

Diversity and evolution of macrohabitat use, body size and morphology in a monophyletic group of Neotropical pitvipers (*Bothrops*)

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(Accepted 16 October 2000)

Abstract

The Neotropical pitviper genus *Bothrops* comprises about 40 species, which occur in all main ecosystems of cis-Andean South America. We explored the relationships of body size and form (tail length and stoutness) with macrohabitat use in 20 forms of *Bothrops*. Semi-arboreal habits appeared only in forest forms. Semi-arboreals are significantly more slender and have longer tails than terrestrials; body size is not significantly different between terrestrials and semi-arboreals. Within *Bothrops*, independent contrasts for macrohabitat use were significantly correlated with contrasts of tail size (positively) and stoutness (negatively); thus, the more arboreal the species, the longer its tail and the more slender its body. Contrasts of adult body size seems to remain constant over the lower range of macrohabitat use, but to decrease in species of *Bothrops* which are more arboreal. Reconstructions of character states indicate that: (1) the ancestor of *Bothrops* was a small, stout, terrestrial species; (2) semi-arboreal habits appeared one to three times in the genus; (3) a decrease in stoutness and an increase in tail length occurred along with an increase in arboreality in some clades. Although macrohabitat use seems to be important in determining body form in *Bothrops*, our results also indicate that tail size, stoutness and body size may also be affected by selective agents other than macrohabitat use. The selective agents responsible for the shifts in macrohabitat use in *Bothrops* are still uncertain, although they may have included prey availability and/or predation pressure. The plasticity of macrohabitat use, morphology and body size described in this study may have been key features that facilitated the highly successful ecological diversification of *Bothrops* in South America.

Key words: Serpentes, Viperidae, ecomorphology, macrohabitat

INTRODUCTION

The way that an animal uses the available macrohabitats (cf. Cadle & Greene, 1993), and its physical implications, is thought to strongly influence the evolution of body form in vertebrates (e.g. Moermond, 1979; Miles & Ricklefs, 1984; Wikramanayake, 1990). Even in limbless, elongate vertebrates such as snakes, closely related species may be included in different morphological syndromes depending on which macrohabitat is explored (see e.g. Vitt & Vangilder, 1983; Guyer & Donnelly, 1990; Cadle & Greene, 1993; Lillywhite & Henderson, 1993). Lillywhite & Henderson (1993) summarized the morphological changes associated with arboreality in snakes (see also Parker & Grandison, 1986). For example, arboreal snakes generally have a small mass/length ratio, laterally compressed body, long tail, large eye, enlarged vertebral scale row and the centre of gravity shifted posteriorly.

The implications of habitat use in the body form of snakes may be better approached by analysing monophyletic groups where these characters could be interpreted under an evolutionary framework (see e.g. Brooks & McLennan, 1991, 1994; Harvey & Pagel, 1991). However, all studies on snake ecomorphology (e.g. Kaufman & Gibbons, 1975; Vitt & Vangilder, 1983; Guyer & Donnelly, 1990) have not separated species by lineages, thus, providing results that may include noise resulting from phylogenetic effects. The recent development of comparative methods (see e.g. Brooks & McLennan, 1991, 1994; Harvey & Pagel, 1991; E. P. Martins & Hansen, 1996) allowed the evaluation of hypotheses about the evolution of ecological characters, including those related to morphological changes associated with macrohabitat use in vertebrates (see e.g. Losos, 1994, 1996; Miles, 1994; Klingenberg & Ekau, 1996).

The Neotropical genus *Bothrops* (including

Bothriopsis) is a recent monophyletic assemblage (Wüster, Salomão, Quijada-Mascareñas *et al.*, in press) of about 40 viperid snakes, distributed from Mexico to Argentina (Hoge & Romano, 1972; Hoge & Romano-Hoge, 1981a,b; Rage, 1987; Campbell & Lamar, 1989; Greene, 1992; Salomão *et al.*, 1997). Species of *Bothrops* occupy several types of habitats, from lowland and montane rainforests to grasslands and other dry habitats (Campbell & Lamar, 1989; M. Martins, Marques & Sazima, in press). The genus includes exclusively terrestrial species (e.g. *B. alternatus* and subspecies of *B. newwiedi*), as well as many that use vegetation, from the semi-arboreal *B. jararaca* (Sazima, 1992) to the almost completely arboreal *B. bilineatus* (Duellman, 1978; Dixon & Soini, 1986). In at least some species, juveniles are found more frequently on the vegetation than adults (Sazima, 1992; Campbell, 1998; M. Martins & Oliveira, 1999).

Recent molecular systematics studies indicate that the species of *Bothrops* may be allocated in at least seven monophyletic species groups: *alternatus*, *atrox*, *jararaca*, *jararacussu*, *microphthalmus*, *newwiedi* and *taeniatus* (Salomão *et al.*, 1997, 1999; Parkinson, Campbell & Chippindale, in press; Wüster, Salomão, Quijada-Mascareñas *et al.*, in press). The monophyly of and relationships within the clade formed by the *taeniatus*, *atrox* and *jararacussu* groups is well supported by several studies (Werman, 1992; Wüster, Thorpe *et al.*, 1996; Salomão *et al.*, 1997, 1999; Wüster, Salomão, Thorpe *et al.*, 1997; Wüster, Salomão, Quijada-Mascareñas *et al.*, in press), as well as the basal position of the *microphthalmus* and *alternatus* groups (Salomão *et al.*, 1997, 1999; Gutberlet, 1998b; Parkinson *et al.*, in press; Wüster, Salomão, Quijada-Mascareñas *et al.*, in press). However, the position of the *newwiedi* group within *Bothrops* is still controversial. The *microphthalmus*, *newwiedi* and *alternatus* groups share the absence of a lacunolabial scale (which is present in all other groups); *newwiedi* and *alternatus* appeared together in a study by Werman (1992) using morphological and immunological data. However, in a recent study using molecular data, the *newwiedi* group appears as a sister clade of the *jararaca* group (Wüster, Salomão, Quijada-Mascareñas *et al.*, in press; see also Parkinson *et al.*, in press). Furthermore, a current study on the systematics of the *newwiedi* group indicates that most of its known forms are good species (V. X. da Silva, pers. comm.). Comprehensive studies on the systematics of crotalines (Gutberlet, 1998a,b; Parkinson, 1999; Parkinson *et al.*, in press; see also Werman, 1992) indicate that the clade composed by *Atropoides*, *Cerrophidion* and *Porthidium* is the sister group of *Bothrops* (but see Kraus, Mink & Brown, 1996; Vidal *et al.*, 1999).

In his inspiring approach to the evolution of the Crotalinae, Greene (1992) explored how behaviour and ecology have been associated with morphological diversification within this subfamily. Based on a preliminary phylogenetic hypothesis of the Crotalinae and the high diversity of macrohabitat use, body size and form in this highly successful radiation, Greene (1992) concluded

that early pitvipers were terrestrial snakes and that arboreality has evolved at least three times within this clade. Herein we explore the relationships of body size and form with macrohabitat use within a sub-clade of pitvipers, the lanceheads of the genus *Bothrops*. We addressed the following questions: (1) was the radiation in macrohabitat use followed by shifts in body size, tail length and stoutness in *Bothrops*?; (2) did arboreality evolve once or multiple times within *Bothrops*?; (3) which were the presumed macrohabitat, body size and morphology of the ancestor of *Bothrops*?

METHODS

Because of the presence of hemipenes, male snakes have a limitation to the extent to which their tails may become shorter, for instance when a semi-arboreal lineage becomes increasingly terrestrial. This limitation may add unwanted noise in analyses of relative tail length, and even in relative mass analyses, since a part of the mass of a snake is represented by the mass of its tail. To avoid this problem, we used only female snakes in our analyses, provided that they were not pregnant; for *Bothrops insularis*, we used functional females, despite the presence of hemipenis-like structures (intersexes in Hoge *et al.*, 1961). Furthermore, to avoid eventual problems related to ontogenetic shifts in body form in comparisons among species, samples included specimens from the entire size range of each species. Samples of 15–20 adult females were analysed for 20 forms of *Bothrops*, as well as for *Atropoides nummifer mexicana* (J. A. Campbell, pers. comm.), *Porthidium yucatanicum* (C. L. Parkinson, pers. comm.) and *P. nasutum*. Almost all samples included specimens from several localities within the distribution of each species. For the populations currently assigned to *B. atrox*, the populations of eastern Amazonia were treated separately from those that occur in central Amazonia, based on their molecular distinctiveness (cf. Wüster, Salomão, Thorpe *et al.*, 1997; Wüster, Salomão, Duckett *et al.*, 1999). The same reasoning was applied when treating *B. leucurus* and *B. moojeni* as distinct species from *B. atrox* (see Wüster, Salomão, Thorpe *et al.*, 1997; Wüster, Salomão, Duckett *et al.*, 1999). Populations of *Bothrops* for this study were chosen based on their availability in Brazilian collections. Therefore, only few specimens from outside Brazil were included in the samples. Brazil is the country with the highest diversity of *Bothrops* (Campbell & Lamar, 1989), with members of all species groups. Thus, we assume that the 20 forms chosen for this study are representative of the genus.

For each preserved specimen, we recorded snout–vent length (SVL), tail length (TL), and mass (after draining the excess of preservative liquid through ventral incisions). For *A. n. mexicana*, only SVL and TL were available; thus, this species was not included in the analyses of snake stoutness (see below). Females with large follicles or embryos were not included in the

Table 1. Summary of mean female snout–vent length (mfSVL, in mm), macrohabitat use (Mac, proportion of individuals found on vegetation, see Methods; RTL, relative tail length; RST, relative stoutness, see Methods) of *Bothrops* spp. (arranged by species groups) and of *Atropoides nummifer mexicana*, *Porthidium nasutum* and *P. yucatanicum*. Morphology data for females only (see Methods). N_{mac} , sample size for observations on macrohabitat use; N_{morf} , sample size for morphological data; SD, standard deviation

	mfSVL	SD	Mac	N_{mac}	RTL	SD	RST	SD	N_{morf}
<i>Bothrops hyoprurus</i>	501.5	94.2	–	–	0.195	0.063	0.463	0.280	20
<i>Bothrops alternatus</i>	1104.0	80.7	0.00	30	–0.297	0.106	0.381	0.430	20
<i>Bothrops cotiara</i>	802.7	55.3	–	–	–0.143	0.145	0.201	0.306	20
<i>Bothrops fonsecai</i>	835.5	57.0	0.00	13	–0.084	0.079	0.471	0.251	20
<i>Bothrops itapetingae</i>	502.4	46.9	0.04	24	–0.244	0.107	0.070	0.336	20
<i>Bothrops erythromelas</i>	551.7	88.3	–	–	–0.043	0.095	0.086	0.227	20
<i>Bothrops neuwiedi mottogrossensis</i>	714.9	81.2	0.00	11	0.020	0.071	–0.125	0.292	19
<i>Bothrops n. pauloensis</i>	687.9	72.6	0.00	86	–0.035	0.069	0.105	0.288	20
<i>Bothrops n. pubescens</i>	836.2	128.5	0.00	36	–0.058	0.092	0.263	0.350	20
<i>Bothrops n. urutu</i>	733.9	50.6	0.08	13	–0.070	0.098	0.213	0.191	17
<i>Bothrops jararaca</i>	946.9	92.4	0.13	64	0.087	0.104	–0.184	0.247	20
<i>Bothrops insularis</i>	666.1	86.7	0.32	273	0.163	0.089	–0.326	0.319	20
<i>Bothrops bilineatus</i>	678.4	72.5	0.90	33	0.124	0.078	–0.713	0.256	20
<i>Bothrops taeniatus</i>	1182.5	73.2	0.50	10	0.103	0.048	–0.747	0.160	20
<i>Bothrops brazili</i>	1050.4	129.4	0.00	11	0.034	0.110	0.222	0.301	20
<i>Bothrops jararacussu</i>	1193.1	88.8	0.00	61	0.026	0.090	0.205	0.395	20
<i>Bothrops atrox</i> (Manaus)	1207.5	97.8	0.28	107	0.086	0.086	–0.293	0.335	20
<i>Bothrops atrox</i> (Pará)	997.0	96.3	0.20	10	0.123	0.060	–0.250	0.214	20
<i>Bothrops leucurus</i>	1046.9	176.4	0.15	20	0.104	0.102	–0.250	0.307	16
<i>Bothrops moojeni</i>	1055.6	171.7	0.18	22	0.114	0.081	–0.117	0.392	20
<i>Atropoides nummifer mexicana</i>	649.1	67.6	–	–	–0.013	0.114	–	–	20
<i>Porthidium nasutum</i>	331.0	67.6	–	–	–0.213	0.104	0.259	0.170	15
<i>Porthidium yucatanicum</i>	446.6	36.3	–	–	–0.023	0.074	0.107	0.643	20

analyses and those with prey in the gut were weighed after removing prey. The information on macrohabitat use (see Table 1) for 18 forms of *Bothrops* is based mostly on original field data, but also on the literature (Duellman, 1978; Dixon & Soini, 1986; Campbell & Lamar, 1989; Sazima, 1992; Strüssmann & Sazima, 1993; Starace, 1998). We failed to obtain data on macrohabitat use for *B. cotiara* and *B. erythromelas*. McCoy & Censky (1992) state that *P. yucatanicum* is terrestrial, *P. nasutum* is commonly found on the ground (Campbell, 1998; but see Greene, 1992) and *A. n. mexicana* is terrestrial (Campbell, 1998); thus, these 3 species are treated here as terrestrials. For *Bothrops*, a species was considered semi-arboreal when >10% of the individuals found in the field were on the vegetation. Although arbitrary, this distinction decreases the chance of considering a species as semi-arboreal when it only rarely uses the vegetation.

Tail length and mass were compared between terrestrial and semi-arboreal species, as well as among species and among species groups, with 1-way analyses of covariance (ANCOVA; all variables transformed to their natural log), with SVL and total length (TTL) as covariates, respectively. Mean female SVL (mfSVL; using the 8 largest individuals of each sample) was compared between terrestrials and semi-arboreals with a *t*-test, and among species and species groups with a 1-way analysis of variance (ANOVA; all variables transformed to their natural log). All statistical analyses were performed using Statistica (StatSoft, 1998).

Tail length, stoutness, body size (mfSVL) and macrohabitat use were reconstructed through linear parsimony in MacClade (Maddison & Maddison, 1992). For the reconstructions of tail length and mass (stoutness), the residuals of simple regressions between these variables and SVL and TTL, respectively, were used (all of them transformed to their natural log), including data for all species (for tail length $r^2=0.955$, including *Porthidium* spp. and *A. n. mexicana*; for mass $r^2=0.945$, including *Porthidium* spp.); these residuals are treated here as relative tail length (RTL) and relative stoutness (RST), respectively (see Forsman, 1991).

Possible relationships between macrohabitat use and RTL, RST and mfSVL were examined using independent contrasts (Felsenstein, 1985) generated by the software COMPARE (E. P. Martins, 1999), using a phylogenetic hypothesis adapted from Wüster, Salomão, Quijada-Mascareñas *et al.* (in press; information on *B. n. pubescens* provided by V. X. Silva, pers. comm.). Only species for which quantitative data for macrohabitat use were available were used for generating contrasts (all *Bothrops*, except *B. cotiara*, *B. erythromelas* and *B. hyoprurus*). Proportions of macrohabitat use (proportion of individuals found on the vegetation) were transformed to the arc sine of their square root (Zar, 1984). All branch lengths were set to 1. Relationships between contrasts of macrohabitat use and those of RTL, RST and mfSVL were analysed through linear regressions forced through the origin (i.e. with the intercept set to 0; see e.g. E. P. Martins & Hansen, 1996).

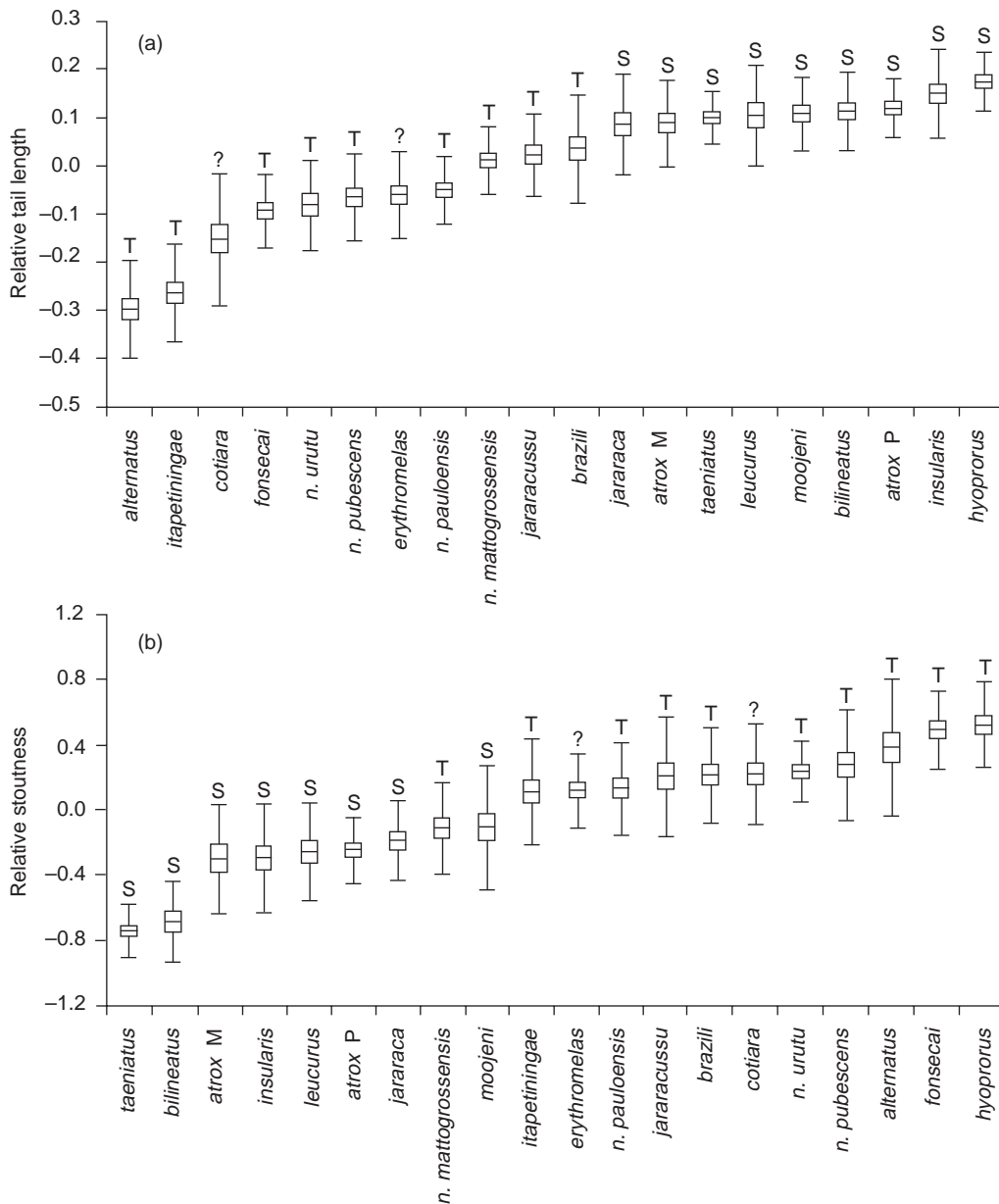


Fig. 1. Mean (middle horizontal line), standard errors (boxes) and standard deviations (vertical bars) of relative tail length (a) and relative stoutness (b; see Methods) in 20 forms of *Bothrops*. T, terrestrial; S, semi-arboreal; ?, unknown macrohabitat. *B. atrox M*, population from the Manaus region (central Amazonia); *B. atrox P*, population from Pará (eastern Amazonia). Note that, in general, semi-arboreals have longer tails and are more slender than terrestrials.

RESULTS

Macrohabitat use and body size (mfSVL) are diverse among the species of *Bothrops* studied (Table 1). All species in the *alternatus* and *neuwiedi* groups for which macrohabitat is known are found almost exclusively on the ground. Species of the *alternatus* group are small (*B. itapetingae*) to large (*B. alternatus*) and of the *neuwiedi* group, small (*B. erythromelas*) to moderate-sized (*B. n. pubescens*). In the *jararaca* group, both species are found mostly on the ground, but also on vegetation; *B. jararaca* is larger than *B. insularis* (Sazima, 1992; Duarte, Puerto & Franco, 1995). Besides

using the vegetation more frequently, *B. insularis* may reach higher spots on the vegetation (up to c. 8 m; pers. obs.) than *B. jararaca* (Sazima, 1992). Juveniles of *B. jararaca* tend to be more arboreal than adults, but even large adults may be occasionally found on the vegetation (Sazima, 1992). In the *taeniatus* group, both species are frequently found on the vegetation and *B. bilineatus* is smaller than *B. taeniatus* (Cunha & Nascimento, 1975, 1978, 1982; Duellman, 1978; Dixon & Soini, 1986). All members of the *atrox* group are large species found mostly on the ground but also on the vegetation; juveniles of all forms are more arboreal than adults (Cunha & Nascimento, 1978, 1982; Duellman,

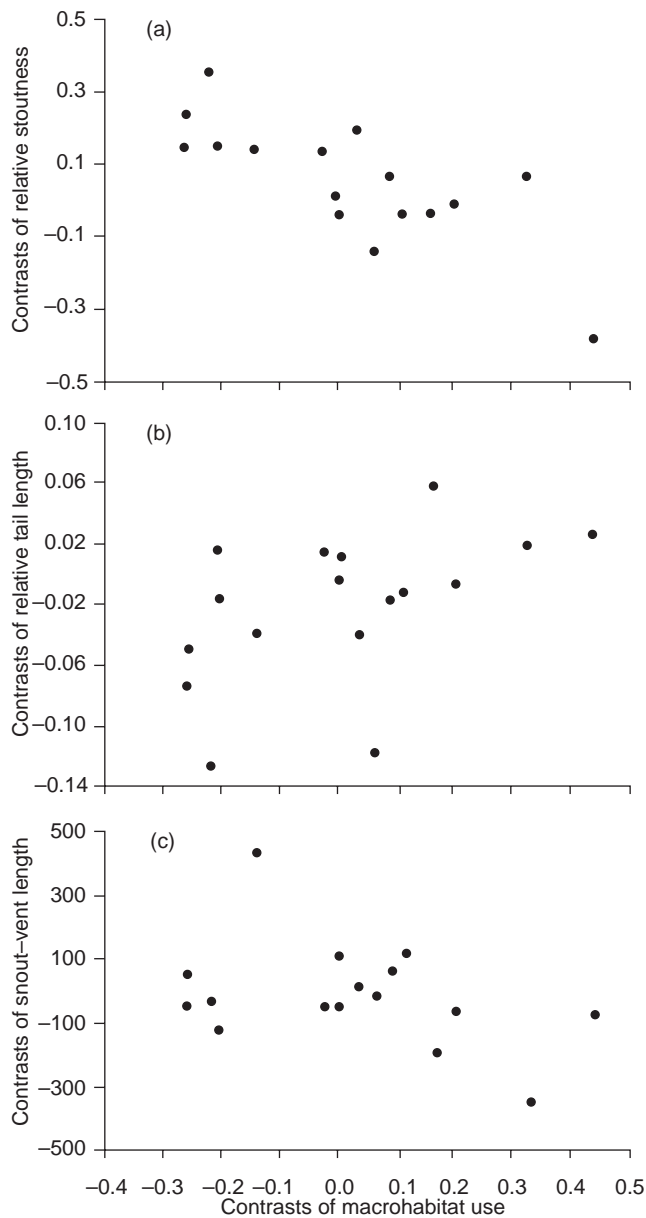


Fig. 2. Relationships between independent contrasts of macrohabitat use with those of relative stoutness (a), relative tail length (b) and mean female snout-vent length (c) in 17 species of *Bothrops* (see Methods). Note that stoutness decreases and tail length decreases with increasing arboreality and that adult body size seems to remain constant over the lower range of macrohabitat use, but to decrease in species of *Bothrops* which are more arboreal.

1978; Dixon & Soini, 1986; M. Martins & Oliveira, 1999; pers. obs.). Both species of the *jararacussu* group treated herein are large and found exclusively on the ground; even juveniles of both species are terrestrial (Cunha & Nascimento, 1978, 1982; Duellman, 1978; Dixon & Soini, 1986; Starace, 1998).

In general, within *Bothrops*, semi-arboreals have longer tails and are more slender than terrestrials (Fig. 1a, b). Based on their RTL and RST, *B. cotiara* and *B. erythromelas* seem to be terrestrial (Fig. 1a, b).

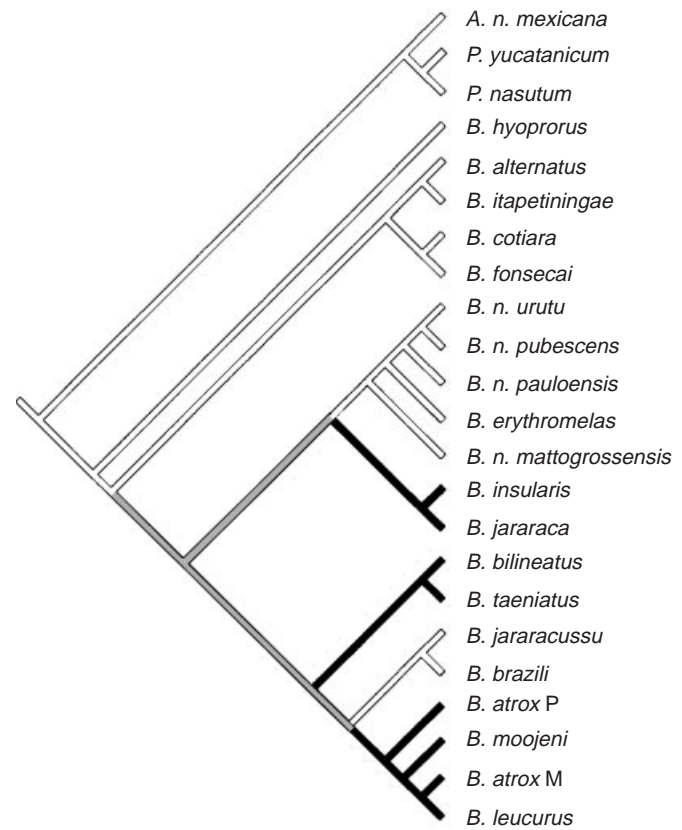


Fig. 3. Reconstruction of macrohabitat use on a phylogenetic hypothesis for the species of *Bothrops* treated herein (adapted from Wüster, Salomão, Quijada-Mascareñas *et al.*, in press), with *Porthidium nasutum*, *P. yucatanicum* and *Atropoides nummifer mexicana* as the outgroup. White, terrestrial habits; black, semi-arboreal habits; grey with black borders, branches in which the character is equivocal. *B. atrox M*, population from the Manaus region (central Amazonia); *B. atrox P*, population from Pará (eastern Amazonia). Note that the ancestor of *Bothrops* may have been a terrestrial species and that semi-arboreal habits may have appeared one to three times in the genus.

The tail is significantly shorter in terrestrials than in semi-arboreals (ANCOVA, $F_{[1,349]} = 146.9$, $P < 0.001$; both species with unknown macrohabitat excluded), and also significantly different among species (ANCOVA, $F_{[17,333]} = 47.8$, $P < 0.001$) and among species groups (ANCOVA, $F_{[6,344]} = 100.2$, $P < 0.001$). Mass is significantly higher in terrestrials than in semi-arboreals (ANCOVA, $F_{[1,349]} = 271.4$, $P < 0.001$; both species with unknown macrohabitat excluded), and also significantly different among species (ANCOVA, $F_{[17,333]} = 32.9$, $P < 0.001$) and among species groups (ANCOVA, $F_{[6,344]} = 79.3$, $P < 0.001$). Although mfSVL is significantly different among species (ANOVA, $F_{[17,126]} = 5.6$, $P < 0.001$; both species with unknown macrohabitat excluded) and among species groups (ANOVA, $F_{[6,137]} = 5.0$, $P < 0.001$), this character is not significantly different between semi-arboreals and terrestrials ($t = 1.65$, 142 d.f., $P = 0.101$).

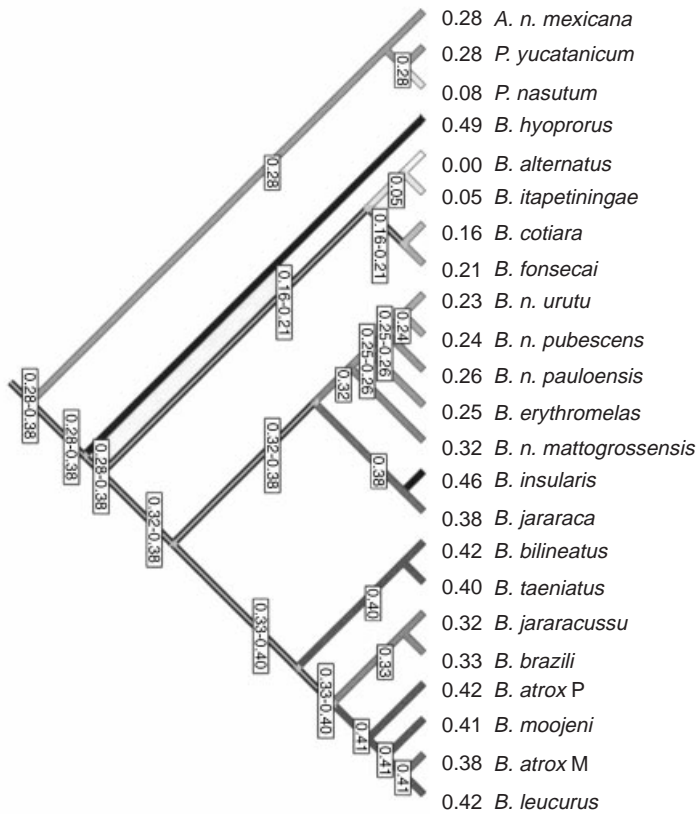


Fig. 4. Reconstruction of relative tail length (see Methods) on a phylogenetic hypothesis for the species of *Bothrops* treated herein (adapted from Wüster, Salomão, Quijada-Mascareñas *et al.*, in press), with *Porthidium nasutum*, *P. yucatanicum* and *Atropoides nummifer mexicana* as the outgroup. Darker branches, longer tails; grey with black borders, branches in which the character is equivocal. *B. atrox M*, population from the Manaus region (central Amazonia); *B. atrox P*, population from Pará (eastern Amazonia). Note that the ancestor of *Bothrops* had a moderate-sized to long tail and that tail length seemed to increase in semi-arboreals, as well as in the terrestrial *B. hyoprurus*.

After removing the effect of phylogeny from our data, a highly significant negative relationship was found between independent contrasts of macrohabitat use and those of RTL (Fig. 2a; $r^2 = 0.501$, $F_{[1,15]} = 15.08$, $P = 0.001$). The relationship between contrasts of macrohabitat and those of RTL is positive and marginally significant (Fig. 2b; $r^2 = 0.215$, $F_{[1,15]} = 4.12$, $P = 0.061$). Thus, within *Bothrops*, the more arboreal the species, the longer its tail and the more slender its body. On the other hand, the relationship of contrasts of macrohabitat with those of mfSVL was not significant (Fig. 2c; $r^2 = 0.167$, $F_{[1,15]} = 3.00$, $P = 0.104$). However, there seems to be a breakpoint of macrohabitat use over which mfSVL decreases with increasing arboreality (Fig. 2).

The reconstruction of macrohabitat use (using *A. n. mexicana* and *Porthidium* spp. as the outgroup; Fig. 3) indicates that the ancestor of *Bothrops* was a terrestrial

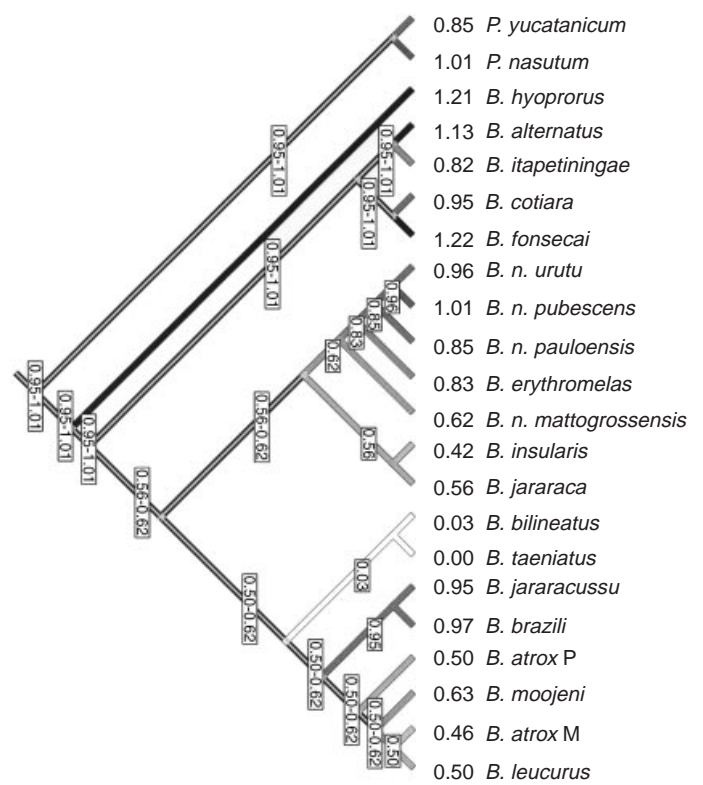


Fig. 5. Reconstruction of relative stoutness (see Methods) on a phylogenetic hypothesis for the species of *Bothrops* treated herein (adapted from Wüster, Salomão, Quijada-Mascareñas *et al.*, in press), with *Porthidium nasutum* and *P. yucatanicum* as the outgroup. Lighter branches, more slender bodies; grey with black borders, branches in which the character is equivocal. *B. atrox M*, population from the Manaus region (central Amazonia); *B. atrox P*, population from Pará (eastern Amazonia). Note that the ancestor of *Bothrops* may have been a stout species and that arboreal habits apparently led to slender bodies (see Table 1).

species and that semi-arboreal habits may have appeared once to three times in *Bothrops*. The reconstruction of RTL (Fig. 4) indicates that the ancestor of *Bothrops* had a moderate-sized to long tail, and that the tail increased in the terrestrial *B. hyoprurus* and several semi-arboreals, while it decreased in two species of the *alternatus* group (*B. alternatus* and *B. itapetiningae*). The reconstruction of RST (Fig. 5) indicates that the ancestor of *Bothrops* had a stout body and that semi-arboreals became slender, especially in the *taeniatus* group. Although showing several equivocal branches, the reconstruction of mfSVL (Fig. 6) indicates that the ancestor of *Bothrops* was a small species (500–650 mm) and that body size increased in *B. alternatus*.

DISCUSSION

Greene (1992) suggested that *Bothrops* (*sensu stricto*, excluding the *taeniatus* group) and *Crotalus* were intra-

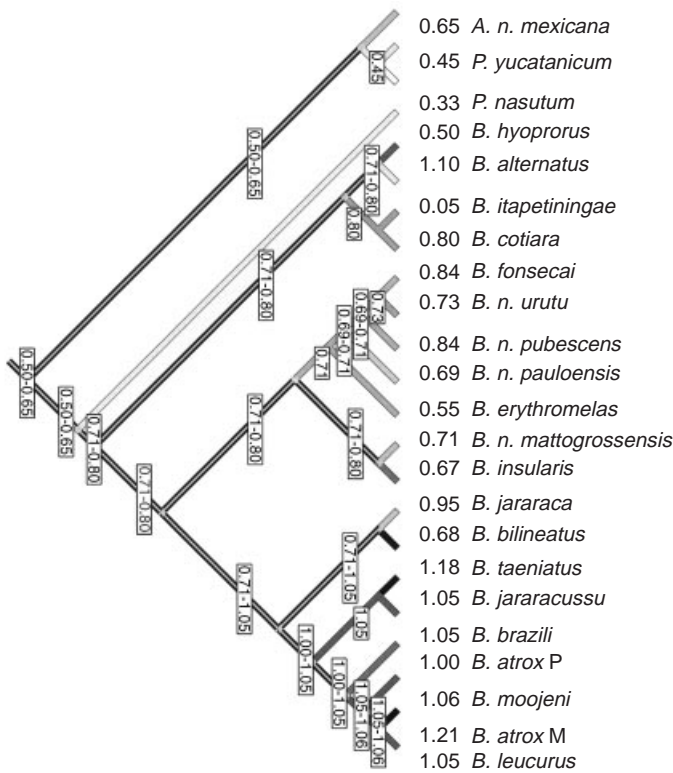


Fig. 6. Reconstruction of body size (mean female snout–vent length, m; see Methods) on a phylogenetic hypothesis for the species of *Bothrops* treated herein (adapted from Wüster, Salomão, Quijada-Mascareñas *et al.*, in press), with *Porthidium nasutum*, *P. yucatanicum* and *Atropoides nummifer mexicana* as the outgroup. Darker branches, larger species; grey with black borders, branches in which the character is equivocal. *B. atrox M*, population from the Manaus region (central Amazonia); *B. atrox P*, population from Pará (eastern Amazonia). Note that the ancestor of *Bothrops* was probably a small species and that there is no clear relationship between body size and arboreality in the genus, although in the *jararaca* and *taeniatus* groups arboreality seems to have resulted in smaller body size (see Table 1).

generically similar in relation to macrohabitat use when compared to *Trimeresurus*. However, the results presented here show a high diversity of macrohabitat use in *Bothrops*, perhaps similar to that found in *Trimeresurus*. Most species of *Bothrops* and *Trimeresurus* are found in forests, in contrast with most species of *Crotalus*, which inhabit open habitats (see e.g. Klauber, 1972). Thus, a higher diversity in macrohabitat use in pitvipers may be associated with inhabiting structurally more complex habitats, such as tropical forests.

Our results strongly indicate that tail length increased and stoutness decreased with increasing arboreality in *Bothrops*. Tail elongation and a decrease in stoutness resulting from arboreality in snakes were suggested in several studies (e.g. Vitt & Vangilder, 1983; Guyer & Donnelly, 1990; Cadle & Greene, 1993; Lillywhite & Henderson, 1993), although the present study is the first to address these trends comparatively in a monophyletic

group of snakes. These shifts in morphology associated with arboreality may be related mainly to the instability and discontinuity of the arboreal macrohabitat, as well as with physiological problems associated with climbing (see review in Lillywhite & Henderson, 1993; see also Lillywhite & Smits, 1992). Therefore, the shifts in tail length and stoutness described here for *Bothrops* are in the directions predicted by previous studies on snake ecomorphology.

The supposed terrestriality in *B. cotiara* and *B. erythromelas* (see Fig. 1a, b) is consistent with their inclusion in terrestrial groups (*alternatus* and *neuwiedii*, respectively). Although apparently terrestrial, *B. n. mattogrossensis*, another member of the *neuwiedii* group, has a relatively slender body and long tail when compared to other species in the *neuwiedii* group (Table 1). A possible reason for such a result may be that this subspecies could occasionally be forced to use vegetation during seasonal floods where it lives (see e.g. Strüssmann & Sazima, 1993).

Although our results indicate that macrohabitat use is an important factor in determining stoutness in *Bothrops*, variations in stoutness in snakes may reflect the action of additional selective agents, such as those related to feeding and reproductive biology (e.g. a larger body can house larger prey as well as larger and/or more eggs or embryos; see e.g. Shine, 1991). For instance, in contrast with most species of *Bothrops*, juveniles of three species of the *alternatus* group (*B. alternatus*, *B. cotiara* and *B. fonsecai*) feed exclusively on mammals, a bulky prey that would require a stout body (M. Martins *et al.*, in press). In fact, M. Martins *et al.* (in press) found that the proportion of mammals in the diet of 17 species of *Bothrops* is positively correlated with snake stoutness. A study on reproductive strategies in *Bothrops* would probably uncover potential effects of litter and neonate size on female stoutness in this genus.

Similarly, variations in tail length in snakes may reflect selective agents other than macrohabitat, as indicated by some of our results. For instance, the extremely long tail of the very stout, terrestrial *B. hyoprurus*, which is even longer than that of the highly arboreal *B. bilineatus* (Fig. 1a), may be related to factors such as foraging behaviour (e.g. caudal luring, tail poking behaviour; see e.g. Strüssmann & Sazima, 1990; Sazima, 1991) or defence (e.g. tail display, tail breakage; see e.g. Greene, 1988; Savage & Slowinski, 1996).

Adult body size seems to remain constant over the lower range of macrohabitat use, but to decrease in species of *Bothrops* that are more arboreal (Fig. 2c). This apparent trend is not surprising since there seems to be an upper limit of body size (c. 1 m) for arboreality in vipers, because of cardiovascular limitations (Lillywhite & Smits, 1992). Suggestively, within the *taeniatus* and *jararaca* groups, more arboreal species (*B. bilineatus* and *B. insularis*, respectively) are smaller than their less arboreal relatives (*B. taeniatus* and *B. jararaca*; Table 1, Fig. 6). This apparent decrease in adult size with

relatively high levels of arboreality in *Bothrops* deserves further attention and similar studies on additional monophyletic clades would show whether such a trend is widespread in snakes.

The number of times arboreal habits appeared in *Bothrops* remains doubtful; the inclusion of additional species in the reconstructions would probably help to answer this question. Total arboreality, such as that observed in some colubrids (e.g. *Xenoxybelis argenteus*, Martins, 1993; M. Martins & Oliveira, 1999; see also Lillywhite & Henderson, 1993), apparently did not evolve in *Bothrops*, although *B. bilineatus* is seldom found on the ground. The invasion of the arboreal habitat by *Bothrops* agrees with the general trend of higher arboreality in tropical snakes (see Cadle & Greene, 1993; Lillywhite & Henderson, 1993), especially those that inhabit forests, such as all semi-arboreal *Bothrops* treated herein. Suggestively, in both lineages in which most species invaded open areas (the *alternatus* and *neuwiedi* groups), no trend towards arboreality appeared.

The possible selective agents responsible for the shifts in macrohabitat reported, with the consequent changes in body form, probably included prey availability and predation. For prey availability, in *B. insularis*, for instance, an increase in ornithophagy (M. Martins *et al.*, in press) may have been followed by an increase in arboreality. However, it is very difficult to reconstruct the evolutionary scenario in which shifts in macrohabitat use took place within *Bothrops*, thus suggestions regarding these agents are speculative. Detailed observations on the natural history of each species of *Bothrops* may uncover subtle differences among species or populations that could help to understand which were the main selective agents in the macrohabitat diversification that occurred in the genus. Techniques that allow detailed behavioural studies in the field (e.g. radio-tracking) are certainly promising (see Greene, 1986).

The ancestor of *Bothrops* was probably a small, stout, terrestrial (this study), forest inhabitant that originated in Central America (Kraus *et al.*, 1996; Parkinson, 1999; M. Martins *et al.*, in press; Parkinson *et al.*, in press; Wüster, Salomão, Quijada-Mascareñas *et al.*, in press) and invaded South America in the late Miocene (11–12 mya; Wüster, Salomão, Quijada-Mascareñas *et al.*, in press). Furthermore, this early *Bothrops* was probably a prolific species which preyed upon centipedes and a wide array of small, terrestrial vertebrates (M. Martins *et al.*, in press; M. Martins, pers. obs). This ancestor gave rise to an extremely diverse clade with about 40 South American forms, which represents five times the number of species of the most diverse clade of Central American pitvipers (*Porthidium*, with eight species; Campbell & Lamar, 1989, 1992). In fact, few snake lineages were so successful in South America (see e.g. Cadle & Greene, 1993; Greene, 1997). Perhaps the characters above (see also Greene, 1992) associated with the relatively high plasticity in macrohabitat use and morphology described here were key features which facilitated the successful radiation of *Bothrops*. Knowl-

edge on which habitats, prey, predators and potential competitors were present during the early invasion and later radiation of *Bothrops* in South America would probably help to uncover the ecological factors involved in this successful history, including those associated with form and size (cf. Greene, 1992).

Acknowledgements

Valuable help in fieldwork was provided by M. T. Almeida, L. A. Anjos, V. Bonato, C. A. Brasileiro, C. Z. Cechin, M. Duarte, S. G. Egler, F. Franco, E. Haller, M. C. Kiefer, O. A. V. Marques, C. C. Nogueira, W. Y. Oda, J. B. Rocha, I. Sazima and P. H. Valdujo. Unpublished field data was kindly provided by L. J. Vitt, J. P. Caldwell, J. L. Gasparini, C. P. A. Prado, C. F. D. Rocha, M. T. U. Rodrigues, I. Sazima and J. Solorzano. Raw morphometric data was provided by M. T. Almeida, J. A. Campbell, H. W. Greene and C. L. Parkinson. Permission to examine museum specimens was kindly provided by T. C. S. Ávila-Pires, U. Galatti and R. N. Yuki (Museu Paraense Emílio Goeldi, Belém, Pará); M. Di-Bernardo (Museu de Ciências da PUCRS, Porto Alegre, Rio Grande do Sul); R. Fernandes (Museu Nacional do Rio de Janeiro, Rio de Janeiro); M. F. D. Furtado and F. L. Franco (Instituto Butantan, São Paulo); P. F. Bührnheim (Instituto de Medicina Tropical de Manaus, Amazonas); C. J. Cole and C. W. Myers (American Museum of Natural History, New York); and R. McDiarmid (National Museum of Natural History, Washington). Help in laboratory work was provided by J. Lima and C. Yamashita. Advice in statistical analyses was generously provided by R. Fernandes, P. S. Santos-Filho and L. Monteiro. Unpublished phylogenies of *Bothrops* were kindly made available by W. Wüster and C. L. Parkinson. Previous drafts of the manuscript were read critically by R. Fernandes, H. W. Greene, H. Lillywhite, O. A. V. Marques, C. Nogueira, I. Sazima, G. Shuett and an anonymous referee. Their comments significantly enhanced the quality of the final version. This study is part of the project Natural History and Evolution of *Bothrops*, funded by Fundação de Amparo à Pesquisa do Estado de São Paulo (grant 95/09642-5).

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