 1994b; James, 1995), where extant populations of *C. amoenus* have not been documented and are assumed to be absent. Therefore, effort should be made to survey for *C. amoenus* at sites with native earthworms in these two southern states. During the Pleistocene Epoch *Carphophis amoenus* was present well south of its current range, in Alachua, Citrus, Marion and Sumpter counties in Florida (Holman, 2000).

The western worm snake, *C. vermis*, like the eastern worm snake, is a small (to 39.1 cm TL [Ernst and Ernst 2003]) snake species with a dark gray to gray-violet dorsum, and pinkish ventral surface. It is also similar to *C. amoenus* in having morphological features that facilitate burrowing (e.g., smooth scales; small, flattened head; etc.).

Carphophis vermis is found from southern Iowa and southeastern Nebraska south to northwestern Louisiana and northeastern Texas. Isolated populations occur in west-central Illinois,

Table 2. The degree of overlap between the geographic distributions of vermivorous snakes and exotic earthworms. Obligate vermivores are listed in bold italics; facultative vermivores are listed in regular italics. Y indicates that significant (90–100%) overlap does occur. P indicates partial overlap occurs, with 25, 50, and 75 representing the approximate percentage of partial overlap. N indicates that there is very little (less than 10%) to no overlap in the ranges.

	Exotic earthworm genera						
Snake species	*Allolobophora*	*Aporrectodea*	*Dendrobaena*	*Dendrodrilus*	*Lumbricus*	*Octolasion*	*Amynthas*
Carphophis amoenus	P75	Y	Y	Y	P75	Y	Y
C. vermis	N	Y	P50	P50	P50	P50	Y
Clonophis kirtlandii	Y	Y	Y	Y	Y	Y	P25
Diadophis punctatus	Y	Y	Y	Y	Y	Y	P50
Seminatrix pygaea	N	P75	N	N	N	P50	P50
Storeria dekayi	Y	Y	Y	Y	Y	Y	Y
Thamnophis brachystoma	Y	Y	Y	Y	Y	Y	P25
T. butleri	Y	Y	Y	Y	Y	Y	N
T. sirtalis	Y	Y	Y	Y	Y	Y	Y
Tropidoclonion lineatum	N	Y	N	N	N	N	P25
Virginia pulchra	Y	Y	Y	Y	Y	Y	N
V. striatula	N	Y	P50	P50	P25	P50	P75
V. valeriae	P25	Y	P50	P50	P50	P50	P75

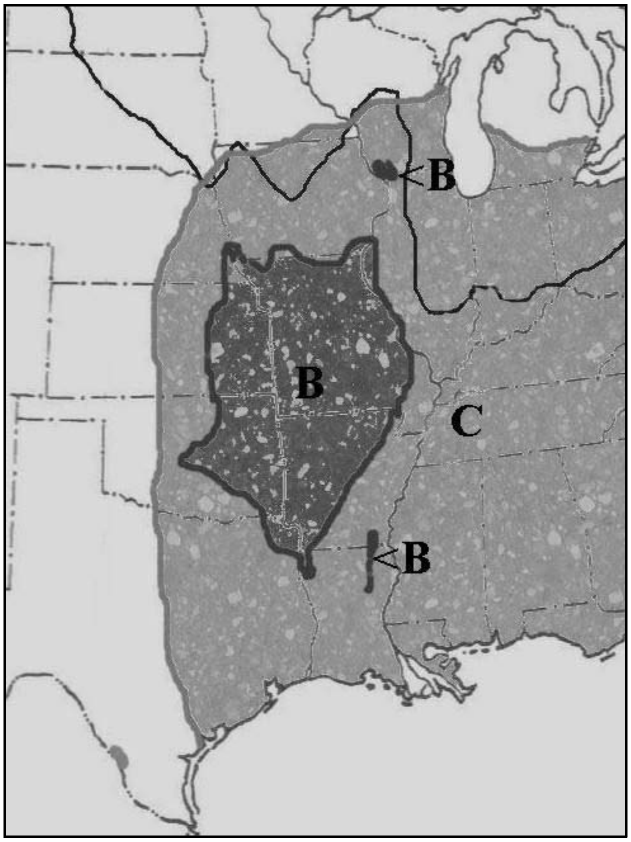

Figure 1. The approximate range of *Carphophis vermis* (adapted from Ernst and Ernst, 2003) and the combined ranges of native earthworms. Dark shaded areas labeled "B" represent areas of overlap between *C. vermis* and native earthworms. Areas of lighter shading labeled "C" represent the combined ranges of native earthworms. The black line represents the southernmost extension of the Wisconsinan Glaciation. The combined ranges of approximately 100 Nearctic earthworm species, some tentative and some with very limited distribution, are adapted from Hendrix and Bohlen (2002).

southwestern Wisconsin, southeastern Arkansas and northeastern Louisiana (Figure 1). The western worm snake has been reported from moist, rocky woodlands, and in prairies may be found along wooded streams (Ernst and Ernst, 2003). Pisani (2009) found *C. vermis*—and *Virginia valeriae*—beneath shelters in Tall Grass Prairie habitat with a dense thatch layer. *Carphophis vermis* and *C. amoenus* have similar soil moisture preferences, 10–83% and 16–42%, respectively (Clark, 1970; Elick and Sealander, 1972; Orr, 2006). Such soil moisture levels not only aid in preventing desiccation in *C. vermis*, but are also necessary for optimum cutaneous respiration of the earthworms this snake consumes. Moist substrates are also selected by snakes seeking suitable egg-laying sites. Furthermore, earthworms of temperate climates prefer similar soil temperatures (10–20°C) and soil pH (5.0–7.4) as *Carphophis* spp. (Curry, 2004; Orr, 2006).

The native earthworm genera *Bimastos, Diplocardia, Eisenoides* and *Sparganophilus* all have ranges that overlap with the range of *C. vermis* (Table 1), as do most exotic genera considered herein (Table 2). Only exotic earthworm species (*Allolobophora tuberculata, A. turgida*, *A. trapezoides* and *Lumbricus* spp.) have been documented as prey of *C. vermis* (Clark, 1970; Ernst and Ernst, 2003). These earthworms are endogeic (soil-dwelling) species, suggesting that *C. vermis* burrows in search of prey. In addition to the above exotic species, *Eisenia* sp. and *Octlasion* sp. have been listed as possible prey (Clark, 1970). However, within the range of *C. vermis*, *Eisenia hortensis* is uncommon (only found in Arkansas [Reynolds and Wetzel, 2008]) and *E. foetida* has a pungent coelomic fluid reportedly toxic to snakes (Rossman et al., 1996); it is therefore not likely to be consumed. *Octolasion*, on the other hand, is only found in the eastern part of the range of *C. vermis*. Incidentally, *Allolobophora caliginosa* was found to be a group of 3–4 species in the larger *trapezoides* complex of up to seven earthworm species in the genus *Aporrectodea* (Reynolds, 1995; Reynolds and Wetzel, 2004). Therefore, unless preserved specimens are available, it may not be possible to positively identify to which species older records listing *A. caliginosa* as a food item refer.

Since exotic species of earthworms primarily have been reported in the diet of *C. vermis*, it can be assumed that a shift from native to exotic species of earthworms in the diet may have taken place in some populations (Clark, 1970). Efforts should be made to document native earthworm species in the diet of the western worm snake. If sites are found with both native and exotic species of earthworms, studies could be done to determine if one is favored or more accessible than the other, and verify whether a shift from natives to exotics occurs. Clovis Period (ca. 11,100 ybp) fossils of *C. vermis* have been found in Lubbock County, Texas, well west of the limits of the current range of this species (Holman, 2000). It is reasonable to assume that native earthworms occurred at the site as well.

The mountain earth snake, *Virginia pulchra*, is a tan to reddish-brown, small (to 38.1 cm TL) snake. Compared to *Carphophis*, species in the genus *Virginia* have stouter bodies, more cone-shaped heads (Ernst and Ernst, 2003), and stronger tendencies toward surface foraging (Pisani, 2009).

Virginia pulchra is found on the Allegheny Plateau and Allegheny Mountains of western Pennsylvania, the western panhandle of Maryland, eastern West Virginia, and a small portion of northern Virginia. Grassy hillsides and ecotonal areas at the edge of deciduous forests and fields are favored habitats.

Although earthworms are listed in the diet (e.g., Green and Pauley, 1987; Hulse et al., 2001), they are not identified to genus or species. Therefore, the documentation and identification of any earthworm species in the diet of *V. pulchra* would be of interest. All genera of native earthworms are known from within the range of *V. pulchra* (Table 1); *Amynthas* is the only exotic earthworm genus that is not sympatric with the mountain earth snake (Table 2). In captivity, this species fed upon exotic *Aporrectodea tuberculata, Lumbricus rubellus* and *L. terrestris* (pers. obs.).

The rough earth snake, *Virginia striatula*, is a small (to 34.8 cm TL [Ernst and Ernst, 2003]), nondescript, gray-brown to reddish-brown snake. Unlike *Carphophis*, rough earth snakes have keeled dorsal scales, slightly stouter bodies, and cone-shaped heads (Ernst and Ernst, 2003).

Ernst and Ernst (2003) delineate the distribution of *V. striatula* as ranging from southeastern Virginia south to northern

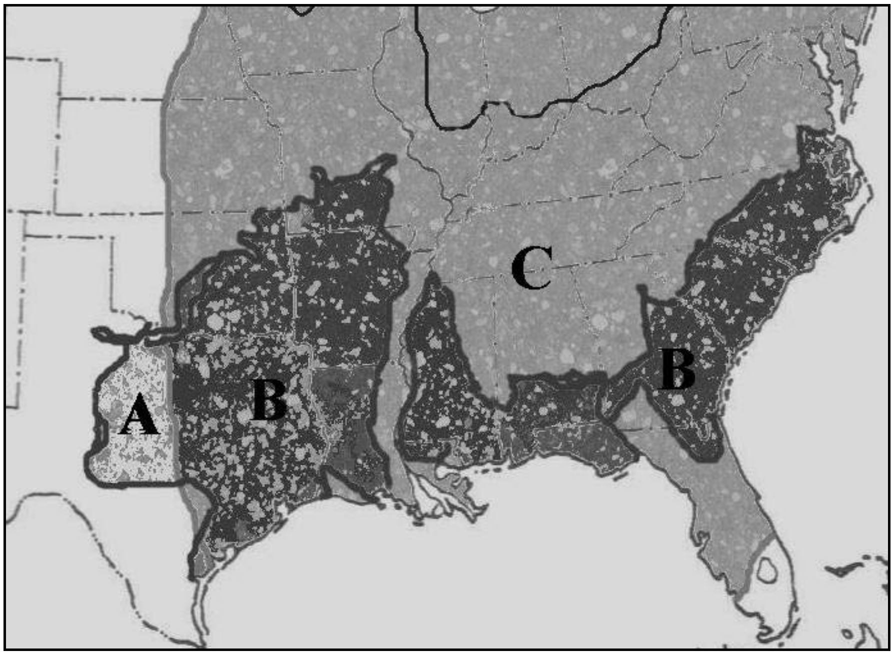

Figure 2. The approximate range of *Virginia striatula* (adapted from Ernst and Ernst, 2003) and the approximate combined ranges of native earthworms. Lightly shaded areas labeled "A" represent western portion of *V. striatula*'s range that does not overlap that of native earthworms. Darker shaded areas labeled "B" represent the portion of *V. striatula*'s range that overlaps that of native earthworms. Moderately shaded area labeled "C" is the remainder of the combined ranges of native earthworms. The black line represents the southernmost extension of the Wisconsinan Glaciation. The combined ranges of approximately 100 Nearctic earthworm species, some tentative and some with very limited distribution, are adapted from Hendrix and Bohlen (2002).

Florida, west across Georgia, Alabama and most of Mississippi to southeastern Louisiana, and from southern Missouri and extreme southeastern Kansas southward through western Arkansas, western Louisiana, eastern Oklahoma, and eastern Texas. *Virginia striatula* prefers wooded areas and ecotones, and can be found beneath rocks, logs, and under bark (Allen, 1932; Cook, 1954; Ernst and Ernst, 2003).

The geographic distribution of *V. striatula* and that of native earthworms (*Bimastos* spp., *Diplocardia* spp., *Eisenoides* spp., and *Sparganophilus* spp.) overlap considerably (Table 1) (Figure 2), yet no reports specifically identify native earthworms in the diet of the rough earth snake (Clark and Fleet, 1976; Linzey and Clifford, 1981; Palmer and Braswell, 1995; Trauth et al., 2004). Populations of *V. striatula* in central Texas are outside the documented range of native earthworms, and it is likely that *Aporrectodea* is fed upon there. Alternatively, it is possible that native earthworm populations exist, but have not been discovered yet. Of the exotic earthworm genera, only the distribution of *Allolobophora* does not overlap with that of the rough earth snake (Table 2). Researchers should make an effort to determine which native earthworms are consumed by *V. striatula*.

The eastern earth snake, *Virginia valeriae*, is a small (to 39.3 cm TL [Smith and Brodie, 1982]) nondescript, tan to light brown snake. Unlike *V. pulchra* and *V. striatula*, the eastern earth snake has smooth scales.

Virginia valeriae is distributed in unglaciated territory from New Jersey, Delaware, Pennsylvania and southern Ohio west to southwestern Illinois and southern Iowa, and south to northern Florida and central Texas (Ernst and Ernst, 2003). Cook (1954) noted that *V. valeriae* burrowed under rotten leaves and bark, and in decayed wood in forested areas—habitat similar to that favored by some native earthworms in the genus *Bimastos*. In Kansas, Pisani (2009) observed that *V. valeriae* utilized dense thatch in Tall Grass Prairie.

Earthworms are listed as the main food item (Conant, 1938; Hulse et al., 2001; Pisani, 2009), but have not been identified to specific taxa. All genera of native earthworms (Table 1) and all genera of exotic earthworms (Table 2) have ranges sympatric with *V. valeriae*. Efforts to identify the earthworm species preyed upon would be of interest to both herpetologists and oligochaetologists.

The short-headed garter snake, *Thamnophis brachystoma*, is the smallest of the garter snake species (up to 57.8 cm TL [Lethaby, 2004]). It has a narrow head and the typical garter snake pattern of lateral and vertebral stripes on the body.

Thamnophis brachystoma is endemic to the Allegheny High Plateau of northwestern Pennsylvania and adjacent southwestern New York; isolated populations also exist in eastern Ohio (Novotny, 1990; Novotny, pers. com.) and Horseheads, New York (Wright and Wright, 1957). It prefers open areas such as old fields and meadows, and avoids deep woodlands (Rossman et al., 1996).

Earthworms are the only prey item presently documented from wild *T. brachystoma* (Asplund, 1963; Wozniak and Bothner, 1966); however, it is unknown whether these represent native or exotic species. In captivity *T. brachystoma* fed on *Aporrectodea* sp., *Lumbricus rubellus* and *Lumbricus terrestris* (pers. obs.). In glaciated territory *T. brachystoma* most certainly preys upon ubiquitous exotic earthworms. Within the range of *T. brachystoma* the following native earthworm species have been documented (Reynolds, 2007, 2008a and b): *Bimastos tumidus*, *B. parvus*, *Diplocardia* spp., *Eisenoides lonnbergi* and *Sparganophilus eiseni* (Table 1). However, because *S. eiseni* is a mud-dwelling species, it is not likely to be available as a food item in this snake's diet. Also, *E. lonnbergi* and *Bimastos* spp. prefer forested areas with high organic matter present (James, 1995; Reynolds, 2008a), and these differences in habitat preferences would cause these earthworms to rarely be encountered by *T. brachystoma*. Therefore, *Diplocardia* spp. constitute the most likely group of native earthworms to be fed on by *T. brachystoma*. All genera of exotic earthworms considered herein have ranges that overlap with *T. brachystoma* (Table 2).

Weatherhead and Madsen (2009) noted that some snake species have benefited from invasive species. One example given was the Lake Erie water snake (*Nerodia sipedon insularum*) which feeds on the now abundant invasive round goby (*Neogobius melanostomus*). Likewise, the vermivorous snakes discussed in this paper may have benefited from the introduction of exotic earthworms. In glaciated regions in Erie County, Pennsylvania, and Horseheads, New York, *T. brachystoma* has successfully been established in areas for the most part devoid of native earthworms (Engelder, 1988; Gray, 2005); the presence of exotic earthworm species probably facilitated these establishments. Alternatively, there is anecdotal evidence that *T. brachystoma* may include a greater diversity of prey items (e.g., leeches, fish and amphibians) in its diet than previously thought, which may have aided in colonization into glaciated areas prior to the introduction of exotic earthworms (Gray, 2008). Fossils from Blair County, Pennsylvania, and Pendleton County, West Virginia, indicate that during the Pleistocene, *T. brachystoma* had a range that extended much further south than it does presently (Holman, 2000). Very little sampling has been done for earthworms within the core range of *T. brachystoma*—for instance, in Pennsylvania there are no earthworm records (native or exotic) for Clarion, Forest, Jefferson, McKean or Warren Counties, and only single collections from Allegheny, Clearfield, Elk, and Venango Counties (Reynolds, 2008a). In New York, Allegany, Cattaraugus, Chautauqua, and Chemung Counties have 1–2 collections each (Reynolds, 2008b). Therefore, records of earthworms found in association with, or consumed as prey by, *T. brachystoma* in these regions could add significantly to our knowledge of the distribution of earthworms, and the feeding habits of the short-headed garter snake.

The following snake species are facultative vermivores, and most adults share the following characteristics: 1) earthworms may form the bulk of their diet, yet other food items are reported among populations; 2) their distributions extend well into glaciated regions where native earthworms would have been absent post-glaciation; 3) they may be found in damp or moist situations, but also drier settings; 4) they usually attain a TL greater than 50 cm; and 5) their gape can accommodate larger prey that may not be elongate. *Diadophis punctatus* is an exception to this last characteristic, as it is very gape limited.

Holman (1992) proposed a model for herpetological reoccupation of formerly glaciated Michigan. He used a variety of data from geological, paleobotanical and paleovertebrate assemblages, as well as from ecological tolerances of modern herpetofauna. In Holman's model there are primary invaders, the first species of amphibians and reptiles to begin colonizing. Their ecological tolerances included adaptation to coniferous forests; *Diadophis punctatus* and *Thamnophis sirtalis* are examples. Secondary invaders were next to colonize, and have ecological tolerances including an adaptation to mixed coniferous–broadleaf areas; *Thamnophis butleri* is an example. Finally, the third and last group of colonizers is named tertiary invaders, and is adapted to exist in broadleaf forest areas; *Clonophis kirtlandii* exemplifies this group. Because earthworms were absent after the retreat of the glaciers, all these snakes must have fed on something other than earthworms during reoccupation; for example, primary colonizers may have fed on other primary colonizers (e.g., *Diadophis punctatus* on *Plethodon cinereus*, or *T. sirtalis* on *Lithobates* (= *Rana*) spp.); secondary colonizers may have fed on primary and other secondary invaders, etc. Whatever they fed upon during that time, a shift to exotic earthworms has occurred within the past 500 years.

Kirtland's snake, *Clonophis kirtlandii* (to 62.2 cm TL [Smith and Brodie, 1982]), has a brownish dorsum with dark, almost black, alternating blotches; the ventral surface is orangish to red. *Clonophis kirtlandii* is a snake of the Prairie Peninsula and is known from west-central Pennsylvania westward through southern Ohio, Indiana, southern Michigan, north-central Kentucky and central Illinois (Ernst and Ernst, 2003).

Throughout the range of *C. kirtlandii*, earthworms are the most commonly found prey in the diet (Conant, 1943; Smith, 1961; Minton, 1972; Hulse et al., 2001; Holman and Harding, 2006), and since this snake is distributed mainly in glaciated regions it is assumed the earthworms represent exotic species; identification of regurgitated stomach contents of live snakes or dissection of preserved specimens may verify this. In the southern part of the range of *C. kirtlandii*, native earthworms in the genera *Bimastos, Diplocardia, Eisenoides, Komarekiona,* and *Sparganophilus* occur, and efforts to identify earthworms preyed upon or in association with *C. kirtlandii* in this region are needed. It cannot be known what *C. kirtlandii* fed on south of the glacier during the Pleistocene; however, assuming prey preferences then were similar to those today, Kirtland's snake may have fed on native earthworms, as well as slugs and leeches.

The ring-necked snake, *Diadophis punctatus*, is usually some shade of gray to bluish black dorsally with a cream, yellowish, or reddish collar on the nape. In the eastern part of its range it is yellowish ventrally; in the west it is more orange to red. *Diadophis punctatus* attains a maximum TL of 85.7 cm (Ernst and Ernst, 2003); however, the subspecies *punctatus* and *edwardsii* are usually less than 50.0 cm TL.

The ring-necked snake is widely distributed throughout much of the United States and Canada, from New Brunswick and Nova Scotia west to Lake Superior, southern Quebec and Ontario, south to the Florida Keys and west to Texas, New Mexico, Arizona and southern California. Isolated populations occur in the Great Basin from southeastern Washington to northwestern Arizona, and in southeastern California (Ernst and Ernst, 2003).

Across the range of the ring-necked snake, there is a great deal of variety in the diet (see Ernst and Ernst [2003] for a summary), with populations predominantly feeding on one, or a combination of, the following: earthworms, salamanders, and other snakes. In parts of North Carolina, ground skinks (*Scincella lateralis*) are occasionally eaten (Jeff Beane, pers. com.). There are some interesting observations to be made regarding the diet of *D. punctatus*; for instance, in North Carolina, earthworms are more frequently observed as prey in the Coastal Plain, whereas in the mountains, plethodontid salamanders dominate (Palmer and Braswell, 1995). One would expect earthworms to be more abundant than salamanders in the Coastal Plain, and the converse to be true in the mountains. As noted above in the discussion of the worm snake, earthworms are usually absent from mountainous areas, due in part to shallow soil or bare rock, wind-induced desiccation, elevated ultraviolet radiation, reduced oxygen, and limited suitable food, all of which act as barriers to earthworm migration (Reynolds and Wetzel, 2004). Hulse et al. (2001) mention that in the eastern United States where salamanders are common, they are the major component of the diet of *D. punctatus*; where salamanders are rare, earthworms are the major prey. It would also be expected that north of the glacial boundary, where native earthworms are absent, *D. punctatus* would feed predominantly on salamanders, and in Michigan, glaciated regions of Pennsylvania, New England, and Ontario this seems to be the case (Blanchard, 1942; Logier, 1958; Serrao, 2000; Krulikowski, 2004; Gray and Lethaby, 2008). In northeastern Kansas, exotic earthworms (*Allolobophora caliginosa*) are the predominant prey (Fitch, 1975; Pisani, 2009). The range of *D. punctatus* overlaps that of all native earthworm genera (Table 1) and all exotic genera (Table 2). As noted above, *Sparganophilus* is a mud-dwelling species and therefore unlikely to be available as prey for the ring-necked snake. In areas south of the glacial boundary, effort should be made to identify the species of earthworms being preyed upon, whether native or exotic.

The swamp snake, *Seminatrix pygaea*, like other vermivorous snake species is relatively small (to 55.5 cm TL [Ernst and Ernst, 2003]); however, unlike them it is a more aquatic species, preferring plant-choked wetlands, and much of its feeding is reportedly in water. It is distributed in the southeastern United States along the Atlantic Coastal Plain from North Carolina to Florida and adjacent southern Alabama.

Seminatrix pygaea has a more diverse diet, consisting of oligochaete worms, leeches, fish, and amphibians (Dowling, 1950; Tennant and Bartlett, 2000; Ernst and Ernst, 2003). *Seminatrix pygaea* is reported from the type locality of *Sparganophilus helenae* (Reynolds, 1980), and possibly feeds on this native earthworm species. *Komarekiona* is the only native earthworm genus not sympatric with *S. pygaea* (Table 1); the exotic genera *Amynthas, Aporrectodea* and *Octolasion* overlap this snake's range (Table 2).

The brown snake, *Storeria dekayi*, is a small species (to 52.7 cm TL [Smith and Brodie, 1982]), and is widely distributed in the eastern United States and southern Ontario, Canada. It is found in glaciated and unglaciated regions. Because *S. dekayi* has keeled scales and a blunt head it probably does not burrow,

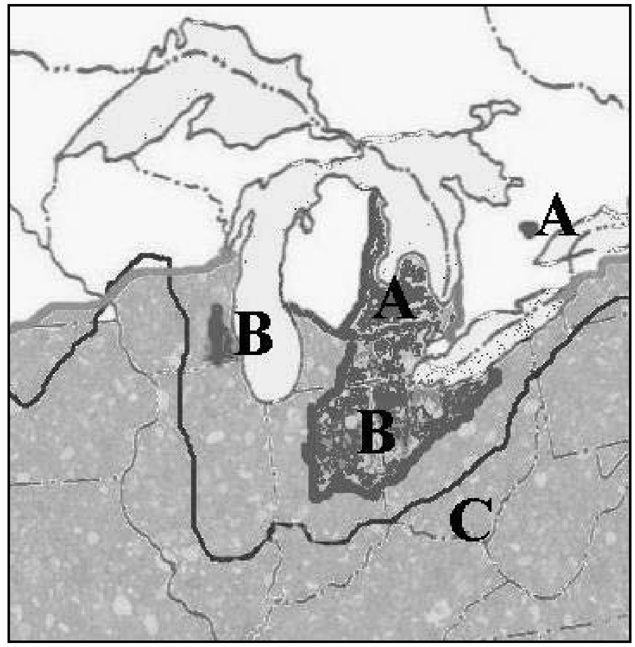

Figure 3. The approximate range of *Thamnophis butleri* (adapted from Ernst and Ernst, 2003) and the approximate combined ranges of native earthworms. The dark shaded areas labeled "A" represent the portion of the range of *T. butleri* that does not overlap the combined ranges of native earthworms. The dark areas labeled "B" represent the portions of the range of *T. butleri* that overlap the combined ranges of native earthworms. The area labeled "C" represents the remainder of the combined ranges of native earthworms. The black line represents the southernmost extension of the Wisconsinan Glaciation. The combined ranges of approximately 100 Nearctic earthworm species, some tentative and some with very limited distribution, are adapted from Hendrix and Bohlen (2002).

and likely feeds on the surface.

In northeastern Kansas, Pisani (2009) observed that *S. dekayi* feeds predominantly on earthworms. In other areas, however, brown snakes feed on slugs and earthworms (Logier, 1958; Mitchell, 1994; Palmer and Braswell, 1995; Hulse et al., 2001; Trauth et al., 2004). In northwestern Pennsylvania, slugs are preferentially taken by captives, although some individuals have eaten *Lumbricus terrestris* (pers. obs.). Incidentally, like earthworms, slugs are rarely identified to species and it is not known whether they represent native or exotic taxa. The range of *S. dekayi* overlaps significantly with all native earthworm genera (Table 1), as well as all exotic genera (Table 2).

Butler's garter snake, *Thamnophis butleri*, is similar in appearance to, but larger than (to 73.7 cm TL [Ernst and Ernst, 2003]) its closest relative, the short-headed garter snake. Unlike *T. brachystoma*, however, *T. butleri* is distributed mainly in formerly glaciated regions of Ohio, Indiana, Michigan, Wisconsin and southern Ontario. Butler's garter snake prefers wet, open areas such as prairies and pastures, but may also be found in urban settings (Ernst and Ernst, 2003).

Thamnophis butleri feeds on earthworms, leeches, and occasionally other prey such as small frogs (Rossman et al., 1996). The range of Butler's garter snake overlaps that of the native earthworm genera *Bimastos*, *Diplocardia*, and *Sparganophilus* (Table 1) (Figure 3); all genera of exotic earthworms except *Amynthas* also have overlapping ranges with *T. butleri*

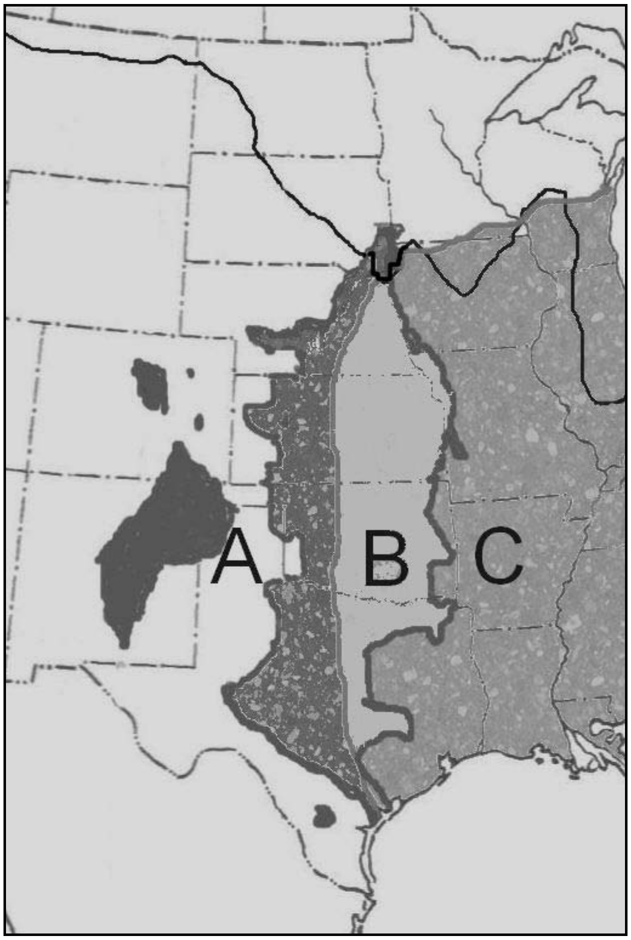

Figure 4. The approximate range of *Tropidoclonion lineatum* (adapted from Ernst and Ernst, 2003) and the approximate combined ranges of native earthworms. Dark shaded areas labeled "A" represent the western portion of *T. lineatum* range that does not overlap that of native earthworms. Lightly shaded area labeled "B" represents the eastern portion of *T. lineatum* range that overlaps that of native earthworms. Moderately shaded area labeled "C" is remainder of combined native earthworm ranges. The black line represents the southernmost extension of the Wisconsinan Glaciation. The combined ranges of approximately 100 Nearctic earthworm species, some tentative and some with very limited distribution, are adapted from Hendrix and Bohlen (2002).

(Table 2). Earthworms in the genus *Bimastos* are usually found in forested areas under logs, bark or leaf packs (James, 1995; Reynolds, 2007), and therefore are less likely to be utilized as food by *T. butleri*. Only exotic species of earthworms (*Allolobophora chlorotica*, *Aporrectodea* sp., *Lumbricus terrestris*, and *Lumbricus* sp.) have been reported in the diet of *T. butleri* (Catling and Freedman, 1980).

Holman (1992) considered *T. butleri* a secondary invader of formerly glaciated Michigan. As earthworms were absent during the recolonization, *T. butleri* must have fed on some other prey; Catling and Freedman (1980) suggested leeches. It is also possible that *T. butleri* fed on primary invaders, such as *Plethodon cinereus, Hyla versicolor, Pseudacris* spp., and *Lithobates* (=*Rana*) spp. which would have preceded it in colonizing glaciated terrain.

The common garter snake, *Thamnophis sirtalis* (to 137.2 cm TL [Ernst and Ernst, 2003]) has a striped pattern, with lateral stripes on dorsal scale rows 2 and 3; a vertebral stripe is also usually present. In the Great Lakes region, some populations contain a high percentage of melanistic individuals.

The common garter snake is distributed from the Atlantic Coast to the Pacific Coast, and is found further north in Canada than any other snake (Ernst and Ernst, 2003). It has been documented from every state except Arizona; it is uncommon in most of the Southwest, however.

When it comes to diet, adult *Thamnophis sirtalis* are generalists, feeding on amphibians, earthworms, nestling birds, and even carrion (Ernst and Barbour ,1989; Gray, 2002); however, juveniles in some populations may feed exclusively on earthworms (Fitch, 1965; Holman and Harding, 2006). Kirschenbaum et al. (1986) demonstrated that earthworms (*Lumbricus terrestris*) produce a cuticle collagen-like substance, readily detected by the vomeronasal apparatus of *T. sirtalis* that enables the snakes to locate their prey. The range of *T. sirtalis* overlaps in whole or in part with all native and exotic genera of earthworms (Tables 1 and 2). Only exotic earthworms, *Allolobophora caliginosa* (= *Aporrectodea* spp.), *Lumbricus rubellus* and *L. terrestris*, have been recorded in the diet of wild *T. sirtalis* (Uhler et al., 1939, cited in Mitchell [1994]; Hamilton, 1951; Fitch, 1999). In captivity *Lumbricus terrestris* and *L. rubellus* were consumed (pers. obs.). Reports of predation by this snake on earthworms that identify the prey as to species would be noteworthy.

Holman and Harding (2006) noted that in urban areas *T. sirtalis* may be able to survive on an exclusive diet of earthworms. Fitch (1965, 2006) over the course of his studies at the Fitch Natural History Reservation, noted that during drought years when earthworms are less available, the survival of first-year young *T. sirtalis* was negatively affected. Droughts likely affect other vermivorous snakes similarly.

Thamnophis sirtalis is considered a primary invader of formerly glaciated regions (Holman, 1992). Like *T. butleri*, some populations of *T. sirtalis* in glaciated northern regions have presumably shifted their diet from primary invaders such as amphibians during recolonization, to exotic earthworms.

The lined snake, *Tropidoclonion lineatum*, is a small (to 57.2 cm TL [Ernst and Ernst, 2003]) snake that resembles a garter snake in pattern; the body has a brownish dorsal surface with light lateral stripes on dorsal scale rows 2 and 3, and a light vertebral stripe.

Ernst and Ernst (2003) give the range of this species as extending from southeastern South Dakota to the Gulf Coast of Texas, with scattered populations in northern and central Illinois, southeastern Iowa, east-central Missouri, eastern Colorado, and New Mexico.

Earthworms are the primary prey of lined snakes (Force, 1931; Collins and Collins, 2006). The western range limits of *Bimastos* spp. and *Diplocardia* spp. overlap with most of the range of *T. lineatum*; however, other than *Diplocardia* spp. in northeastern New Mexico (Reynolds and Damoff, 2009), native earthworm species have not been documented from the westernmost portion of the range of *T. lineatum* (Figure 4). Lined snakes in Colorado present an interesting area of study for both herpetologists and oligochaetologists. In the eastern half of

Colorado *T. lineatum* is patchily distributed, being documented from Adams, Arapahoe, Baca, Bent, Boulder, Cheyenne, Douglas, Elbert, Jefferson, Lincoln, Otero and Prowers Counties (Hammerson, 1999). Of these counties, only six (Adams, Boulder, Douglas, Ebert, Jefferson, and Lincoln) have been sampled for earthworms; however, with five or fewer records each, these counties are under-surveyed for earthworms (Damoff and Reynolds, 2004). No native earthworms have been documented within the state (Reynolds and Reeves, 2003; Damoff and Reynolds, 2004). However, Damoff and Reynolds (2004) noted that "it is reasonable to expect the presence of native earthworms in Colorado, especially in consideration of the occurrence of native species in those adjacent states in which records of earthworms have been reported." Future surveys by oligochaetologists in Colorado may wish to search for *Diplocardia* in undisturbed habitats in the counties listed above, especially where populations of *T. lineatum* are known. A similar strategy could be used in New Mexico, where records of native earthworms are few. Oligochaetologists working in New Mexico may wish to consult the range map for *T. lineatum* in Degenhardt et al. (1996). Exotic earthworms in the genus *Aporrectodea* occur throughout the range of *T. lineatum*; a small portion of the eastern end of the range overlaps that of *Amynthas* spp. With much of the western range of *T. lineatum* lacking documented occurrences of native earthworms, one must consider the possibility that the lined snake may have fed on other prey, such as sowbugs and soft-bodied insects and insect larvae (Wright and Wright, 1957) prior to the introduction of exotic earthworms, and now feeds on exotic earthworms because they are ubiquitous and an easily obtained food source. It seems more probable, however, that native earthworms (*Diplocardia* spp.) will be found within much of the western range of *T. lineatum*. Such a finding would support considering *T. lineatum* as an obligate vermivore. Like the earth snakes, *T. lineatum* is likely a surface feeder, although it is capable of burrowing (Ernst and Ernst, 2003). During the Pleistocene, *T. lineatum* was present in the Lubbock Lake / Plainview faunas, somewhat south of the species' present-day range in the Texas Panhandle and somewhat west of its current range in the central part of that state (Johnson, 1986; Holman, 2000).

Several other North American snake species (*Storeria occipitomaculata*, *Thamnophis elegans*, *T. marcianus* and *T. radix*) are known to occasionally feed on earthworms; however, earthworms do not constitute as significant a portion of the diet as they do in the species discussed above. Although the current discussion focuses on North American (north of Mexico) forms, vermivorous snakes also occur in other regions, for instance *Adelophis* spp. in western Mexico; *Adelphicos* spp. and *Atractus* spp. in Central America and South America respectively; as well as *Aspidura* spp., *Calamaria* spp., *Haplocercus ceylonensis*, *Pseudotyphlops philippinus*, *Rhabdops bicolor*, *Rhinophis* spp., *Trachischium* spp. and *Uropeltis* spp. in Burma, India, Sri Lanka and surrounding regions (Parker and Grandison, 1977; Mahendra, 1984; Ernst and Zug, 1996; Mattison, 2007).

Conservation and the possible effects of nonnative earthworms on snakes

Many aspects of snake biology are affected by the abundance of their prey; therefore an understanding of predator–prey interactions is critical for management and conservation of snake species (Weatherhead and Madsen, 2009). Despite earthworms being an important component in the natural diet of many birds, mammals, and reptiles (including snakes), virtually no work has been done to examine the trophic relationship(s) between these predators and various earthworm species (Reynolds, 1980). In addition, to my knowledge, no studies testing whether there are differences in nutritional content between native and exotic earthworm species have been done. What effects will exotic earthworms have on snake populations in areas that were once earthworm-free?

Pisani (2009) noted that populations of vermivorous snakes are very susceptible to land use and management practices that affect hibernacula and availability of earthworms. In areas where droughts are common, native earthworms in the genus *Diplocardia* are able to survive soil temperatures that are fatal to exotic earthworms in the family Lumbricidae (James and Hendrix, 2004). What effects will climate change have on vermivorous snakes in these regions if *Diplocardia* spp. are replaced by lumbricid earthworms?

Finding and preserving areas lacking exotic earthworms, but having native earthworms and vermivorous snakes should be a priority. Kalisz and Wood (1995) speculated that native earthworms would not survive over long periods in wildland remnants in fragmented landscapes, especially those less than 30 ha in area. Habitat destruction and fragmentation are detrimental to both snake and native earthworm populations (Hendrix, 1995; Mullin and Seigel, 2009) and both taxa may benefit from a conservation strategy that aims to conserve intact ecosystems of suitable size that support both vermivorous snakes and native earthworms. Unfragmented old growth forest sites south of the glacial boundary have the greatest potential of having earthworm populations consisting solely of native species (Kalisz and Wood, 1995; Kalisz and Powell, 2000); if such sites also have vermivorous snakes, they also have the best potential of documenting snake predation on native earthworms. Disturbance facilitates invasion of forested habitats by exotic earthworms, and while there is no direct evidence that exotic earthworms have negative effects on snakes, there is a growing body of literature showing that negative effects (e.g., reduction of percent organic matter, loss of forest floor mass, changes in microflora and microarthropods, and decreased plant biodiversity) do occur in northern forests that were previously worm-free (Hale et al., 2005; Hale et al., 2006; Eisenhauer et al., 2007). Removal of the forest floor could also negatively affect salamander populations, and the snakes that feed on them (e.g., *Diadophis punctatus* in northern areas). Once established, it is probably not feasible to attempt to eliminate exotic earthworms from an area (James and Hendrix, 2004); therefore preventing the establishment of exotic earthworms would be prudent. Areas containing exotic earthworms, with and without vermivorous snakes, could be used to test whether there are significant differences in the effects of exotic earthworms on ecosystems. For instance, are earthworm invasions slowed, and the negative effects reduced at sites with vermivorous snakes?

Earthworms often have clumped distributions, corresponding to such factors as vegetation, soil texture, or soil organic matter content (Hendrix and Bohlen, 2002). It would be expected that vermivorous snake species, especially the obligate ones, would have similar distributions; the patchy distribution of *Virginia valeriae* in Kansas observed by Pisani (2009) may partially be explained by such factors. With the introduction of exotic earthworm species into areas formerly devoid of native earthworms, vermivorous snakes may have been given an opportunity to expand their ranges; *T. brachystoma* in Erie County, northwestern Pennsylvania, may be such a species (Gray, 2005, 2008).

It is hoped that this paper will encourage collaboration amongst herpetologists and oligochaetologists. When studying vermivorous snake species, it would benefit the herpetologist to consult any earthworm surveys done within the state in which they are working. By doing so, they may familiarize themselves with the distribution and habitat preferences of earthworm species most likely to be prey of their study subjects. John W. Reynolds has published earthworm surveys, with county-level distribution maps, for most of the continental United States (for available surveys visit: http://www.inhs.uiuc.edu/~mjwetzel/megadrilogica.home.html). There are several areas where earthworm surveys have not been done, and the potential for discovery of new species still exists (Reynolds, 2004). Reynolds and Wetzel (2008) list Kansas, Nebraska, New Mexico, Texas and Wisconsin (all states with at least one species of vermivorous snake) as being under-surveyed for earthworms. Therefore, earthworms identified as prey to snakes in these states have the potential of augmenting our knowledge of the distribution and ecological interactions of earthworms. As noted above in the short-headed garter snake discussion, even in states that have been more extensively surveyed (i.e., New York and Pennsylvania), opportunity still exists to make significant contributions in understanding the distribution of earthworms found in association with vermivorous snakes. In the Great Lakes region, exotic earthworms found in proximity to vermivorous snakes may be of interest to the Great Lakes Worm Watch Project (www.greatlakeswormwatch.org). For these reasons I would encourage herpetologists to collect, preserve, and deposit in a museum collection any earthworms found in association with their study subjects. Reynolds and Wetzel (2004) provide information on how to properly collect data and preserve earthworms for future study. I also encourage oligochaetologists to take note of which snake species are found in habitats with earthworms in their studies—not only because they may represent possible predators, but also because such reports may augment our understanding of predator–prey associations, geographic distributions of earthworms and snakes, and habitat preferences of vermivorous snakes. The current paper is essentially an annotated checklist of which snake species I consider most useful in evaluating the points I have raised. Oligochaetologists wishing to make snake identifications should consult Conant and Collins (1998). Herpetologists wishing to identify earthworms should review Reynolds (1977b, 1995) and Hale (2007) for an introduction to terms and characteristics useful in proper identifications. To guarantee positive identification of earthworm species and to initiate collaboration, contacting an oligochaetologist to identify the specimens is encouraged.

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The Distribution of the Burmese Python, *Python bivittatus*, in China

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We here provide a revision of the distribution of the Burmese python, *Python bivittatus*, in China, as reported previously in Barker and Barker (2008). Information provided to us since the publication of that article allows a more detailed depiction of the natural distribution of the Burmese python in China. We discuss the distribution of the Burmese python in each province from which the species has been recorded.

Fujian

The easternmost dot on the map represents the vicinity of Nanping [Yenping]. Pope (1935) reports that the python was killed in the vicinity of Yenping at an elevation of about 1000 feet (330 m). Pope also mentions that there are "several records for this province" but goes on to say that the Nanping record is the only specific locality. The dot at the southern tip of Fujian refers to the Kinmen Archipelago, where pythons are reported to occur on Queymoy Island (Hsiang, 2009).

Jiangxi

Zhong (1993) reported the presence of Burmese pythons in the extreme southern tip of this province on the basis of a sighting and a shed skin.

Guangdong

Pope (1935) mentioned that the Burmese python could be found in Kwantung Province (now Guangdong) along the southern coastal region from Swatow to Yeungkong. He goes on to state that this species "probably occurs over considerable areas in *extreme southern* China" [italics ours]. The easternmost dot on the coast of this province refers to Hong Kong and the adjacent mainland; there the species is well-known, although considered a rare species (Karsen et al., 1986). The dot just to the west refers to Macao (Zhao and Adler, 1993). The locality in north-central Guangdong is based on the report of Xu and Jim (2003) and refers to the Shimentai Nature Reserve situated in Yingde. It is the northernmost record in Guangdong of which we are aware; we placed the northern limit of the range about 50 km north of this record, as indicated by the shaded area on our map, because of similar elevation and habitat.

Hainan

The species is well-known from Hainan Island. Pope (1935) examined several specimens from this locality.

Guangxi

We are unable to find specific locality records of Burmese pythons for this province. It is widely accepted in the literature that pythons are found across the southern half of this province. We have illustrated the range with two northward extensions on the basis of river drainages.

Guizhou

There are three closely grouped localities for Burmese pythons in south-central Guizhou (Zhao et al., 1998). The elevation of the westernmost locality, listed as Wangmo [Wang Mo], is about 600 m. To the east, the elevation of Luodian is about 500 m. The town of Ziyun [Zi Yun] is the northernmost of the three, located at an elevation of 1100 m; we note that nearby to Ziyun, about 2 km southwest, is a deep valley, the bottom of which is 500 m elevation.

Yunnan

Much of Yunnan is a high rocky plateau, the Shan Plateau, dissected with river courses, many of which are tributaries of the main rivers draining the Tibetan Plateau. Most of the ten Burmese python localities listed by Zhao et al. (1998) are associated with various drainages that offer lower elevations and far warmer conditions than up on the plateau.

The easternmost locality is on the Vietnamese border at Hekou, at an elevation of about 150 m on the Yuan Jiang; upon crossing into Vietnam the river is known as the Song Koi (Red River), flowing on to the coast at Hanoi. Further upstream on the Yuan Jiang, northwest of Hekou, is the locality of Yuanjiang [Yuankiang], and the specimen from there was collected at