



At the lower size limit in snakes: two new species of threadsnakes (Squamata: Leptotyphlopidae: *Leptotyphlops*) from the Lesser Antilles

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Abstract

Islands are viewed as natural evolutionary laboratories for terrestrial organisms because they have boundaries that limit dispersal and often reveal evolutionary patterns and mechanisms. One such pattern is that the smallest and largest species of different types of tetrapod animals are frequently found on islands. Here I describe two new diminutive species of snakes of the genus *Leptotyphlops* from the Lesser Antilles: one from Saint Lucia and the other from Barbados. The one from Barbados is the smallest species of snake and has a total adult length of approximately 100 mm. Limited evidence indicates a clutch size of one and a greatly elongated egg shape (length /width). Comparison of egg shapes in snakes indicates that the shape is a packaging phenomenon, related primarily to the shape of the available body cavity and clutch size. For a clutch size of one, expected egg shape is eight whereas expected egg shape drops to two at a clutch size of ten. The body shape of snakes, defined as snout-to-vent length divided by width, also varies and influences the shape of snake eggs. The smallest snakes are typically stout-bodied with shapes of 30–35 whereas the longest snakes usually are more elongate, with shapes of 45–50. The allometry of organ size also affects clutch size and shape, because the smallest snakes have the smallest proportion of body cavity space available for reproduction. The best explanation for the observation of body size extremes on islands is that colonizing species have adapted to open ecological niches that would otherwise be occupied on the mainland. Island colonists encounter novel environments and reduced interspecific competition, allowing species to evolve physical traits, including extremes in size, not normally seen on continents. However, the lower limit of adult size appears to be constrained by the allometry of morphology, physiology, and reproduction. The smallest tetrapods have small clutches, usually one egg or young, and offspring that are relatively large. In the smallest snakes, offspring are one-half of the length of adults, compared with 10% adult length in the case of large species of snakes. Thus the evolutionary tradeoff between number and size of offspring appears to have reached a size boundary in these species, limiting the evolution of yet smaller species.

Key words: adaptive radiation; allometry; body shape; egg shape; evolutionary constraint; extremophile; Lesser Antilles; miniaturization; speciation; West Indies

Introduction

Size is the best-studied trait of an organism, primarily because it is correlated with evolutionary fitness traits and is easy to measure (Blanckenhorn, 2000). Nonetheless, the evolutionary limits of size are not well understood. In some cases there are physical and physiological limitations. For example, there must be sufficient space for critical cellular molecules (e.g., DNA, RNA) placing a lower limit on the size of a prokaryote (National Research Council, 1999; Morris *et al.*, 2002). Also, atmospheric oxygen levels may bear on the upper limits of body size in animals (Falkowski *et al.*, 2005). In other cases, organisms at size extremes show major changes in morphology suggesting possible design limitations of a given body form (Hanken & Wake, 1993). However, it is usually difficult to determine whether physical or biological constraints play a part in the extremes in size that we observe among organisms. The fact that some of the smallest and largest animals are

found on islands (Estrada & Hedges, 1996; Hedges & Thomas, 2001) suggests that further study of island faunas may help reveal the evolutionary constraints of body size.

Here, I describe two new species of threadsnakes (Leptotyphlopidae) from Caribbean islands. One of those, from Barbados, is the smallest of the ~3000 known species of snakes and measures approximately 100 mm in adult length. It also has a clutch size of one. A survey of other groups of tetrapod vertebrates revealed a similar pattern: species at the lower extreme in size are also at the lower extreme in number of offspring and often are restricted to islands. For these vertebrates that normally have many more young, the convergence of two lower extremes, body size and clutch size, appears to be more than a coincidence. Thus I explore here both the association of size extremes with islands, and the possibility that the lower limit in body size is tied to a life history trait, the minimum size of offspring.

Materials and methods

Morphological data

Field and laboratory research was approved by the Institutional Animal Care and Use Committee of Pennsylvania State University (#17632). Specimens were collected and exported with permission of governmental authorities from the countries of origin and additional specimens were borrowed from museums. Partial or complete data were available for the following numbers of specimens: Martinique (12), St. Lucia (ten), and Barbados (five). However, several old museum specimens from Martinique had prior damage and therefore sample sizes were smaller for some measurements and characters. In addition to standard scale counts and measurements (Thomas *et al.*, 1985), length, width, and suture length measurements, made with digital calipers (0.01 mm accuracy) were taken for selected head scales showing variation and used in plots. Head scale and pattern drawings were made from digital images. Sex was determined by gonadal examination.

In the case of newly collected material, ethanol (buffered with Tris EDTA) was used for fixing and preserving, to conserve tissue for use in DNA analyses. In some cases, total length (TOL) was used for comparison, rather than snout-vent length (SVL) as is typical for snakes, because TOL has been the length measurement of choice in the history of *Leptotyphlops* systematics (Broadley & Wallach, 2007). Nonetheless, SVL was taken and reported (Table 1) for all specimens. Samples sizes differ in Table 1 because adults were used for lengths and only well-preserved specimens could be used for scale measurements. Although the largest specimens of each species were females, suggesting sexual size dimorphism, limited sample sizes precluded separate analysis of character data by sex. Also the mixture of males and females among each of the three species suggests that this factor is not related to average size differences among the species. Sexual size dimorphism in *Leptotyphlops* is discussed in detail below.

The following specimens of *Leptotyphlops bilineatus* Schlegel from Martinique were examined: Natural History Museum, London (BM) 53.2.4.36 (missing many scales), no specific locality; KU (University of Kansas, Museum of Natural History) 269642, Tartane, Morne Jesus; MNHN (National Museum of Natural History, Paris) 3234 (head missing), syntype, no specific locality, although restricted to Martinique (Thomas, 1965); MNHN 2006.0516, Le Lamentin; MNHN 2006.0517, Rivière Salée; United States National Museum of Natural History, Smithsonian (USNM) 119168 (desiccated), no specific locality; USNM 236657 (skin only), Plage du Diamant; USNM 564808–809, Le Lamentin. Some measurements and scale count data listed for three additional specimens from a small museum in Martinique (unavailable for this study), reported by Thomas (Thomas, 1965), were included in Table 1. Specimens from St. Lucia and Barbados are listed below in species descriptions. No other specimens of *L. bilineatus* were located in museums.

The 16 morphological characters used in the comparisons were: middorsal scale counts, subcaudal scale counts, head width (HW), prefrontal (PF)-rostral (RO) suture length (SL), prefrontal (PF)-postnasal (PN) suture length, ocular-postnasal suture length, ocular (OC)-supraocular (SO) suture length, parietal-1 (PA1)

length (L), parietal-2 (PA2) length, length of first 4 middorsals—prefrontal + frontal (FR) + interparietal (IP) + interocular (IO), ocular length, supraocular width (W), parietal-1 width, parietal-2 width, average middorsal scale width at midbody, and parietal-1/parietal-2 suture length. Midbody diameter (MBD) was also measured.

TABLE 1. Variation in three species of threadsnakes (*Leptotyphlops*) from the Lesser Antilles.

Character*	<i>L. bilineatus</i> (Martinique)	<i>L. breuili</i> , n. sp. (St. Lucia)	<i>L. carlae</i> , n. sp. (Barbados)
Animal dimensions			
TOL (mm)	93–108 (101.6)	102–113, 113 (106.8)	93–104, 104 (99.4)
SVL (mm)	88–102 (95.6)	96–105, 105 (99.9)	87–98, 98 (93.7)
TAL (mm)	5.3–6.2 (6.0)	6.3–7.6, 7.6 (6.9)	5.0–6.1, 5.6 (5.7)
TAL (% TOL)	5.6–6.3 (5.8)	6.1–6.9, 6.7 (6.5)	5.1–6.4, 5.4 (5.7)
MBD (mm)	2.33–2.99 (2.65)	2.28–3.47, 3.28 (2.98)	2.09–3.04, 3.04 (2.51)
TOL/MBD	36–40 (38.2)	31–40, 34 (33.7)	34–47, 34.2 (40.3)
HW (% SVL)	2.53–2.68 (2.63)	2.47–2.95, 2.54 (2.63)	2.38–2.49, 2.44 (2.45)
Scale counts			
Middorsals	170–187 (177.2)	176–183, 176 (179.4)	185–192, 190 (188.2)
Subcaudals	12–13 (13.3)	13–15, 15 (13.6)	12–14, 13 (12.8)
Scale measurements			
PA1 W/L	1.84–1.93 (1.89)	2.08–2.28, 2.17 (2.19)	1.56–1.74, 1.71 (1.66)
PA2 W/L	1.82–2.01 (1.91)	2.03–2.48, 2.15 (2.17)	1.71–1.93, 1.82 (1.80)
PF-RO/PF-PN SL	0.35–0.59 (0.45)	0.31–0.61, 0.43 (0.43)	0.78–1.2, 0.90 (0.97)
PA1-PA2 SL (% SVL)	0.73–0.82 (0.77)	0.69–0.85, 0.76 (0.79)	0.63–0.68, 0.66 (0.66)
Middorsal W (% SVL)	0.84–0.95 (0.90)	0.79–0.96, 0.92 (0.89)	0.75–0.84, 0.80 (0.81)
OC-SO/OC-PN SL	1.55–2.29 (1.86)	2.23–3.31, 2.74 (2.76)	1.42–2.08, 2.08 (1.73)
SO W (% SVL)	0.78–0.99 (0.93)	0.99–1.16, 0.99 (1.04)	0.87–0.96, 0.87 (0.92)
OC L (% SVL)	0.78–0.84 (0.80)	0.63–0.76, 0.67 (0.69)	0.65–0.73, 0.65 (0.68)
PF+FR+IP+IO L (% SVL)	2.28–2.55 (2.40)	2.07–2.28, 2.12 (2.13)	2.06–2.16, 2.06 (2.13)

Ranges and means (in parenthesis) are given for all specimens, with holotype data listed after range for new species (St. Lucia, Barbados).

Sample sizes are 10, 6, and 5 (Martinique, St. Lucia, Barbados) for animal dimensions (adults only); 12, 10, and 5 for scale counts, and 5, 8, and 5 for scale measurements (excludes damaged specimens).

*See text for abbreviations.

Comparative data on egg shape and body shape in snakes

Snake egg shape (length/width) and clutch size data were taken from the literature for 193 species of snakes (Appendix 1). In addition, intraspecific data were assembled for four species, totaling 82 individuals (Appendix 2), and for different clutches of the same female snakes, in four species (Appendix 3). A distinction was made between measurements of oviductal eggs and those of eggs that had been laid (oviposited), although the difference was not significant and therefore both types of data were combined for analysis.

Snake body shape data were taken from preserved snakes in the collection of the Smithsonian Institution. Snout-vent length and width at midbody (one-half SVL) were measured on 829 individuals representing 334 species from eight families. For interspecific comparisons, measurements of one individual or an average of 2–5 adult individuals was used. A least squares regression analysis was performed on log width versus log SVL, measured in centimeters, and allometric equations were generated. Deviations from isometry (slope =

1.0) were tested for significance using the t-test. Because of the diversity of body shapes found among species at comparable body sizes, body shape data were analyzed by taxonomic and ecological groups rather than all species combined, although global averages for slope and intercept are reported.

Comparative data on body size and reproduction in other tetrapods

To draw comparisons on size and reproductive characteristics of other terrestrial vertebrates, data were assembled from the literature. The sources for the number of species were: anurans (Amphibiaweb, 2006), salamanders (Amphibiaweb, 2006), caecilians (Amphibiaweb, 2006), lizards (Uetz, 2006), amphisbaenians (Uetz, 2006), snakes (Uetz, 2006), turtles (Uetz, 2006), mammals (Wilson & Reeder, 2005), and birds (Sibley & Monroe, 1990). For the maximum number of eggs and young they were: anurans (Pough *et al.*, 2003), salamanders (Rose & Armentrout, 1976), caecilians (Kupfer *et al.*, 2004), lizards (Fitch, 1970), amphisbaenians (Colli & Zamboni, 1999), snakes (Greene, 1997), turtles (Ernst & Barbour, 1989), mammals (Nowack, 1991), and birds (Van Tyne, 1976).

The smallest species, and sources used for their size and number of eggs and young were: anurans (*Eleutherodactylus iberia* Estrada & Hedges, *Brachycephalus didactylus* Izecksohn) (Estrada & Hedges, 1996), salamanders (*Thorius arboreus* Hanken & Wake) (Hanken & Wake, 1994) (clutch size unknown, but probably <10 based on the number of enlarging ova in other species of the genus; J. Hanken, pers. comm.), caecilians (*Grandisonia brevis* Boulenger) (Taylor, 1968; Duellman & Trueb, 1986) (clutch size unknown, but probably <10 based on clutch sizes of other small species of caecilians), lizards (*Sphaerodactylus ariasae* Hedges & Thomas/*S. parthenopion* Thomas) (Hedges & Thomas, 2001), amphisbaenians (*Chirinda* sp.) (Spawls *et al.*, 2002), snakes (*Leptotyphlops carlae*, this study), turtles (*Homopus signatus* Schoepff) (Loehr *et al.*, 2004), mammals (*Craxonycteris thonglongyai* Hill) (Nowack, 1991), and birds (*Mellisuga helenae* Lembeye) (Garrido & Kirkconnell, 2000). The largest species, and sources used for their size were: anurans (*Conraua goliath* Boulenger) (Duellman & Trueb, 1986), salamanders (*Andrias davidianus* Blanchard) (Duellman & Trueb, 1986), caecilians (*Caecilia thompsoni* Boulenger) (Duellman & Trueb, 1986), lizards (*Varanus komodoensis* Ouwens) (Pianka & King, 2004), amphisbaenians (*Amphisbaena alba* Linnaeus) (Pough *et al.*, 2003), snakes (*Python reticulatus* Schneider) (Greene, 1997), turtles (*Geochelone nigrita* Duméril & Bibron) (Ernst & Barbour, 1989), mammals (*Loxodonta Africana* Blumenbach) (Nowack, 1991), and birds (*Dinornis robustus* Owen, recently extinct) (Benton, 2000). The two largely marine or aquatic groups, sea turtles (7 sp.) and crocodylians (23 sp.), were excluded.

Molecular data and analyses

The following 14 specimens of *Leptotyphlops* were available for sequence analysis (sample identification numbers used in figures are in parentheses): Martinique, MNHN 2006.0516 (M1), USNM 564808–809 (M2–3), MNHN 2006.0517 (M4); St. Lucia, USNM 564813–814 (S1–2), 564810–812 (S3–5), 564815–817 (S6–8); and Barbados, USNM 564818–819 (B1–2). DNA sequences of four mitochondrial genes (12S and 16S ribosomal RNA, tRNA-Valine, and cytochrome b) were collected, totaling 3,470 aligned base pairs. An intron of a nuclear gene (rhodopsin; 432 bp), also sequenced, had only a single variable site and was therefore not used. A Hispaniolan species, *L. leptepileptus* (Thomas *et al.*, 1985) belonging to the same species group was used as the outgroup (USNM 564820). Genomic DNA was extracted, amplified (PCR) with primers spanning defined regions of genes, and sequenced. DNA sequencing was performed with an ABI 3730 Genetic analyzer and all fragments were sequenced in both forward and reverse directions.

The following is a list of primers used in PCR reactions, with gene indicated in prefix of primer name). The first six pairs cover the continuous region of 12S rRNA, tRNA-Valine, and 16S rRNA: 12L2 (AAA GCA WRG CAC TGA ARA TGC TWA GAT) and 12H3 (CGR GGK KTA TCG ATT AYA GAA CAG GCT CCT CTA G), 12L17 (CAA ACT AGG ATT AGA TAC CCT ACT ATG C) and 12H11 (CAC TTT CCA GTA CGC TTA CCA TGT TAC G), 12L3 (TGA RGC RCG YAC ACA CCG CCC GTC ACC CTC) and 16H22

(TTT WTT GRT GGC TGC TTT ARG GCC TAC), 16L4 (ACC AAG TTA CCC TAG GGA TAA CAG CGC A) and 16H17 (GCW RRR GGR KAT GTT TTT GGT AAA CA), and 16L39 (CTG TTT ACC AAA AAC ATA GCC TTT AG) and 16H1 (CTC CGG TCT GAA CTC AGA TCA CGT AGG). The following amplify and sequence the cytochrome b gene: CytbS1L (GAA AAA CCG CYR TTG TWW TTC AAC TA) or CytbL1L (GAA AAA CCM CCG TTG TWW TTC AAC TA) and CytbS1R (YTT TGG TTT ACA ARA ACA ATG CTT TR) or CytbLtyph4R (GTG TTA ATG TGG CGT TGT TTA CTG A), CytbLtyph3L (CAT ATA TCG GAC AAA CTC TTG TCA) and CytbLtyph2R (AGY TTG TTT GGG ATK GCT CGT AGR AT). The following were used to amplify and sequence an intron of the rhodopsin nuclear gene: RHO6L (ATT ATM TTC TTC TGC TAY GGA CGC CT) and RHO5R (CAG AKC CTT GGT GRG TGA AGA TGT A) or RHO9L (TTC TGC TAY GGA CGC CTY STC TG) and RHO7R (AGA KCC TTG GTG RGT GAA GAT GTA).

Sequences were aligned using CLUSTAL (Thompson *et al.*, 1997). Secondary structure alignment in the ribosomal RNA region was unnecessary because of the high sequence conservation. Phylogenies were constructed with maximum likelihood using PHYML (Guindon & Gascuel, 2003), minimum evolution (ME) using MEGA 4.0 (Kumar *et al.*, 2004), and with Bayesian methods of inference using MRBAYES 3.1 (Ronquist & Huelsenbeck, 2003). MODELTEST 3.06 (Posada & Crandall, 1998) was used to select the model (GTR + proportion of invariable sites) and estimate model parameters using the Akaike Information Criterion for the ML analysis: base frequencies A = 0.3643, C = 0.2736, G = 0.1676; rate matrix AC = 4.0938, AG = 52.5945, AT = 1.9586, CG = 0.3383, CT = 36.1350; proportion of invariable sites = 0.7134). The ME tree was constructed with maximum composite likelihood distances (Tamura *et al.*, 2004). For Bayesian analysis a mixed model approach was used with two partitions corresponding to the combined RNA genes (GTR + gamma) and the cytochrome b gene (GTR + proportion of invariable sites), based on results of MODELTEST. Model parameters were estimated from the data using one cold and three heated Markov chains. The Monte Carlo Markov chain length was 2,000,000 generations, sampled every 100 generations. The first 5000 samples were discarded as burnin. Statistical significance was evaluated with bootstrapping (2000 replications) for ML and ME.

DNA sequences were obtained from the following species of blindsnakes (*Typhlops*) at the mitochondrial gene cytochrome b, to compare levels of sequence divergence in two sympatric species pairs: *T. hypomethes* Hedges & Thomas (USNM 300581; Puerto Rico, San Juan) and *T. platycephalus* Duméril & Bibron (Puerto Rico, 12.3 km SSE Arecibo); and *T. eperopeus* Thomas & Hedges (USNM 564785, holotype, from Barahona, 3.9 km SSW Barahona) and *T. titanops* Thomas (USNM 266302; Dominican Republic, Pedernales, 22 km N. Pedernales). Sequence divergence (maximum composite likelihood) was estimated (MEGA 4.0; Between Group Means) between the two species pairs and among groups of species *Leptotyphlops*. The same 918 bp region of the gene was used in both cases.

Systematic accounts

Leptotyphlops carlae sp. nov.

Fig. 1A

Barbados Threadsnake

Holotype. USNM 564819, adult female, collected on 9 June 2006 under rock on ground near Bonwell, St. Joseph Parish, Barbados (Fig. 2A), 280 m (13° 11.196' N, 59° 32.445' W), by S. Blair Hedges and Carla Ann Hass. Field tag number 267708.

Paratypes. USNM 564818, from same locality; BM 89.7.5.27, from Barbados (no specific locality); BM 1969.792, from Codrington College, St. John Parish, Barbados, 100 m (13° 10.543' N, 59° 28.481' W); Cali-

ifornia Academy of Sciences (CAS) 49279, “St. John, Antigua,” collected by W. K. Fisher in July, 1918, on the Barbados-Antigua Expedition. This locality is interpreted to be in error; it is likely from St. John Parish, Barbados (see discussion below).

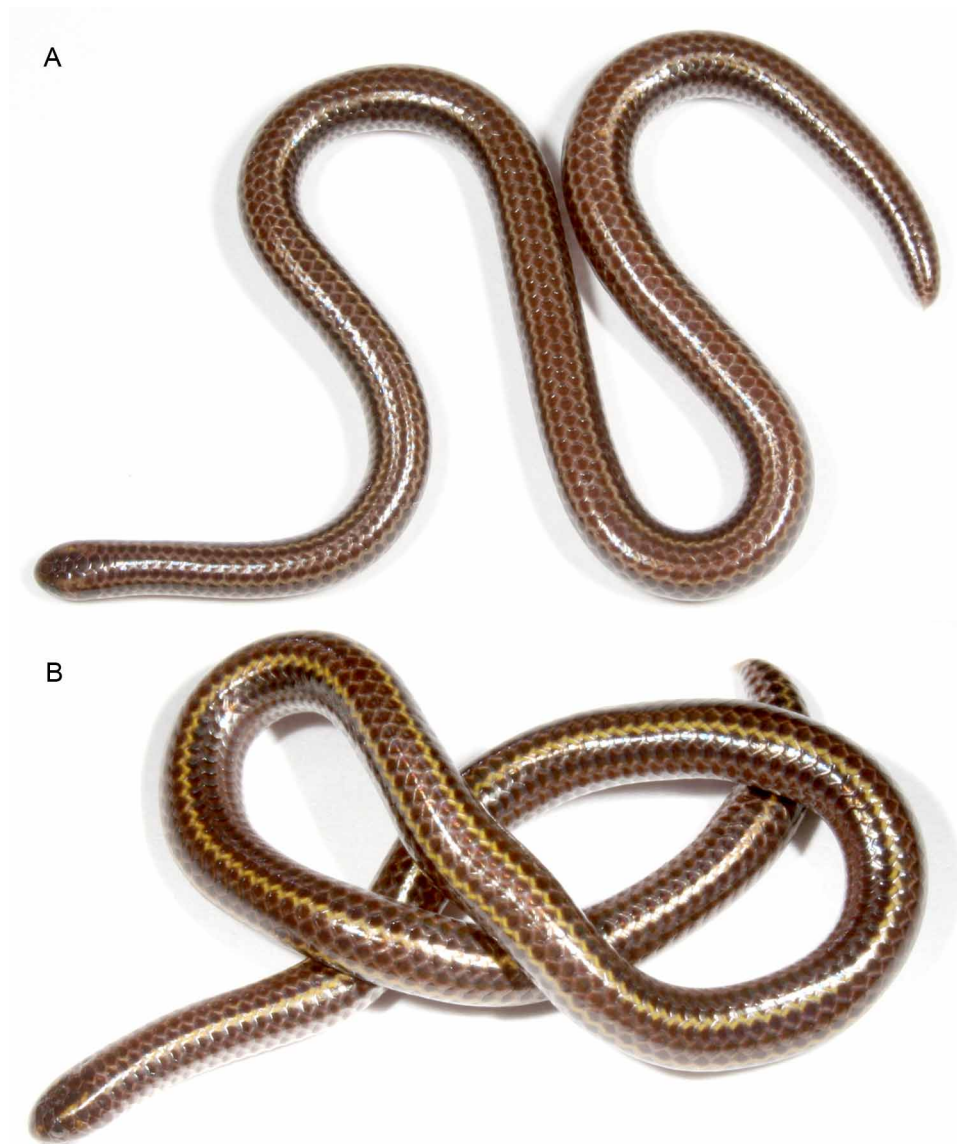


FIGURE 1. Two species of threadsnakes (*Leptotyphlops*) from the Lesser Antilles. (A) *Leptotyphlops carlae* (101 mm TL), adult female paratype (USNM 564818). (B) *Leptotyphlops breuili* (108 mm TL), adult male paratype (USNM 564811).

Diagnosis. A small species of the genus (104 mm maximum total length, TOL) and member of the West Indian *bilineatus* group (Thomas *et al.*, 1985) in having the ocular and lip separated by labial scales. It is most closely related to *Leptotyphlops bilineatus* (Martinique) and an undescribed species from St. Lucia (see below) in having fewer than 290 middorsal scales, large eyes, and a dark body color with two pale dorsolateral stripes. In color pattern it differs from both in having continuous stripes from eyes to tip of tail with an additional pair of narrow middorsal lines (Fig. 2A–B). In scale characters (Figs. 3–4, Table 1) it differs from both species in having a narrower PA1 (width/length 1.56–1.74 vs. 1.84–2.28), a wider contact (suture) of PF and RO (PF-RO/PF-PN 0.78–1.2 vs. 0.31–0.61), and a shorter PA1-PA2 suture (0.63–0.68 vs. 0.69–0.85 % snout-vent length, SVL). In addition, it differs from *L. bilineatus* in having a narrower head (2.38–2.49 vs. 2.53–2.68 % SVL), a shorter OC (0.65–0.73 vs. 0.78–0.84 % SVL), and shorter anterior middorsals, PF+FR+IP+IO

(2.06–2.16 vs. 2.28–2.55). From the new *St. Lucia* species, it differs in having more middorsal scales (185–192 vs. 176–183), a shorter OC suture (SO-OC/PN-OC 1.42–2.08 vs. 2.23–3.31), and a narrower SO (0.87–0.96 vs. 0.99–1.16). Measurements and scale counts, including those of the holotype, are in Table 1.

Description. Body with 14 scale rows, reducing in region of vent; middle of tail with ten rows; four supralabials and four infralabials. Body stout; head narrow, tapering from behind eyes to snout and covered with numerous tubular scale organs; rostral narrow, tapering posteriorly to rounded margin, widest (and slightly protuberant) at tip of snout, narrower and concave on ventral portion; spine at tip of tail. In average width, $PF > IO > IP > F$. Eye large, 43–51% distance from naris to posterior edge of eye. Coloration in life dark brown to black above and below, with pale grayish-yellow dorsolateral lines extending from PA1 to tip of tail, defining a reddish-brown and slightly iridescent middorsal zone three scales in width, with narrower (inner) pair of lines along outer border of middorsal scale row; lower sides and venter pale grayish-brown, beginning 1.8 scales below dorsolateral lines; two pale spots on each PN scale, with occasional white markings on SO and PF scales; 5–11 white scales around vent. Live weight, 0.60 g (holotype).

Etymology. The species name is dedicated to my wife, Carla Ann Hass.

Comments. Until now, the two BM specimens of this species, one from 1889 (Fielden, 1889; Boulenger, 1893) and the other from 1963 (Underwood, 1963), have been the only documented evidence of the occurrence of *Leptotyphlops* on Barbados. Both have been confused with *L. bilineatus* of Martinique. The second BM specimen requires discussion because it has had a confused history. It was first reported by Underwood (Underwood, 1963) as coming from “the vicinity of Codrington College,” St. John Parish, having been collected by Father E. J. Pearce. Several years later, Emsley (Emsley, 1966) reported on what appears to be the same specimen, although he makes no mention of the earlier report by Underwood. However, Underwood is mentioned in the note as having examined the specimen for him and compared it with the 1889 BM specimen and one from Martinique. Although Emsley (Emsley, 1966) mentioned that the specimen was in the collection of the Department of Zoology, University of the West Indies, Trinidad, it must be the same specimen as BM1969.762, now in the Natural History Museum (NHM), London. The collection dates (January, 1963), collector, and ecological notes correspond. Also, a check of the collection in Trinidad (A. Hailey, pers. comm.) confirmed that the specimen is no longer there. The possibility that this specimen is different from the one reported initially by Underwood (Underwood, 1963) was considered because the date of publication of his book is reported in all literature as “1962,” which would predate the collection of the specimen. The 1962 date derives from a date of May, 1962 in the foreword of the book, written by Hector Wynter. However, Underwood’s supplement to the book, dated June, 1964, states that 12 months have passed since publication of the original book, giving a likely date of June, 1963 (not 1962) as the publication date of the original book. This would be consistent with the mention of the Barbados specimen collected in January, 1963. Therefore, I consider BM1969.762 to be the same snake reported by Underwood (Underwood, 1963) and Emsley (Emsley, 1966).

The CAS paratype (CAS 49279) has an equally confusing history. It has gone unnoticed by herpetologists studying West Indian snakes for nearly a century since it was collected, despite being in a major U.S. collection. The specimen locality is “St. John, Antigua,” collected by W. K. Fisher in July, 1918. However, it is 400–500 km north of the ranges of *L. bilineata*, *L. breuili*, and *L. carlae*, and it is consistent in all aspects with *L. carlae* of Barbados. After some investigation, it was revealed that the collector and date of the specimen implied that it was collected on the Barbados-Antigua Expedition of the University of Iowa (Nutting, 1919). Also, the major city of Antigua is St. John’s, whereas the Parish in Barbados where *L. carlae* is found is St. John, again consistent with the locality of the specimen. Reptiles were not a major group studied on the expedition, and the collector (Fisher) studied echinoderms. The few other reptiles collected on Antigua came from only two sites, English Harbor and Monk’s Hill (not St. John’s). The account of the expedition mentions field work in St. John (Parish), Barbados (Nutting, 1919). Considering all of this information, I conclude that this specimen is from St. John Parish, Barbados, not “St. John, Antigua.”

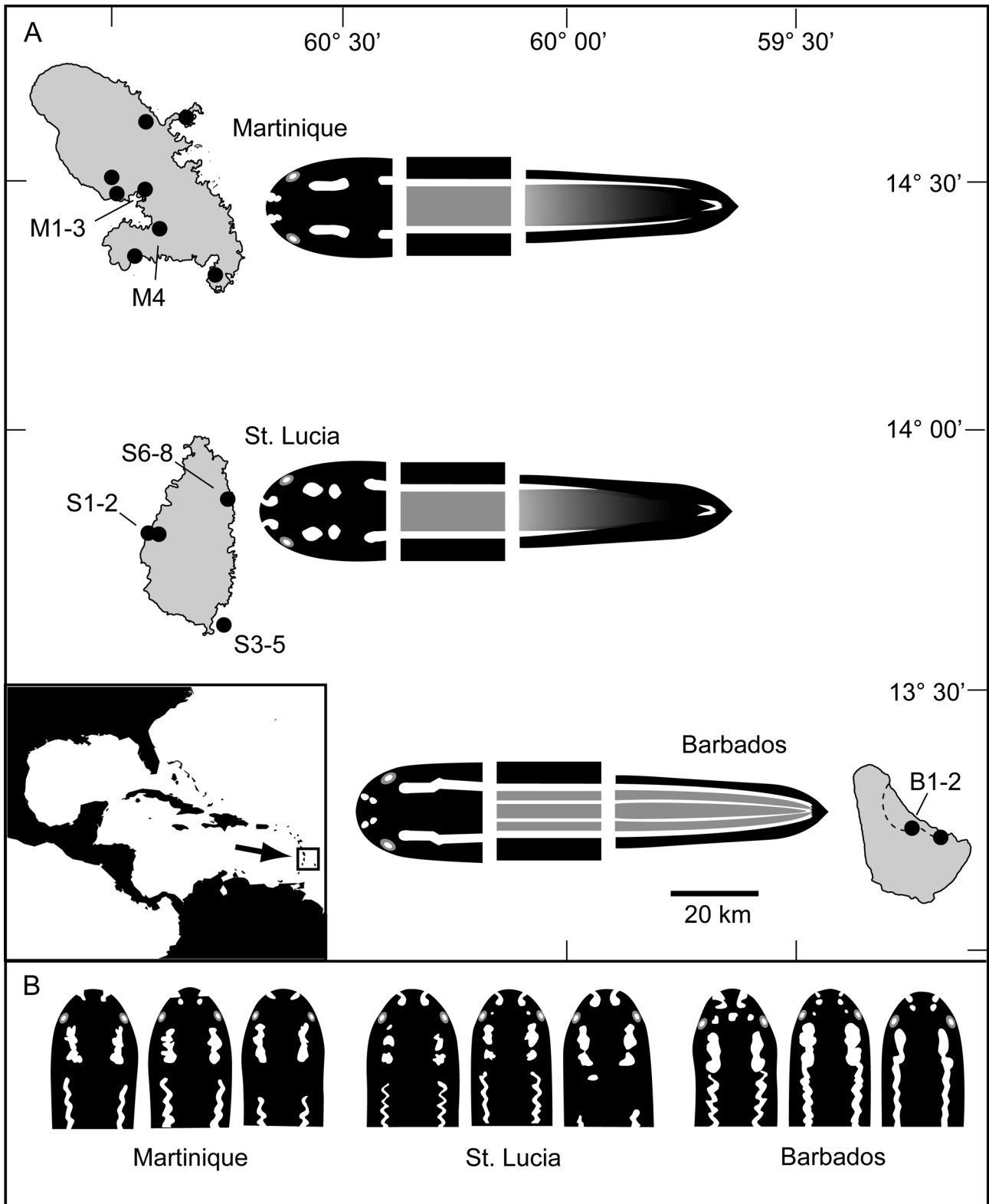


FIGURE 2. Distribution and pattern variation in threadsnakes (*Leptotyphlops*) from three islands in the Lesser Antilles. (A) Distribution and generalized color pattern differences (head, midbody, and tail). The location of samples used in sequence analyses is indicated. (B) Head pattern in three individuals from each island, illustrating variation (MNHN 2006.0516, USNM 564808, 564809; USNM 564810, 564815, 564816; BM1969.792, USNM 564819, 564818). Dashed line in Barbados indicates geologic region of sub-reef outcrop.

The two new specimens were collected adjacent to a small patch of secondary forest near Bonwell in the Parish of St. Joseph. This locality and the only other known locality, Codrington College (Fig. 2A), lie within a small, geologically unique area (Speed, 1994) in east-central Barbados lacking a Pleistocene reef cap. This upland area comprises ~40 km² or about one-tenth of the total land area of Barbados and corresponds to the parishes of St. Andrew, St. Joseph, and a small portion of St. John close to the coast. Numerous other localities in these parishes were searched intensely for several days in June 2006, including coastal and upland habitats, without success. The imprecise locality for CAS 49279, “St. John,” is consistent with the species being restricted to the same region of Barbados as the other specimens. This was the first part of Barbados to emerge above sea level about one million years ago (Speed, 1994) and establishes the maximum age for the colonization of Barbados by *Leptotyphlops*, although molecular clock time estimates in anoline lizards inhabiting Barbados have conflicted with this geologic date (Thorpe *et al.*, 2005).

There is little known about the ecology of these new Antillean snakes. Threadsnakes are burrowers and usually feed on the adults and larvae of ants and termites (Greene, 1997). It is almost certain that this native species, which evolved in the presence of forests, requires such forest habitat for survival. However, Barbados is one of the ten most densely populated countries in the World (World Resources Institute, 2006) and has essentially no original forest remaining (FAO, 2005). Assuming that secondary forest is sufficient to provide habitat for the survival of this species, and if such habitat comprises 5–10% of the east-central sub-reef region, then the suitable habitat for *L. carlae* is probably is no more than a few square kilometers. An additional concern is the recent introduction to Barbados of the Flowerpot Blindsnake, *Ramphotyphlops braminus* Daudin, a parthenogenetic species native to the Australasian region. On our visit in 2006 we examined specimens of this species collected in Bridgetown (St. Michael) and near Lowland (Christ Church) indicating that it is probably now widespread in Barbados, at least in urban areas. As a potential competitor, it could pose an additional threat to the survival of *L. carlae*.

***Leptotyphlops breuili* sp. nov.**

Fig. 1B

St. Lucia Threadsnake

Holotype. USNM 564810, adult male, collected on 13 June 2006 under rock on ground on north slope of Maria Major Island, St. Lucia (Fig. 2A), 60 m (13° 43.430' N, 60° 55.897' W), by S. Blair Hedges and Carla Ann Hass. Field tag number 267731.

Paratypes. USNM 564811–812 from type locality; 564813–814 from Anse Galet (near Anse La Raye), St. Lucia, 5 m (13° 56.080' N, 61° 02.950' W); 222954 from 0.1 mi E Anse Galet River; 564815–817 from 1.6 km N Praslin, St. Lucia, 40 m (13° 52.875' N, 60° 53.418' W); Museum of Comparative Zoology, Harvard University (MCZ) 10693 from St. Lucia (exact locality unknown).

Diagnosis. A small species of the genus, reaching 113 mm maximum TOL (preserved specimens); up to 119 mm TOL in live specimens (Buley *et al.*, 1997). It is a member of the West Indian *bilineatus* group having two dorsolateral lines, most closely related to *Leptotyphlops bilineatus* and *L. carlae*. It differs from both in having a typical pattern of two spots behind the head and a dark tail (Fig. 2A–B). In scale characters (Figs. 3–4, Table 1) it also differs from both species in having a wider PA1 (width/length 2.08–2.28 vs. 1.56–1.93) and a wider PA2 (2.03–2.48 vs. 1.71–2.01). In addition, it differs from *L. bilineatus* in having a wider SO (0.99–1.16 vs. 0.78–0.99), a shorter OC (0.63–0.76 vs. 0.78–0.84), and shorter anterior middorsals, PF+FR+IP+IO (2.07–2.28 vs. 2.28–2.55). From *L. carlae*, it differs in the three characters noted above in the diagnosis of that species. Measurements and scale counts, including those of the holotype, are in Table 1.

Description. Body with 14 scale rows, reducing in region of vent; middle of tail with ten rows; four supralabials and four infralabials. Similar in body proportions to previous species. In average width, PF = IO

> IP > F. Eye large, 37–49% distance from naris to posterior edge of eye. Coloration in life dark brown to black above and below, with pale yellow dorsolateral lines extending from two scales behind PA2 to base of tail, defining a reddish-brown middorsal zone three scales in width; tail dark to black, lacking stripes completely, or with faint indication or stripes; usually a dorsal v-marking on last two scales of tail (Fig. 2A); lower sides and venter pale grayish-brown, beginning 1.8 scales below dorsolateral lines; pale markings on PA1 and PA2, usually in the form of two irregular spots in line with the dorsolateral lines; pale markings also on each PN scale; 7–18 white scales around vent. Live weight, 0.50–0.70 g (mean = 0.61 g; n = 4 adults).

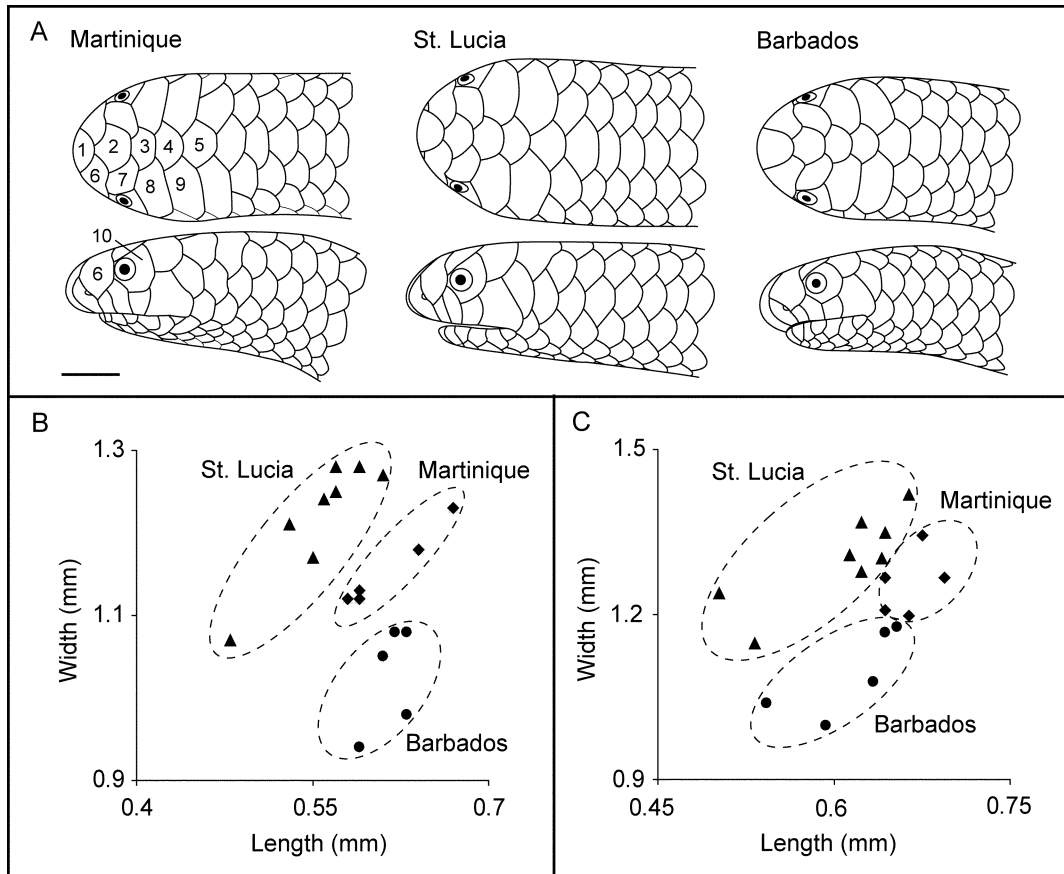


FIGURE 3. Variation in scalation of threadsnakes (*Leptotyphlops*) from three islands in the Lesser Antilles. (A) Head scalation (top and side of head) in representatives from each island (USNM 564809, 564810, 564819). Scale bar = 1 mm. Numbered head scales are rostral, RO (1); prefrontal, PF (2); frontal, FR (3); interparietal, IP (4); interoccipital, IO (5); postnasal, PN (6); preocular, PO (7); parietal-I, PA1 (8); parietal-II, PA2 (9); and ocular, OC (10). (B) Plot of parietal-1 scale width versus length. (C) Plot of parietal-2 scale width versus length.

Etymology. The species name is dedicated to Michel Breuil for his contributions to the herpetology of the Lesser Antilles.

Comments. The species is known from only two areas on Saint Lucia and a third locality on Maria Major Island off the southeast coast. Buley *et al.* (1997) reported collecting six specimens under rocks and in leaf litter on Maria Major in 1997 (22–24 September), measuring (in life) 58–113 SVL (62–119 TOL). They were not sexed, and all were released. All localities for this species have been in forested areas, on slopes, and there are no reports of it being encountered in open areas or beach habitats. Several other suitable localities in eastern and western St. Lucia were searched during a visit by the author in June 2006 (and during an earlier visit by the author in April 1996) without success, although more effort is needed to better delineate the distribution of *L. breuili*. The genetic difference between the eastern and western populations on Saint Lucia, ~1.4% (Fig. 4C) is much greater than between the eastern locality and Maria Major, suggesting a relatively long

period of differentiation on the island. Development of forested areas on Saint Lucia, for housing, roads, tourism, and other activities, is likely to continue reducing the available habitat of this species.

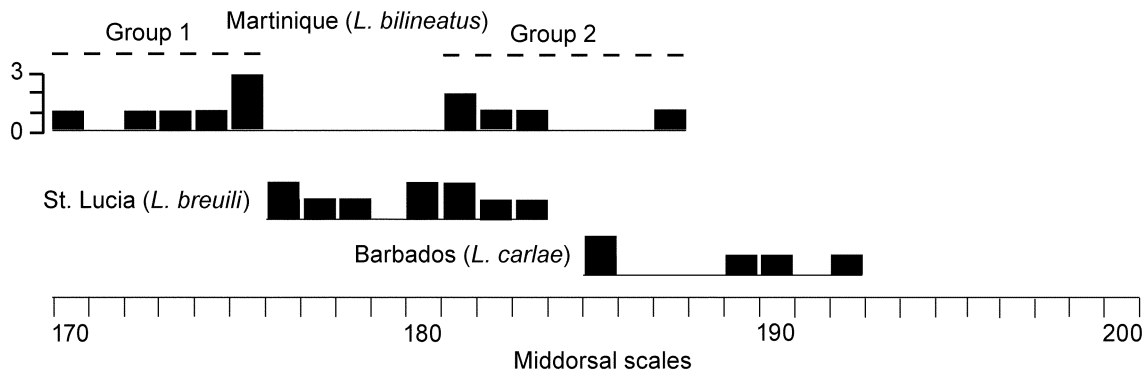


FIGURE 4. Variation in the number of middorsal scales in *Leptotyphlops* from the Lesser Antilles. The two groups identified for *L. bilineatus* are suspected to be different species.

Discussion

Molecular evidence for species differences

Besides the diagnostic morphological differences, the two new species are distinguished from each other and from *Leptotyphlops bilineatus* in a phylogenetic analysis of DNA sequences (Fig. 5). The sequence analysis also shows that genetic divergence among populations has occurred within Martinique and St. Lucia (only one locality was sampled in Barbados). The ML and ME topologies were identical. The Bayesian topology was similar except for the non-significant nodes involving the position of *L. bilineatus* sample M4 which in that topology appeared basal to the cluster of *L. carlae* + *L. bilineatus*.

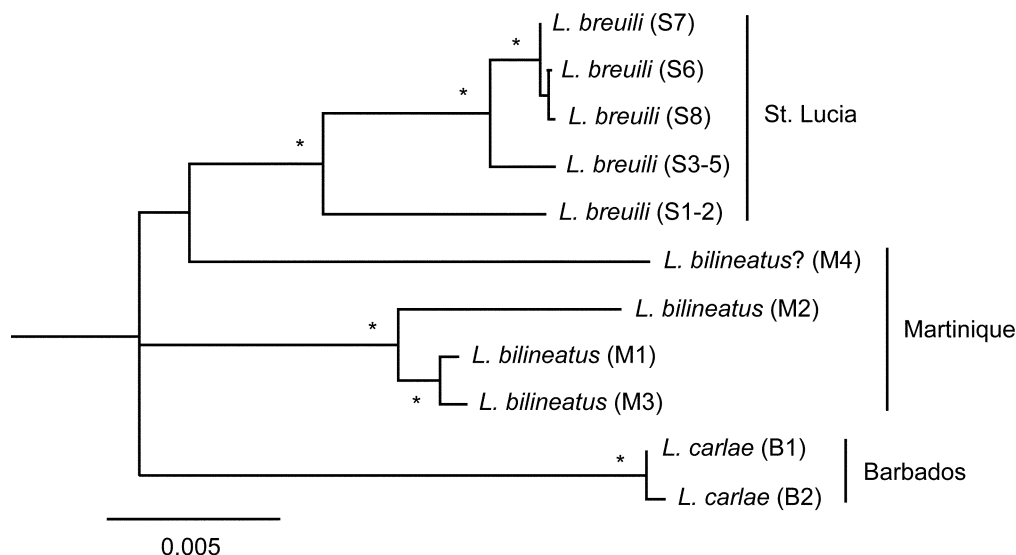


FIGURE 5. Molecular variation in threadsnakes (*Leptotyphlops*) from three islands in the Lesser Antilles. Maximum likelihood phylogenetic tree from sequences of four mitochondrial genes, totaling 3,470 aligned base pairs. The tree was rooted with a species from the Greater Antilles, *L. leptepileptis* (not shown). Asterisks indicate significant nodes (>95%) in both maximum likelihood and minimum evolution analyses.

Specimen M4 from Martinique may represent an additional undescribed species, co-occurring with *L. bilineatus* on Martinique. It has a high number of middorsal scales (Fig. 4, Group 2) whereas the other three

individuals examined from that island have a low number of middorsal scales (Group 1). Also, it is as divergent genetically from *L. bilineatus* as that species is from the other two species (Fig. 5). As noted, its position was different in the ML/ME trees versus the Bayesian tree, but in both cases the topological difference was not significant. Morphologically, specimen M4 also differs from the other three specimens of *L. bilineatus* in having a larger number of pale scales around the vent (17 versus 3–6) and a narrower supraocular scale (0.72 mm versus 0.84–0.94 mm). Although it has a narrower head and body, it is also slightly desiccated, which would affect length measurements. If the middorsal scale difference corresponds to two species, they are sympatric and similar in size (maximum total length of each, 108 mm). Additional specimens will be needed to confirm the presence of a second species on Martinique, because more than half of the existing museum specimens from that island are old and have prior damage, making it impossible to compare any additional morphological characters with middorsal scale counts.

Average levels of mitochondrial sequence divergence (cytochrome b, maximum composite likelihood) among these species of *Leptotyphlops* in the Lesser Antilles are low (5.1%), but comparable to that estimated here between other pairs of West Indian burrowing snakes known to be sympatric (Thomas & Hedges, 2007), including *Typhlops hypomethes* and *T. platycephalus* (5.8%), and *T. eperopeus* and *T. titanops* (4.7%), further supporting the species status of the new *Leptotyphlops*. As noted above, Barbados is thought to have been above sea level for approximately one million years (Speed, 1994).

The smallest snakes

Body sizes of vertebrates are most often compared in terms of maximum length, because mass, size of offspring, and size at sexual maturity are unavailable for many species, and mean measurements depend on the distinction of adults from juveniles. Even using maximum length, it is often difficult to order species by size because of the small number of specimens typically available for tropical species (Estrada & Hedges, 1996; Hedges & Thomas, 2001). Also, given that snakes shrink up to 28% (average, 7%) in length after preservation (Reed, 2001) and that different preserving fluids and their concentrations yield different amounts of shrinkage of vertebrate specimens (Smith & Walker, 2003), small differences in size among specimens are unlikely to be significant.

The smallest snakes are in the genus *Leptotyphlops*, where six species have maximum lengths that are less than 105 mm. Four are known only from their holotypes (*L. dissimilis* Bocage, *L. nicefori* Dunn, *L. pungwensis* Broadley and Wallach, and *L. yemenicus* Scortecchi); one of those (*L. pungwensis*) is a juvenile female whereas the adult status of the other three is not known. Thus, no conclusions regarding the maximum size of those species can be drawn until more specimens, including adults, become available. For example, until recently, the Socotra island species *L. wilsoni* was known from two specimens with total lengths of 100 and 101 mm (Hahn, 1978). However, the maximum size increased substantially—to 129 mm—when six additional specimens were reported (Rösler & Wranik, 2004). Similarly, the current maximum TOL of *L. collaris* Hoogmoed is 109 mm (Nicolas Vidal, personal communication), although the largest in the type series was 104 mm (Hoogmoed, 1977).

Of the two remaining species, *Leptotyphlops carlae* (Barbados) and *L. tanae* Broadley and Wallach (Kenya), only *L. carlae* is known from adults of both sexes. The largest specimen of the type series of *L. tanae* is 103 mm in total length (Broadley & Wallach, 2007), but only two specimens were sexed and both were males. While the sex of specimens of *Leptotyphlops* is infrequently reported in the literature, it is known in a scattering of accounts and in several studies with sufficient sample sizes to examine sexual dimorphism. In those cases, females of *Leptotyphlops* are known to be larger than males, although the dimorphism appears to be more pronounced in African species than in New World species. In *L. scutifrons* Peters (n = 164) and *L. conjunctus* Jan (n = 177), both from Africa, females averaged 27% longer than males in each species (Webb *et al.*, 2000). In a third African species, *L. macrops* Broadley & Wallach (n = 7), the longest female was 40% longer than the longest male (Broadley & Wallach, 1996). In the New World, sexual dimorphism in two well-

sampled species was noticeably less: 12% in *L. fuliginosus* (n = 45) (Passos *et al.*, 2006) and 11% in *L. leptepileptus* (n = 70) (Thomas *et al.*, 1985). Size dimorphism in seven other New World species with smaller sample sizes (*L. anthracinus* Bailey, *L. bilineatus*, *L. breuili*, *L. carlae*, *L. koppesi* Amaral, *L. salgueiroi* Amaral, and *L. tricolor* Orejas-Miranda and Zug) averaged 7.5% (Bailey, 1946 ; Zug, 1977; Passos *et al.*, 2005;2006). Based on this, I examined all specimens of *L. tanae* that could be obtained (n=18), to determine length and sex.

Nine specimens of *Leptotyphlops tanae* are adult males (MCZ 40093–94, 40096–97, 40101–03, 40106, and 40108), one is an immature female (MCZ 40095), two are small juveniles (USNM 120801–02), and six could not be sexed because of their poor condition of preservation (MCZ 40100, 40104–05, 40107, and 40110–11). Of the latter specimens, none appeared to contain enlarged eggs. An additional specimen (MCZ 40098) was missing from the museum collection and presumed lost. Thus, surprisingly, no adult females of *L. tanae* were present among the 12 specimens that could be sexed. Given the maximum length of the adult males (100 mm) and the size dimorphism ratios of the four species noted above with large sample sizes, the females of *L. tanae* would be expected to be ~111–127 mm. The series of *L. carlae*, although small (n = 5, all adults), includes males and females, with the largest being a female and with both females bearing eggs. Considering all of this, *Leptotyphlops carlae* (maximum TOL 104 mm) is currently the smallest species of snake where adult males and females are known. *Leptotyphlops bilineatus* (maximum TOL 108 mm) is slightly larger and perhaps is the second smallest. Nonetheless, more individuals of these and other species are needed to more accurately assess species-specific size differences.

Reproductive constraints on body size

The holotype of *Leptotyphlops carlae* has a single, greatly elongated (2.2 x 13.7 mm) oviductal egg and one of the paratypes has one enlarging egg. Such a low clutch size is rare in snakes, where the average number of offspring is seven and several species are known to produce as many as 100 eggs or young (Fitch, 1970). However, clutch size is correlated with body size, with the smallest snakes having the smallest clutches and largest offspring relative to adult size (Fitch, 1970; Shine & Seigel, 1996; Webb *et al.*, 2000), consistent with life history theory postulating an optimal (or minimal) offspring size (Smith & Fretwell, 1974; Shine, 2005). Offspring size still varies widely across snakes, but it is the ratio of offspring to adult size that suggests a reproductive constraint. Clutch sizes of 1–3 are known in several other small species of snakes (Fitch, 1970; Wallach & Hahn, 1998; Webb *et al.*, 2000). The unusual egg shape of *L. carlae* is also at the extreme among snakes (Fig. 6A). It is clearly the result of the tradeoff between clutch size and relative offspring size, combined with the morphological constraints of the snake tubular body shape.

Further evidence that egg shape is constrained by snake body shape comes from data on variation among individuals of the same species (Fig. 6B) and among successive clutches of the same female snake (Fig. 6C). In both cases, as in the interspecific comparison, smaller clutches result in eggs that are more elongate. In the case of inter-clutch variation of the same female, the suggestion is that egg shape may have little or no genetic basis. In a study of egg variation in three species of snakes (Ford & Seigel, 1989), egg shape (length/width) was not examined specifically, but the results for length and width were consistent with the general model proposed here. Those authors also proposed that oviduct length is a constraint. Although the eggs are contained within the oviduct, the walls of the oviduct are elastic and unlikely to pose a constraint. Instead, dissections of gravid female snakes show that most or all of the available space in the body cavity is used for eggs, which suggests that it is the snake body cavity, not the oviduct *per se*, that is the constraint.

In snakes, eggs are arranged serially within the body and each egg occupies nearly the entire inside diameter of the body, although in some species with large clutches they may overlap. The proportion of the female SVL occupied by the clutch, termed the relative clutch length, averages one-third (0.33) in terrestrial snakes although is somewhat lower (0.24) in aquatic snakes (Shine, 1988). Relatively large eggs (compared with female size) in small clutches are elongate because they distribute their mass down the available space in the

cylindrical body cavity (the “package”). Relatively small eggs in large clutches are nearly round because their shape is little affected by these constraints (Fig. 6D). In that sense, egg shape in snakes is a packaging phenomenon (Hedges, 1981), a byproduct of the tradeoff between clutch size and offspring size. The interspecific egg shape regression (Fig. 6D) indicates that shape is similar (~1.5–2.0) above a clutch size of about 10–15, presumably because the greater body width of females laying larger clutches does not pose a constraint on shape.

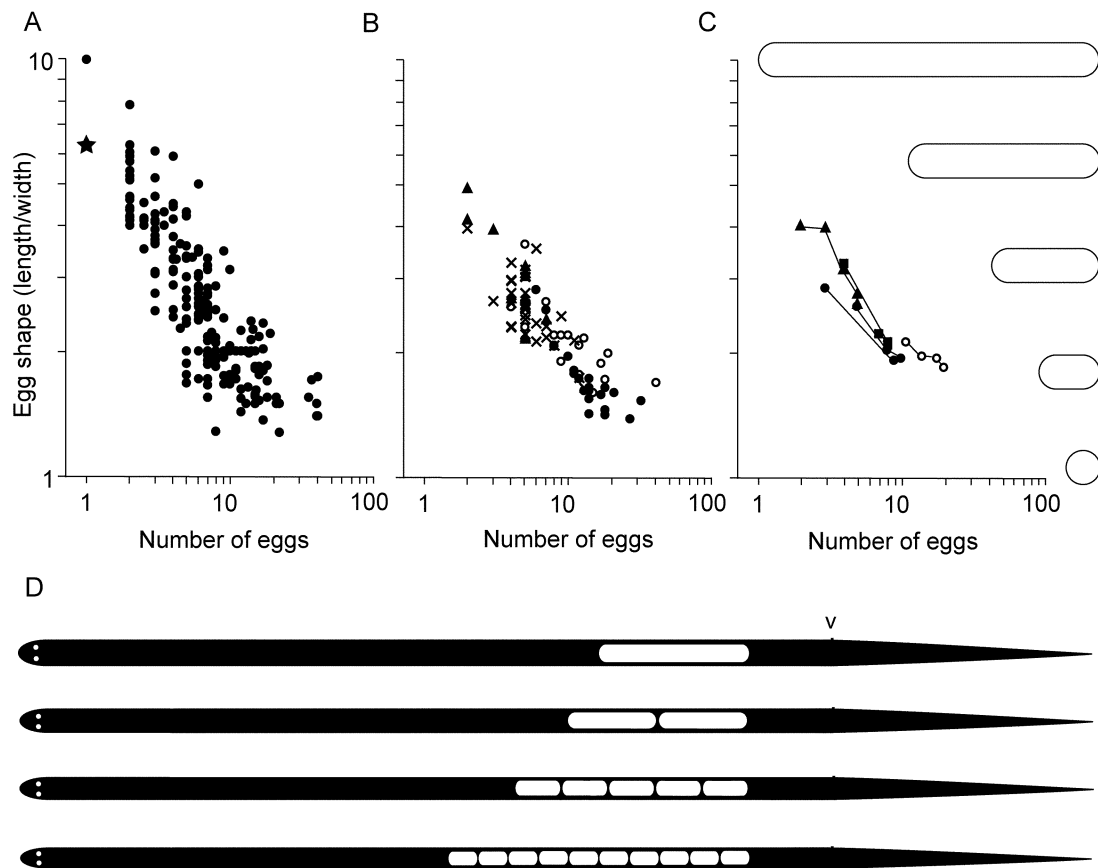


FIGURE 6. Relationship of egg shape, clutch size, and body shape in snakes. (A) A log-log plot of egg shape (length/width) and clutch size (number of eggs) among 193 species of snakes (Appendix 1). The equation for the regression line is: $\log \text{ egg shape} = -0.602 (\log \text{ clutch size}) + 0.877$. Symbols are means of each species; star indicates *L. carlae*; other data from the literature. (B) A similar plot for variation within four species; symbols are individuals of each species (closed circles, *Coluber constrictor* Linnaeus; open circles, *Pantherophis obsoletus*; triangles, *Diadophis punctatus* Linnaeus; “x”s, *Lampropeltis triangulum* Lacépède); data are from Appendix 2. (C) A similar plot for variation among clutches of the same female snake; symbols are means of eggs within a clutch (closed circles, *Lampropeltis mexicana* Garman; open circles, *Naja melanoleuca* Hallowell; triangles, *Elaphe climacophora* Boie; squares, *Lampropeltis triangulum*); lines connect clutches of same snake; data are from Appendix 3. Representations of eggs of different shapes are shown at right for comparison. (D) Relationship of body shape and egg shape in snakes. Shown are the shapes of four snakes of different lengths ranging from 10 cm SVL (top) to 100 cm (bottom). The shapes are derived from the mean of the slopes (0.90) and intercepts (-1.39) determined across all snakes for the log-log regression of SVL and body width (W) at midbody (Table 2), resulting in these average body shapes: 31 (SVL/W) for 10 cm SVL, 34 for 22 cm SVL, 36 for 46 cm SVL and 39 for 100 cm SVL. Average egg shapes are shown for each clutch size indicated, from the relationship in (A) above. The position of the clutch, starting at approximately 10% of SVL anterior to the vent, is based on the results of Shine (1988). A ‘v’ indicates the position of the vent.

The shape of the body space occupied by the clutch can be estimated by summing the lengths of the eggs in a clutch and dividing that total by the average width of the eggs. Considering the interspecific pattern (Fig. 6A), at a clutch size of ten, the expected egg shape is 1.9. Therefore the clutch shape of snakes at this clutch

size is 19. At a clutch size of one, the expected egg shape (and clutch shape) is 7.5. This presents a conundrum because, assuming that snakes with large clutches are equally as full as those with small clutches, the latter have packages that are roughly half as elongate. In other words, while the relative size of eggs and offspring are larger in small snakes, a smaller proportion of the female mass (volume) is being devoted to the clutch. As further evidence of this disparity, the relative clutch length of *L. carlae*, which has an egg shape (6.2) close to the expected, is only 0.14 (13.7 mm/98 mm SVL) compared with the average of 0.33 in terrestrial snakes, noted above. To have that average relative clutch length, and given its egg width of 2.2 mm, *L. carlae* would need to lay an egg that is 32 mm long, with a shape of 14. However, only two eggs have been recorded more elongate than that of *L. carlae*, with shapes of 8 and 10 (Fig. 6A).

These size-related differences in clutch shape and relative clutch length were not detected in earlier studies of variation in relative clutch mass (Seigel *et al.*, 1986) and relative clutch length (Shine, 1988) among snakes, perhaps because of insufficient sampling across a diversity of species. They are best explained by the fact that many body organs are negatively allometric, which means that that relatively more body cavity space is occupied by organs in small animals (Rensch, 1948). This, in turn, leaves less space for eggs and young.

However, an additional compounding factor is that snake body shape (SVL/width) itself is negatively allometric. Thus, in general, large species are more elongate (Table 2); although one group showed a significantly positive allometric slope. Across all snakes (interspecific), the following equation describes the average shape relationship: $\log \text{width} = 0.90 (\log \text{SVL}) - 1.39$, where measurements are in centimeters. For example, the smallest snakes (~10 cm SVL) typically have a stout body shape of 31 whereas in the longest snakes (~1,000 cm) the average shape is ~50. Earlier discussions of body cavity space available for reproduction in snakes had instead assumed a 1:1 relationship (Seigel & Ford, 1992). Nonetheless, differences in squamate body shape have been found to be associated with reproductive traits in other studies (Shine, 1992; Griffith, 1996). Body shape also varies among groups, complicating such patterns, with sit-and-wait predators (e.g., viperids) being wider bodied and less tubular than other species. Some species of small snakes are unusually thin, with body shapes greater than 100, and both *Typhlops* and *Leptotyphlops* are positively allometric in body shape (Table 2), meaning that smaller species, on average, are relatively thinner than larger species. The different feeding mode of scolecophidians—eating prey much smaller than their body, and doing so frequently—compared with other snakes, also may affect their body shape. Nonetheless, *L. carlae* (average body shape = 34) is close to the expected shape for a snake (in general) of that size.

Although no juveniles of *L. carlae* are known, the size range of the four juveniles of *L. breuili* is 59–85 mm TOL and the one juvenile of *L. bilineatus* is 60 mm TOL. Based on this and hatchling size in other *Leptotyphlops* (Webb *et al.*, 2000), the hatchlings of the smallest snakes are probably 40–50 mm, which is about 60% of their size at sexual maturity and 50% of their maximum length. For comparison, in the largest snakes, such as boids and pythonids, hatchlings or newborn are only ~20% of their size at sexual maturity and 5–10% of maximum TOL (Pope, 1961). A similar pattern was seen in some Australian elapid snakes and appears to be a general trend (Shine, 2003). While being at the terminus of an allometric trend does not necessarily imply an adaptive constraint, the production of young—in very small snakes—that are even larger (relative to the adult) may require a larger proportion of the females' body than is available given the morphology and physiology of the snake body plan. Therefore, the lower limit in snake size appears to be tied to basic aspects of snake biology, such as their body form and reproductive strategy.

Islands and size extremes

Islands make up only three percent of the Earth's land area (excluding Antarctica and islands north of, and contacting, the Arctic Circle) yet they have a disproportionately high number of tetrapod species at the extreme of size (Table 3). Recent discussions of animal size differences on islands, compared with continents, have focused on a phenomenon of central tendency, where large species (e.g., elephants) are smaller on islands and small species (e.g., rodents) are larger (Foster, 1964; Case, 1978; Boback, 2003; Lomolino, 2005;

TABLE 2. Variation in body shape among snakes. The results of regression analyses of log body width at midbody (cm) versus log SVL (cm) are shown. All data sets (rows) are independent, and thus in the interspecific comparisons, the category “terrestrial colubroids” excludes *Chironius* and “terrestrial elapids” excludes *Micrurus*.

Group	N	r	m	s(m)	b	s(b)	P
Interspecific							
Terrestrial colubroids	33	0.95	0.796	0.032	-1.23	0.056	<0.01
Arboreal colubroids	32	0.46	0.628	0.120	-1.13	0.223	<0.01
Burrowing colubroids	13	0.69	0.974	0.135	-1.50	0.213	NS
Terrestrial boids	21	0.84	0.867	0.085	-1.27	0.159	<0.05
Terrestrial elapids	50	0.49	0.677	0.098	-1.05	0.173	<0.01
Uropeltids	8	0.86	0.938	0.142	-1.38	0.193	NS
<i>Agkistrodon</i> Linnaeus	12	0.83	1.260	0.169	-1.82	0.297	NS
<i>Bothrops</i> Linnaeus	29	0.65	0.856	0.118	-1.20	0.211	NS
<i>Chironius</i> Linnaeus	11	0.78	0.930	0.155	-1.56	0.300	NS
<i>Leptotyphlops</i> Fitzinger	15	0.74	1.250	0.195	-1.98	0.236	NS
<i>Micrurus</i> Wagler	30	0.71	0.715	0.084	-1.21	0.152	<0.01
<i>Tropidophis</i> Cocteau & Bibron	7	0.79	0.600	0.124	-0.86	0.190	<0.05
<i>Typhlops</i> Oppel	47	0.81	1.250	0.088	-1.92	0.119	<0.01
Mean			0.903		-1.39		
Intraspecific							
<i>Anilius scytale</i> Linnaeus	11	0.52	0.898	0.261	-1.47	0.459	NS
<i>Atractus major</i> Boulenger	20	0.87	0.934	0.081	-1.43	0.130	NS
<i>Carphophis amoenus</i> Say	33	0.89	0.693	0.043	-1.07	0.052	NS
<i>Coluber constrictor</i> Linnaeus	33	0.93	0.959	0.047	-1.52	0.082	NS
<i>Cylindrophis ruffus</i> Laurenti	17	0.95	1.070	0.060	-1.57	0.093	NS
<i>Micrurus fulvius</i> Linnaeus	33	0.89	0.876	0.056	-1.34	0.150	<0.05
<i>Oxybelis aeneus</i> Wagler	33	0.64	0.660	0.097	-1.37	0.159	<0.01
<i>Python reticulatus</i> Schneider	18	0.93	1.010	0.066	-1.62	0.128	NS
<i>Ramphotyphlops braminus</i> Daudin	33	0.91	0.907	0.050	-1.50	0.050	NS
<i>Rhinotyphlops schlegelii</i> Bianconi	33	0.94	0.968	0.043	-1.59	0.056	NS
<i>Typhlops jamaicensis</i> Shaw	11	0.89	1.270	0.139	-1.79	0.188	NS
<i>Typhlops reticulatus</i> Linnaeus	15	0.91	0.882	0.073	-1.27	0.106	NS
Mean			0.927		-1.46		

Abbreviations: N = number of species (interspecific) or individuals (intraspecific), r = correlation coefficient, m = slope, s(m) = standard deviation of slope, b = intercept, s(b) = standard deviation of intercept, P = result of t-test for significance of slope from isometry (1.0), and NS = not significant.

Sander *et al.*, 2006). This is different from the observation here (Table 3) involving extremes in size, although the characterization of “central tendency” versus “extreme” depends in part on the taxonomic scale considered. Nonetheless, both patterns are related and probably have the same general explanation, which is reduced interspecific competition—and possibly resource limitation—leading to the filling of open ecological niches, an old concept (Darwin, 1859). Those niches may be similar to niches of species in the same genus or group on the mainland, or of a completely different group of organisms (Fig. 7). For example, the smallest vertebrates on islands may occupy niches normally occupied by invertebrates on the mainland. An increased rate of morphological change (Millien, 2006) is expected during this process of colonization and adaptation. Such

size change may occur in a single species or in multiple species that have evolved in one area, as in an adaptive radiation. Size extremes in other groups of organisms on islands, such as plants and insects (McIntyre, 2001), suggests that this process is a general one in nature.

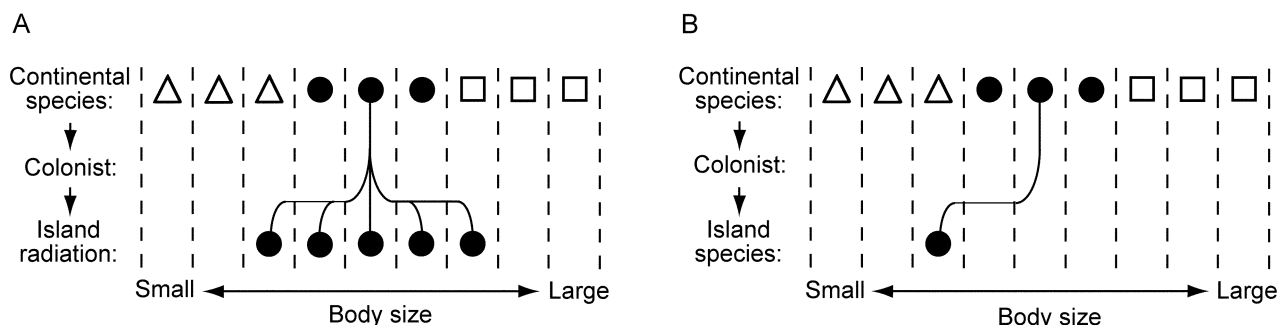


FIGURE 7. Evolution of extreme body size in island species. Vertical columns separated by dashed lines indicate ecological niches defined by body size. Individual symbols represent species whereas different types of symbols (triangles, circles, and squares) represent different taxonomic groups (e.g., genera, phyla, etc.). (A) A single colonizing species leads to an adaptive radiation (multiple species) on the island, some of which are extreme in size after filling of vacant niches. (B) A similar scenario, but in this case the colonizing species evolves an extreme body size by natural selection alone, without adaptive radiation.

TABLE 3. Extremes in size and reproduction of terrestrial tetrapods.

Group	Number of species	Maximum number of eggs or young	Smallest species		Distribution	Largest species	
			Number of Eggs or young	Maximum Length (cm)		Maximum Length (cm)	Distribution
Anurans	5,412	50,000	1	1.0	Island and continent	32	Continent
Salamanders	557	7,631	<10	2.0	Continent	180	Continent
Caecilians	171	101	<10	11.2	Island	152	Continent
Lizards	4,765	60	1	1.8	Island	302	Island
Amphisbaenians	165	16	1	15.0	Continent	80	Continent
Snakes	2,989	156	1	10.4	Island	1,000	Island and continent
Turtles	301	136	1	11.0	Continent	130	Island
Mammals	5,419	32	1	3.3	Continent	400	Continent
Birds	9,672	20	2	6.4	Island	300	Island*

Footnotes: Length is adult total length, except SVL for anurans, salamanders, and lizards; carapace length for turtles, and height for largest mammal and bird. The list excludes tuataras (two species, both on islands) and marine species.

*recently extinct.

Most species of tetrapods at the lower extreme in body size are also at the low extreme (one) in number of offspring—and its correlate, large relative offspring size—suggesting, again, a possible reproductive constraint on miniaturization (Table 3). This observation has been noted earlier, with respect to lower size limits in animals (Rensch, 1948; Estrada & Hedges, 1996). Thus, on the one hand, islands provide open niches for evolutionary experimentation in size extremes, whereas on the other hand, the lower limit of adult size appears to be constrained by the optimal (or minimal) size of the offspring. But as discussed above for snakes, offspring size is itself tied—at least in part—to allometry and the greater filling of body cavity space with organs in small animals, leaving relatively smaller space for offspring. The morphological consequences of

miniaturization can be extreme, involving the reduced function or even loss of some organs (Rensch, 1948), besides loss of digits and simplification of other external structures (Hanken & Wake, 1993; Estrada & Hedges, 1996). One morphological outcome of small size, a high surface-to-volume ratio, likely imposes physiological constraints as well, related to extreme rates of heat loss and evaporative water loss. Nonetheless, if selection is strong enough for attainment of even smaller body size, it might be achievable by only slight modification of the body plan, such as a snake with a stouter body shape.

In summary, miniaturization in animals is intimately tied to the allometry of morphology, physiology, and reproduction. The fact that the smallest species in each of nearly every major group of tetrapods produces only one offspring suggests the reproductive constraint may be the most important, and that they are at or near the lower limit of body size.

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Appendix 1. Interspecific variation in clutch size and egg shape (length/width) for 193 species of snakes. Measurements (mm) were taken before oviposition (po) or after oviposition (o).

Species	Clutch size	Egg length	Egg width	Egg shape	Po/o	Reference
<i>Achalinus spinalis</i> Peters	7	19.0	7.0	2.714	po	(Pope, 1935)
<i>Adenorhinos barbouri</i> Loveridge	10	10.0	6.0	1.667	o	(Spawls <i>et al.</i> , 2002)
<i>Ahaetulla prasina</i> Boie	3	33.3	10.9	3.055	po	(Pope, 1935)
<i>Amblyodipsas polylepis</i> Bocage	7	30.0	15.0	2.000	o	(Spawls <i>et al.</i> , 2002)
<i>Ambylodipsas concolor</i> Smith	11	29.0	16.0	1.813	o	(Branch, 1988)
<i>Ambylodipsas unicolor</i> Reinhardt	7	32.5	15.0	2.167	o	(Pitman, 1974)
<i>Amphiesma craspedogaster</i> Boulenger	5	29.5	8.8	3.371	po	(Pope, 1929)
<i>Amphiesma stolatum</i> Linnaeus	6	22.0	9.0	2.444	po	(Pope, 1935)
<i>Aparallactus capensis</i> Smith	2	31.0	4.0	7.750	po	(Loveridge, 1942)
<i>Aparallactus lunulatus</i> Peters	3	30.0	5.0	6.000	o	(Spawls <i>et al.</i> , 2002)
<i>Aparallactus modestus</i> Günther	7	25.0	8.0	3.125	po	(Loveridge, 1942)
<i>Arizona elegans</i> Kennicott	3	60.0	16.3	3.681	o	(Reynolds, 1943)
<i>Aspidura copei</i> Günther	21	18.8	12.5	1.500	po	(Wall, 1921)
<i>Atractaspis congica</i> Peters	3	62.0	12.0	5.167	po	(Branch, 1988)
<i>Bogertophis subocularis</i> Brown	7	53.3	28.1	1.894	o	(Campbell, 1972)
<i>Boiga blandingii</i> Hallowell	9	40.0	20.0	2.000	o	(Broadley <i>et al.</i> , 2003)
<i>Boiga cynodon</i> Boie	7	52.0	24.6	2.114	o	(Quinn & Neitman, 1978)
<i>Boiga kraepelini</i> Stejneger	14	40.0	17.0	2.353	o	(Pope, 1935)
<i>Boiga multomaculata</i> Boie	5.5	28.5	8.5	3.353	po	(Pope, 1935)

<i>Boiga pulverulenta</i> Fischer	3	32.5	8.0	4.063	po	(Pitman, 1974)
<i>Bothrophthalmus lineatus</i> Peters	5	40.0	20.0	2.000	po	(Spawls <i>et al.</i> , 2002)
<i>Bungarus multicinctus</i> Blyth	4	31.0	7.0	4.429	po	(Pope, 1935)
<i>Calamaria septentrionalis</i> Boulenger	2	22.0	5.0	4.400	po	(Pope, 1935)
<i>Carphophis amoenus</i> Say	4	15.0	6.0	2.500	po	(Wright & Wright, 1957)
<i>Causus bilineatus</i> Boulenger	8	18.0	14.0	1.286	po	(Broadley <i>et al.</i> , 2003)
<i>Causus lichtensteinii</i> Jan	8	10.0	5.0	2.000	po	(Pitman, 1974)
<i>Causus resimus</i> Peters	9	12.0	5.0	2.400	po	(Pitman, 1974)
<i>Causus rhombeatus</i> Lichtenstein	8	15.5	8.0	1.938	po	(Loveridge, 1955)
<i>Cemophora coccinea</i> Blumenbach	6	28.3	10.1	2.802	o	(Palmer & Tregumbo, 1970)
<i>Chilorhinophis gerardi</i> Boulenger	6	30.0	6.0	5.000	po	(Branch, 1988)
<i>Chironius grandisquamis</i> Peters	15	39.0	26.0	1.500	po	(Savage, 2002)
<i>Coluber constrictor</i> Linnaeus	15.2	29.3	18.2	1.608	o	(Fitch, 1963)
<i>Coniophanes imperialis</i> Baird	4.5	21.5	9.5	2.263	o	(Wright & Wright, 1957)
<i>Conopsis vittatus</i> Peters	6	32.0	13.1	2.443	o	(Werler, 1970)
<i>Crotaphopeltis barotseensis</i> Broadley	9.5	19.0	11.0	1.727	o	(Broadley <i>et al.</i> , 2003)
<i>Crotaphopeltis hotamboeia</i> Laurenti	6	27.0	11.0	2.455	po	(Loveridge, 1942)
<i>Cyclophiops major</i> Günther	8	29.5	13.8	2.145	po	(Pope, 1935)
<i>Dasypeltis atra</i> Sternfeld	14	17.0	8.0	2.125	po	(Pitman, 1974)
<i>Dasypeltis fasciata</i> Smith	5	43.0	10.0	4.300	po	(Pitman, 1974)
<i>Dasypeltis scabra</i> Linnaeus	13.5	37.0	18.8	1.973	po	(Pitman, 1974)
<i>Dendrelaphis caudolineatus</i> Gray	3	41.0	10.0	4.100	po	(Wall, 1921)
<i>Dendrelaphis pictis</i> Gmelin	5	32.0	9.0	3.556	o	(Pope, 1935)
<i>Dendroaspis polylepis</i> Günther	13	70.0	35.0	2.000	o	(Branch, 1988)
<i>Diadophis punctatus</i> Linnaeus	4.25	27.9	8.4	3.314	o	(Blanchard, 1936)
<i>Dinodon orientale</i> Hilgendorf	2	41.0	8.0	5.125	po	(Fukada, 1965)
<i>Dinodon rufozontum</i> Cantor	7	38.7	15.3	2.529	o	(Simmons, 1977)
<i>Dipsadoboa aulica</i> Günther	7.5	25.5	11.5	2.217	o	(Branch, 1988)
<i>Dispholidus typus</i> Smith	12	40.0	20.0	2.000	o	(Branch, 1988)
<i>Dromophis lineatus</i> Duméril, Bibron & Duméril	9	25.0	15.0	1.667	po	(Pitman, 1974)
<i>Drymarchon corais</i> Boie	9	65.1	37.3	1.745	o	(Groves, 1960)
<i>Drymobius margaritiferus</i> Schlegel	7	35.7	13.0	2.746	o	(Werler, 1949)
<i>Duberria lutrix</i> Linnaeus	12	10.0	7.0	1.429	po	(Pitman, 1974)
<i>Echis carinatus</i> Schneider	21	17.0	11.0	1.545	po	(Mendelssohn, 1965)
<i>Elaphe carinata</i> Günther	12	47.7	29.5	1.617	o	(Pope, 1935)
<i>Elaphe dione</i> Pallas	8	28.5	15.0	1.900	po	(Pope, 1935)
<i>Elapsoidea loveridgei</i> Parker	2	40.0	10.0	4.000	po	(Pitman, 1974)
<i>Elapsoidea sundevallii</i> Smith	6	21.3	7.5	2.833	po	(Loveridge, 1955)
<i>Farancia abacura</i> Holbrook	40	35.0	25.0	1.400	o	(Wright & Wright, 1957)
<i>Farancia erythrogramma</i> Palissot De Beauvois	22	37.0	29.0	1.276	po	(Wright & Wright, 1957)
<i>Hapsidophrys smaragdina</i> Schlegel	3	56.0	12.0	4.667	po	(Pitman, 1974)
<i>Gongylsoma scripta</i> Theobald	4	24.9	9.9	2.510	o	(Pongsapipatana, 1975)

<i>Grayia smithii</i> Leach	18	46.0	25.0	1.840	po	(Pitman, 1974)
<i>Haplocercus ceylonensis</i> Günther	2	31.0	5.0	6.200	po	(Wall, 1921)
<i>Hapsidophrys lineatus</i> Fischer	2	25.0	6.0	4.167	po	(Loveridge, 1942)
<i>Hemirhagerrhis nototaenia</i> Günther	2	17.5	3.3	5.385	po	(Loveridge, 1955)
<i>Heterodon nasicus</i> Baird & Girard	7	32.1	19.4	1.655	o	(Platt, 1969)
<i>Heterodon platirhinos</i> Latreille	22	27.0	18.0	1.500	o	(Edgren, 1955)
<i>Hierophis spinalis</i> Peters	9	38.0	11.0	3.455	po	(Pope, 1935)
<i>Hypsiglena torquata</i> Günther	3	45.3	12.0	3.775	o	(Vitt, 1975)
<i>Lachesis muta</i> Linnaeus	11	80.0	40.0	2.000	o	(Amaral, 1926)
<i>Lampropeltis calligaster</i> Harlan	11	37.9	21.1	1.796	o	(Shoop, 1957)
<i>Lampropeltis getula</i> Linnaeus	10	37.0	18.0	2.056	o	(Gloyd, 1928)
<i>Lampropeltis mexicana</i> Garman	7	39.0	20.0	1.950	o	(Murphy <i>et al.</i> , 1978)
<i>Lampropeltis triangulum</i> Lacépède	6	35.0	10.0	3.500	o	(Gloyd, 1928)
<i>Lampropeltis zonata</i> Lockington	4	41.0	17.0	2.412	o	(Tryon & Murphy, 1982)
<i>Lamprophis fuliginosus</i> Boie	11	24.0	14.0	1.714	po	(Broadley <i>et al.</i> , 2003)
<i>Lamprophis lineatus</i> Duméril, Bibron & Duméril	5	28.0	12.0	2.333	po	(Loveridge, 1936)
<i>Leioheterodon madagascariensis</i> Duméril & Bibron	10	53.3	32.0	1.666	o	(Campbell & Murphy, 1977)
<i>Leptodeira annulata</i> Linnaeus	7	28.9	12.0	2.408	o	(Haines, 1940)
<i>Leptophis ahaetulla</i> Linnaeus	3	24.9	6.9	3.609	po	(Sexton & Heatwole, 1965)
<i>Leptotyphlops blanfordi</i> Boulenger	1	25.0	2.5	10.000	po	(Fitch, 1970)
<i>Leptotyphlops carlae</i> Hedges	1	13.7	2.2	6.227	po	This study
<i>Leptotyphlops dulcis</i> Baird & Girard	7	15.0	4.5	3.333	po	(Wright & Wright, 1957)
<i>Leptotyphlops humilis</i> Baird & Girard	4	15.0	4.5	3.333	po	(Klauber, 1940)
<i>Leptotyphlops longicaudus</i> Peters	2	21.0	4.0	5.250	po	(Fitch, 1970)
<i>Letheobia caeca</i> Duméril	6	22.0	8.0	2.750	o	(Bogert, 1940)
<i>Limnophis bicolor</i> Günther	5	28.0	15.0	1.867	po	(Broadley <i>et al.</i> , 2003)
<i>Liophis epinephalus</i> Cope	7	19.3	7.5	2.573	po	(Sexton & Heatwole, 1965)
<i>Liophis reginae</i> Linnaeus	3	29.3	11.8	2.496	po	(Test <i>et al.</i> , 1966)
<i>Lycodon ruhstrati</i> Fischer	4	33.0	8.0	4.125	po	(Pope, 1935)
<i>Lycodon subcinctus</i> Reinwardt	5	35.5	12.8	2.784	o	(Pope, 1935)
<i>Lycophidion capense</i> Smith	4	23.0	8.0	2.875	po	(Loveridge, 1942)
<i>Lycophidion laterale</i> Hallowell	3	33.0	12.0	2.750	po	(Spawls <i>et al.</i> , 2002)
<i>Lycophidion nanus</i> Broadley	2	26.0	6.0	4.333	o	(Branch, 1988)
<i>Lycophidion ornatum</i> Parker	5	21.0	5.0	4.200	po	(Pitman, 1974)
<i>Macropisthodon plumbicolor</i> Cantor	7	36.0	21.0	1.714	o	(Wall, 1921)
<i>Madagascarophis colubrinus</i> Schlegel	6	38.0	19.0	2.000	o	(Campbell, 1972)
<i>Masticophis bilineatus</i> Jan	6	54.0	19.2	2.813	o	(Vitt, 1975)
<i>Masticophis flagellum</i> Shaw	9	35.0	21.0	1.667	o	(Cunningham, 1959)
<i>Masticophis lateralis</i> Hallowell	6	47.0	16.5	2.848	o	(Cunningham, 1959)
<i>Masticophis mentovarius</i> Duméril, Bibron & Duméril	17	55.1	30.7	1.795	o	(Werler, 1951)
<i>Masticophis taeniatus</i> Hallowell	4	63.0	14.0	4.500	po	(Johnson <i>et al.</i> , 1948)

<i>Mehelya poensis</i> Smith	8	25.0	10.0	2.500	po	(Spawls <i>et al.</i> , 2002)
<i>Meizodon regularis</i> Fischer	4	35.0	6.0	5.833	po	(Spawls <i>et al.</i> , 2002)
<i>Meizodon semiornatus</i> Peters	2.5	35.0	10.0	3.500	o	(Broadley <i>et al.</i> , 2003)
<i>Micruroides euryxanthus</i> Kennicott	2	36.8	6.2	5.984	po	(Funk, 1964)
<i>Micrurus fulvius</i> Linnaeus	6.5	30.3	11.5	2.635	o	(Sabath & Worthington, 1959)
<i>Micrurus mipartitus</i> Duméril, Bibron & Duméril	18	22.0	13.0	1.692	o	(Savage, 2002)
<i>Naja melanoleuca</i> Hallowell	17	61.5	30.5	2.017	o	(Pitman, 1974)
<i>Naja mossambica</i> Peters	16	35.0	20.0	1.750	o	(Spawls <i>et al.</i> , 2002)
<i>Naja naja</i> Linnaeus	16	56.3	26.1	2.157	o	(Campbell & Quinn, 1975)
<i>Naja nigricollis</i> Reinhardt	10	35.0	17.0	2.059	o	(Pitman, 1974)
<i>Natriciteres olivaceae</i> Peters	7	22.0	9.0	2.444	o	(Branch, 1988)
<i>Ninia sebae</i> Duméril, Bibron & Duméril	2	25.8	6.2	4.195	po	(Greene, 1975)
<i>Oligodon arnensis</i> Shaw	4.5	36.0	10.0	3.600	o	(Daniel, 1983)
<i>Oligodon cinereus</i> Günther	8	19.0	10.0	1.900	po	(Pope, 1935)
<i>Ophedrys aestivus</i> Linnaeus	6	26.0	10.0	2.600	o	(Anderson, 1965)
<i>Ophedrys vernalis</i> Harlan	18	18.6	12.0	1.550	o	(Fritts, 1968)
<i>Ophiophagus hannah</i> Cantor	41	59.5	34.3	1.732	o	(Oliver, 1956)
<i>Opisthotropis latouchii</i> Boulenger	2	34.0	6.0	5.667	po	(Pope, 1935)
<i>Orthriophis moellendorffi</i> Boettger	6	64.6	27.3	2.366	o	(Henderson, 1975)
<i>Orthriophis taeniura</i> Cope	13	36.0	24.0	1.500	po	(Pope, 1935)
<i>Ovophis okinavensis</i> Boulenger	6	38.6	22.6	1.710	o	(Fukada, 1964)
<i>Oxybelis aeneus</i> Wagler	4	39.3	11.3	3.478	po	(Dixon & Soini, 1977)
<i>Oxybelis brevirostris</i> Cope	3	28.7	9.3	3.086	po	(Sexton & Heatwole, 1965)
<i>Oxyrhopus petola</i> Linnaeus	10	32.5	18.5	1.757	o	(Savage, 2002)
<i>Pantherophis guttatus</i> Linnaeus	8	34.8	19.0	1.832	o	(Bechtel & Bechtel, 1958)
<i>Pantherophis obsoletus</i> Say	15	44.3	28.1	1.575	o	(Wright & Wright, 1957)
<i>Pantherophis vulpinus</i> Baird & Girard	15	44.0	24.0	1.833	o	(Wright & Wright, 1957)
<i>Pareas stanleyi</i> Boulenger	6	19.0	8.0	2.375	po	(Pope, 1935)
<i>Philothamnus heterolepidotus</i> Günther	5	21.0	12.0	1.750	po	(Broadley <i>et al.</i> , 2003)
<i>Philothamnus hoplogaster</i> Günther	6	30.0	10.0	3.000	po	(Loveridge, 1942)
<i>Philothamnus irregularis</i> Leach	6	31.0	9.0	3.444	po	(Bogert, 1940)
<i>Philothamnus punctatus</i> Peters	5	30.0	10.0	3.000	po	(Spawls <i>et al.</i> , 2002)
<i>Philothamnus semivariiegatus</i> Smith	4	30.0	8.0	3.750	po	(Pitman, 1974)
<i>Phyllorhynchus decurtatus</i> Cope	2.5	36.0	9.0	4.000	po	(Klauber, 1935)
<i>Pituophis melanoleucus</i> Daudin	12	55.1	35.9	1.535	o	(Anderson, 1965)
<i>Plagiopholis styani</i> Boulenger	7	15.5	5.5	2.818	po	(Pope, 1935)
<i>Prosymna pitmani</i> Battersby	4	23.0	8.0	2.875	o	(Spawls <i>et al.</i> , 2002)
<i>Prosymna ruspolii</i> Boulenger	3.5	28.0	7.0	4.000	o	(Spawls <i>et al.</i> , 2002)
<i>Prosymna ambigua</i> Bocage	3.5	30.0	7.0	4.286	o	(Broadley <i>et al.</i> , 2003)
<i>Psammophis angolensis</i> Bocage	4	16.5	5.0	3.300	po	(Loveridge, 1955)
<i>Psammophis notosticus</i> Peters	3	28.0	6.0	4.667	po	(Branch, 1988)

<i>Psammophis punctulatus</i> Duméril & Bibron	6.5	32.0	13.0	2.462	po	(Pitman, 1974)
<i>Psammophis sibilans</i> Linnaeus	17	30.0	22.0	1.364	o	(Pitman, 1974)
<i>Psammophylax variabilis</i> Günther	7	16.0	5.0	3.200	po	(Loveridge, 1942)
<i>Pseudaspis cana</i> Linnaeus	41	35.0	25.0	1.400	po	(Bogert, 1940)
<i>Pseudohaje goldii</i> Boulenger	15	50.0	25.0	2.000	o	(Spawls <i>et al.</i> , 2002)
<i>Pseudoxenodon macrops</i> Blyth	3	47.0	13.0	3.615	po	(Pope, 1935)
<i>Ptyas dhummades</i> Cantor	10	47.0	15.0	3.133	po	(Pope, 1935)
<i>Ptyas korros</i> Schlegel	9	36.0	18.0	2.000	o	(Pope, 1935)
<i>Ptyas mucosa</i> Linnaeus	12	65.0	29.0	2.241	o	(Pope, 1935)
<i>Python anchietae</i> Bocage	5	62.0	37.0	1.676	o	(Branch, 1988)
<i>Python curtus</i> Schlegel	16	67.0	44.0	1.523	o	(Noble, 1935)
<i>Python molurus</i> Linnaeus	35	98.0	63.5	1.543	o	(Van Mierop & Barnard, 1976)
<i>Python regius</i> Shaw	7	85.0	55.0	1.545	o	(Spawls <i>et al.</i> , 2002)
<i>Python reticulatus</i> Schneider	16	43.0	23.5	1.830	o	(Pope, 1961)
<i>Python sebae</i> Gmelin	40	90.0	60.0	1.500	o	(Pitman, 1974)
<i>Python timorensis</i> Peters	8	93.0	49.0	1.898	o	(Murphy <i>et al.</i> , 1978)
<i>Ramphotyphlops braminus</i> Daudin	2.5	14.5	3.5	4.143	o	(Fukada, 1965)
<i>Rhabdophis nuchalis</i> Boulenger	19	11.0	5.0	2.200	po	(Pope, 1935)
<i>Rhabdophis subminiatus</i> Schlegel	15	20.0	11.0	1.818	po	(Pope, 1935)
<i>Rhabdophis tigrinus</i> Boie	5	32.0	12.0	2.667	po	(Pope, 1935)
<i>Taeniophallus brevirostris</i> Peters	2	24.4	5.3	4.604	po	(Dixon & Soini, 1977)
<i>Rhadinaea calligaster</i> Cope	2	30.8	7.5	4.107	po	(Savage, 2002)
<i>Rhadinaea flavilata</i> Cope	2.5	26.7	6.5	4.108	po	(Myers, 1967)
<i>Rhamnophis aethiopissa</i> Günther	17	35.0	15.0	2.333	o	(Spawls <i>et al.</i> , 2002)
<i>Rhamphiophis oxyrhynchus</i> Reinhardt	10	40.0	20.0	2.000	o	(Pitman, 1974)
<i>Rhinocheilus lecontei</i> Baird & Girard	8	20.0	7.0	2.857	po	(Conant & Downs, 1940)
<i>Rhinotyphlops schlegelii</i> Bianconi	37	17.0	10.0	1.700	po	(Broadley, 1959)
<i>Salvadora hexalepis</i> Cope	5	19.2	7.2	2.672	po	(Tanner, 1941)
<i>Senticolis triaspis</i> Cope	5	52.3	22.0	2.377	o	(Werler, 1970)
<i>Sibynophis collaris</i> Gray	2	35.0	6.0	5.833	po	(Pope, 1935)
<i>Sinomicrurus japonicus</i> Günther	3	36.1	9.6	3.760	o	(Fukada, 1965)
<i>Sinomicrurus kelloggi</i> Pope	14	18.0	9.0	2.000	po	(Pope, 1935)
<i>Sinomicrurus macclellandi</i> Reinhardt	6	33.3	10.9	3.055	po	(Pope, 1935)
<i>Sinonatrix percarinata</i> Boulenger	7	32.5	17.5	1.857	o	(Pope, 1935)
<i>Sonora semiannulata</i> Baird & Girard	4	25.1	8.1	3.085	o	(Staedeli, 1964)
<i>Tantilla coronata</i> Baird & Girard	3	22.5	5.3	4.245	po	(Neill & Boyles, 1957)
<i>Tantilla gracilis</i> Baird & Girard	2.5	22.8	5.1	4.515	o	(Carpenter, 1958a)
<i>Tantilla melanocephala</i> Linnaeus	3	27.3	7.0	3.904	po	(Dixon & Soini, 1977)
<i>Thelotornis kirtlandii</i> Hallowell	6	36.0	13.5	2.667	po	(Pitman, 1974)
<i>Tretanorhinus variabilis</i> Duméril, Bibron & Duméril	8	35.0	16.8	2.090	o	(Petzold, 1967)
<i>Trimorphodon biscutatus</i> Duméril, Bibron & Duméril	15	32.5	20.9	1.555	o	(Werler, 1970)

<i>Typhlops angolensis</i> Bocage	9	27.0	14.0	1.929	o	(Loveridge, 1942)
<i>Typhlops bibronii</i> Smith	5	23.0	9.0	2.556	po	(Bogert, 1940)
<i>Typhlops punctatus</i> Leach	14.5	13.5	6.0	2.250	po	(Loveridge, 1942)
<i>Vipera xanthina</i> Gray	13.3	35.8	21.8	1.642	po	(Mendelssohn, 1963)
<i>Xenocalamus bicolor</i> Günther	2	28.0	6.0	4.667	po	(Branch & Patterson, 1976)
<i>Xenocalamus transvaalensis</i> Methuen	2	28.0	6.0	4.667	o	(Branch, 1988)
<i>Xenochrophis piscator</i> Schneider	91	27.0	18.0	1.500	o	(Daniel, 1983)
<i>Xenoxybelis argenteus</i> Daudin	6	32.7	12.8	2.555	o	(Duellman, 1978)

Appendix 2. Intraspecific variation in clutch size and egg shape (length/width) for four species (82 individuals) of snakes. Measurements (mm) were taken before oviposition (po) or after oviposition (o).

Species	Clutch size	Egg length	Egg width	Egg shape	Po/o	Reference
<i>Coluber constrictor</i>	7	44.7	17.9	2.497	o	(Wright & Wright, 1957)
<i>Coluber constrictor</i>	14	33.4	19.6	1.704	o	(Wright & Wright, 1957)
<i>Coluber constrictor</i>	32	27.8	18.5	1.503	o	S. B. Hedges, personal observation
<i>Coluber constrictor</i>	14	32.4	21.3	1.521	o	(Gillingham, 1976)
<i>Coluber constrictor</i>	14	32.2	19.9	1.618	o	(Munro, 1948)
<i>Coluber constrictor</i>	5	38.2	18.0	2.122	o	(Munro, 1948)
<i>Coluber constrictor</i>	11	35.0	20.0	1.750	o	(Carpenter, 1958b)
<i>Coluber constrictor</i>	6	43.7	15.7	2.783	o	(van de Velde <i>et al.</i> , 1962)
<i>Coluber constrictor</i>	17	26.5	17.0	1.559	o	(Fitch, 1963)
<i>Coluber constrictor</i>	8	33.3	16.3	2.043	o	(Fitch, 1963)
<i>Coluber constrictor</i>	12	29.1	17.1	1.702	o	(Fitch, 1963)
<i>Coluber constrictor</i>	14	26.9	19.2	1.401	o	(Fitch, 1963)
<i>Coluber constrictor</i>	10	31.7	16.5	1.921	o	(Fitch, 1963)
<i>Coluber constrictor</i>	11	29.7	16.7	1.778	o	(Fitch, 1963)
<i>Coluber constrictor</i>	21	28.9	18.4	1.571	o	(Fitch, 1963)
<i>Coluber constrictor</i>	13	30.7	19.3	1.591	o	(Fitch, 1963)
<i>Coluber constrictor</i>	18	29.0	17.9	1.620	o	(Fitch, 1963)
<i>Coluber constrictor</i>	12	30.3	17.8	1.702	o	(Fitch, 1963)
<i>Coluber constrictor</i>	14	30.9	19.4	1.593	o	(Fitch, 1963)
<i>Coluber constrictor</i>	18	28.3	20.3	1.394	o	(Werler, 1970)
<i>Coluber constrictor</i>	27	25.4	18.7	1.358	o	(Werler, 1970)
<i>Coluber constrictor</i>	18	28.9	20.2	1.431	o	(Werler, 1970)
<i>Pantherophis obsoletus</i>	15	44.3	28.1	1.577	o	(Wright & Wright, 1957)
<i>Pantherophis obsoletus</i>	7	65.8	25.3	2.601	o	(Wright & Wright, 1957)
<i>Pantherophis obsoletus</i>	9	44.0	23.5	1.872	o	(Wright & Wright, 1957)
<i>Pantherophis obsoletus</i>	9	40.0	18.5	2.162	o	(Wright & Wright, 1957)
<i>Pantherophis obsoletus</i>	41	32.5	19.5	1.667	o	(Wright & Wright, 1957)
<i>Pantherophis obsoletus</i>	8	49.7	22.9	2.170	o	(Wright & Wright, 1957)
<i>Pantherophis obsoletus</i>	5	56.0	24.7	2.267	o	(Brecke <i>et al.</i> , 1976)
<i>Pantherophis obsoletus</i>	4	57.5	22.7	2.533	o	(Brecke <i>et al.</i> , 1976)

<i>Pantherophis obsoletus</i>	13	34.0	16.0	2.125	o	(Cohen, 1978)
<i>Pantherophis obsoletus</i>	10	39.0	18.0	2.167	o	(Cohen, 1978)
<i>Pantherophis obsoletus</i>	18	52.6	31.0	1.697	o	(McCallion, 1945)
<i>Pantherophis obsoletus</i>	12	42.2	20.6	2.049	o	(Mansueti, 1946)
<i>Pantherophis obsoletus</i>	12	37.6	21.6	1.741	o	(Mansueti, 1946)
<i>Pantherophis obsoletus</i>	8	51.0	25.0	2.040	o	(Shuette, 1978)
<i>Pantherophis obsoletus</i>	5	70.2	19.6	3.582	o	(Werler, 1951)
<i>Pantherophis obsoletus</i>	17	42.7	23.0	1.857	o	(Netting, 1927)
<i>Pantherophis obsoletus</i>	19	46.0	23.5	1.957	o	(Anderson, 1965)
<i>Lampropeltis triangulum</i>	5	50.0	19.5	2.564	o	(Werler, 1949)
<i>Lampropeltis triangulum</i>	12	24.0	14.0	1.714	o	(Marr, 1944)
<i>Lampropeltis triangulum</i>	6	35.0	10.0	3.500	o	(Gloyd, 1928)
<i>Lampropeltis triangulum</i>	2	27.5	7.0	3.929	o	S. B. Hedges, personal observation
<i>Lampropeltis triangulum</i>	5	23.4	9.1	2.571	o	S. B. Hedges, personal observation
<i>Lampropeltis triangulum</i>	13	27.5	17.0	1.618	o	(Blanchard, 1928)
<i>Lampropeltis triangulum</i>	5	27.3	10.8	2.528	o	(Groves & Assetto, 1976)
<i>Lampropeltis triangulum</i>	4	53.2	18.0	2.956	o	(Tryon & Hulsey, 1976)
<i>Lampropeltis triangulum</i>	3	48.0	18.3	2.623	o	(Tryon & Hulsey, 1976)
<i>Lampropeltis triangulum</i>	4	51.2	19.7	2.599	o	(Tryon & Hulsey, 1976)
<i>Lampropeltis triangulum</i>	5	47.6	17.4	2.736	o	(Tryon & Hulsey, 1976)
<i>Lampropeltis triangulum</i>	4	23.7	10.4	2.279	o	(Herman, 1979)
<i>Lampropeltis triangulum</i>	5	32.4	14.9	2.174	o	(Fitch & Fleet, 1970)
<i>Lampropeltis triangulum</i>	5	33.0	13.1	2.519	o	(Fitch & Fleet, 1970)
<i>Lampropeltis triangulum</i>	7	31.6	13.9	2.273	o	(Fitch & Fleet, 1970)
<i>Lampropeltis triangulum</i>	5	49.2	19.6	2.510	o	(Werler, 1951)
<i>Lampropeltis triangulum</i>	11	34.0	16.1	2.112	o	(Condit & Woodruff, 1955)
<i>Lampropeltis triangulum</i>	5	51.6	17.2	3.000	o	(Werler, 1970)
<i>Lampropeltis triangulum</i>	8	41.0	20.0	2.050	o	(Tryon & Murphy, 1982)
<i>Lampropeltis triangulum</i>	4	55.0	17.0	3.235	o	(Tryon & Murphy, 1982)
<i>Lampropeltis triangulum</i>	4	41.0	14.0	2.929	o	(Tryon & Murphy, 1982)
<i>Lampropeltis triangulum</i>	5	53.0	17.0	3.118	o	(Tryon & Murphy, 1982)
<i>Lampropeltis triangulum</i>	4	60.0	20.5	2.927	o	(Tryon & Murphy, 1982)
<i>Lampropeltis triangulum</i>	7	26.1	12.2	2.139	o	(Tryon & Murphy, 1982)
<i>Lampropeltis triangulum</i>	6	44.0	19.0	2.316	o	(Tryon & Murphy, 1982)
<i>Lampropeltis triangulum</i>	6	44.0	21.0	2.095	o	(Tryon & Murphy, 1982)
<i>Lampropeltis triangulum</i>	4	52.0	19.0	2.737	o	(Tryon & Murphy, 1982)
<i>Lampropeltis triangulum</i>	9	56.7	23.5	2.413	o	(Tryon & Murphy, 1982)
<i>Lampropeltis triangulum</i>	7	45.0	21.0	2.143	o	(Tryon & Murphy, 1982)
<i>Lampropeltis triangulum</i>	4	43.0	19.0	2.263	o	(Smith, 1977)
<i>Lampropeltis triangulum</i>	5	38.0	16.0	2.375	o	(Iverson, 1977)
<i>Lampropeltis triangulum</i>	5	34.0	14.0	2.429	o	(Iverson, 1975)
<i>Diadophis punctatus</i>	5	19.6	9.2	2.130	po	(Wright & Wright, 1957)
<i>Diadophis punctatus</i>	4	16.0	6.0	2.667	o	(Wright & Wright, 1957)
<i>Diadophis punctatus</i>	5	19.2	7.2	2.667	po	(Wright & Wright, 1957)

<i>Diadophis punctatus</i>	3	44.0	11.3	3.894	o	(Blanchard, 1936)
<i>Diadophis punctatus</i>	5	23.2	7.6	3.069	o	(Blanchard, 1936)
<i>Diadophis punctatus</i>	5	24.3	8.0	3.022	o	(Blanchard, 1936)
<i>Diadophis punctatus</i>	5	21.3	9.9	2.156	o	(Blanchard, 1936)
<i>Diadophis punctatus</i>	5	23.9	7.5	3.187	o	(Blanchard, 1936)
<i>Diadophis punctatus</i>	7	19.7	8.3	2.373	o	(Blanchard, 1936)
<i>Diadophis punctatus</i>	2	35.6	7.3	4.910	o	(Blanchard, 1936)
<i>Diadophis punctatus</i>	2	31.2	7.6	4.132	o	(Blanchard, 1936)

Appendix 3. Clutch size and egg shape (length/width) data for four species of snakes showing variation among clutches of the same female snake. Measurements (mm) were taken before oviposition (po) or after oviposition (o).

Species	Clutch size	Egg length	Egg width	Egg Shape	Po/o	Reference
<i>Elaphe climacophora</i> , Female A	4	67.2	21.5	3.125	o	(Fukada, 1978)
<i>Elaphe climacophora</i> , Female A	3	85.4	21.6	3.854	o	(Fukada, 1978)
<i>Elaphe climacophora</i> , Female A	5	57.1	22.2	2.572	o	(Fukada, 1978)
<i>Elaphe climacophora</i> , Female A	5	58.2	21.3	2.732	o	(Fukada, 1978)
<i>Elaphe climacophora</i> , Female A	2	89.2	22.3	4.000	o	(Fukada, 1978)
<i>Lampropeltis mexicana</i> , female C	8	42.2	21.2	1.991	o	(Tryon & Murphy, 1982)
<i>Lampropeltis mexicana</i> , female C	10	41.6	21.9	1.900	o	(Tryon & Murphy, 1982)
<i>Lampropeltis mexicana</i> , female C	5	50.8	20.0	2.540	o	(Tryon & Murphy, 1982)
<i>Lampropeltis mexicana</i> , female D	3	56.0	20.0	2.800	o	(Tryon & Murphy, 1982)
<i>Lampropeltis mexicana</i> , female D	9	37.6	20.0	1.880	o	(Tryon & Murphy, 1982)
<i>Lampropeltis triangulum</i> , Female A	7	48.0	22.0	2.182	o	(Tryon & Murphy, 1982)
<i>Lampropeltis triangulum</i> , Female A	8	41.0	20.0	2.050	o	(Tryon & Murphy, 1982)
<i>Lampropeltis triangulum</i> , Female B	8	44.0	21.0	2.095	o	(Tryon & Murphy, 1982)
<i>Lampropeltis triangulum</i> , Female B	4	55.0	17.0	3.235	o	(Tryon & Murphy, 1982)
<i>Naja melanoleuca</i> , Female A	11	58.5	28.2	2.074	o	(Tryon, 1979)
<i>Naja melanoleuca</i> , Female A	14	60.6	31.6	1.918	o	(Tryon, 1979)
<i>Naja melanoleuca</i> , Female A	18	60.9	32.0	1.903	o	(Tryon, 1979)
<i>Naja melanoleuca</i> , Female A	20	57.4	31.8	1.805	o	(Tryon, 1979)