Phylogenetic relationships among the Stiletto Snakes (genus Atractaspis) based on external morphology

Katie Moyer*, Kate Jackson

*Department of Biology, Whitman College, Walla Walla, WA, USA

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**KATIE MOYER & KATE JACKSON***

*Department of Biology, Whitman College, Walla Walla, WA 99362, USA*

**Abstract.**—Stiletto Snakes (genus *Atractaspis*) are the most poorly studied of the three clades of snakes with front-fanged venom-delivery systems. Fossorial and endemic to Africa and the Middle East, *Atractaspis* possess uniquely derived mobile fangs that allow them to perform a ‘side-stabbing’ method of envenomation, rather than the frontal strike of most other venomous snakes. While many studies have examined the functional anatomy of these unique fangs, the evolutionary history of *Atractaspis* has been comparatively neglected by researchers. While several evolutionary hypotheses exist for relationships within the Atractaspididae, no study has focused on the phylogenetic relationships within the genus *Atractaspis* itself. This study presents the first attempt to reconstruct the phylogenetic history of 14 species within this genus, using external morphological data. Using *Macrelaps* and *Homoroselaps* as alternate outgroups, we compare the results of two phylogenies and provide a starting point for an investigation of the evolutionary history of this remarkable yet relatively little-known genus.

**Key words.**—*Atractaspis*, Atractaspididae, evolution, morphology, systematics

Front-fanged delivery systems are found in the snake families Elapidae, Viperidae and Atractaspididae. Within these three clades, Stiletto Snakes (*Atractaspis*) are by far the most poorly-known. *Atractaspis* is a genus of approximately 20 fossorial snakes found in Africa and the Middle East. Species within this genus are morphologically very similar, sharing such characters as smooth scales and brown or black coloration, occasionally with a pale ventrum. Their bodies are cylindrical with a truncated tail, a relatively small depressed head, an indistinct neck and a protruding upper jaw useful for pushing through substrate (Deufel & Cundall 2003). They have a venomous bite that in most species is painful, and some species have highly toxic venoms that are potentially fatal to humans (e.g. *A. irregularis, A. microlepidota*) (Kochva 2002). Clinical understanding of the venoms of different species within the genus is largely anecdotal or based on individual case histories (e.g. Kurnik *et al.* 1999). Perhaps the most distinctive feature of *Atractaspis* is its uniquely derived solenoglyph dentition, which allows these snakes to use a ‘side-stabbing’ method of envenomation rather than the frontal strike characteristic of most venomous snakes. This distinctive strike is accomplished by sliding one fang out sideways and striking backwards into their prey. This method of feeding probably evolved as an adaptation to hunting in confined spaces underground, a challenge common to fossorial atractaspids (Deufel & Cundall 2003).

*Corresponding author. Email: jacksok@whitman.edu*
Although Atractaspidids share several characteristics (Shine et al. 2006), the family as a whole is highly variable in dentition, venom (or Duvernoy’s gland secretion) composition, venom gland morphology and mean head and body size (Greene 1997). For over a century, the phylogenetic placement of Atractaspis has baffled herpetologists, who were unable to reconcile its strange dentition with any known caenophidian family. The first species discovered, A. irregularis (Reinhardt 1843), was originally placed within the Elapidae in the mid-1800s. Two decades later, it was moved into Viperidae, where it remained for the next century (reviewed by Underwood & Kochva 1993). While several herpetologists questioned the placement of Atractaspis within the Viperidae (e.g. Haas 1931; Laurent 1950), no new placement was made until Bourgeois (1968) recognised the distinct differences between the fang-erecting mechanism of Atractaspis and that of vipers during the course of a comparative study of the skulls of African snakes. This led her to erect a separate subfamily for Atractaspis and related genera – the Aparallactinae – within the Colubridae. Later studies of Atractaspis venom glands (Kochva et al. 1967) and jaw musculature (Heymans 1975) confirmed a morphology fundamentally different from that of vipers. Heymans (1982) raised the clade containing Atractaspis and the Aparallactinae to family status, naming it the Atractaspididae. Similarly, Underwood & Kochva (1993) placed Atractaspis and related genera within the family Atractaspididae, on the basis of two shared derived features.

With the advent of molecular systematics, the genus Atractaspis has been proposed as the nearest relative of a diverse range of colubroids. Cadle (1994) determined that Atractaspis represented part of an early African radiation of colubroids and was the sister group to the clade containing both colubroids and elapids. Kraus & Brown (1998) found Atractaspis to be in a clade with the Boodontinae (Madagascarpophis and Leioheterodon) and the sister group to the Elapidae. In contrast, Lawson et al. (2005) found Atractaspis to be the sister group to the Boodontinae (e.g. Bothrophthalmus, Lamprophis) and closely related to Elapidae, Psammophiinae (e.g. Psammophis, Malpolon), and Pseudoxyrhophiinae (e.g. Leioheterodon, Ithycyphus). Gravlund (2001) found Atractaspis to be most closely related to Lamprophis and part of a polytomy with five elapids and three other colubrids (Xenodon, Lycofoothomorphus, and Mehelya), while Vidal & Hedges (2002) found Atractaspis to be most closely related to Pseudoaspis and the sister group to the psammophiines (e.g. Malpolon, Rhamphiophis). Heise et al. (1995) and Pinou et al. (2004) found Atractaspis to be most closely related to the Elapidae (but did not include any other atractaspidid genera in their analysis). Vidal et al. (2007, 2008) placed Atractaspis (along with the genera Lamprophis, Pythonodipsas, Mehelya, Psammophylax, Pseudoaspis, Buhoma, Psammodynastes, Prosymma and Leioheterodon) within the newly erected family Elapoidea, the sister group to Elapidae and the new family Lamprophiidae (corresponding closely to the Boodontinae of Lawson et al. 2005).

Kelly et al. (2008) found that Atractaspis and several other atractaspidid genera represented a basal African radiation of colubroids, closely associated with Buhoma, Psammodynastes, and the Lamprophiidae (e.g. Lamprophis, Mehelya) and Pseudoaspididae (Pseudoaspis and Pythonodipsas). Most recently, Zaher et al. (2009) placed Atractaspis in a clade with aparallactines (Homoroselaps and Aparallactus), lamprophiines (Lycophidion and Bothrophthalmus) and pseudoxyrhophiines (Pseudoxyrhopus and Leioheterodon). This clade is placed as the sister group to
the elapids, and is also closely related to the psammophiines (*Rhamphiophis* and *Psammophis*).

Although the phylogenetic placement of *Atractaspis* within the Colubroidea has been extensively studied, this is the first examination of the evolutionary relationships among species within this genus. As tissue samples have yet to be collected for many of these rare burrowing snakes, this study used external morphology in a preliminary attempt to shed light on the phylogenetic relationships within the genus *Atractaspis*.

The choice of a suitable outgroup for our analysis presented a difficult decision. The most comprehensive phylogenetic analysis of the Atractaspididae to date identified the monospecific genus *Macrelaps* as the sister group to *Atractaspis*, based on internal morphology (Underwood & Kochva 1993). This was strong support for our choice of *Macrelaps microlepidota* as the outgroup for our study of relationships within *Atractaspis*.

However, the only molecular phylogenetic studies to include a significant representation of atractaspid species (Nagy et al. 2005; Vidal et al. 2008) found *Homoroselaps lacteus* to be the sister group to *Atractaspis*, with *Macrelaps* more distantly related. *Homoroselaps* is a problematic genus, considered on the basis of morphology to be most closely affiliated with the Elapidae by some researchers (e.g. Underwood & Kochva 1993) and by others more closely allied with the Atractaspididae (e.g. Bourgeois 1968). Those molecular phylogenies in which it has been included find it to be either ‘unplaced’ (Kelly et al. 2003) or more closely affiliated with the Atractaspididae than with the Elapidae (e.g. Lawson et al. 2005; Vidal et al. 2008; Kelly et al. 2009; Zaher et al. 2009). However, these studies included very few atractaspid species in their analyses. In the absence of many other atractaspid species for comparison, evidence that *Homoroselaps* is affiliated more closely with *Atractaspis* than with the Elapidae does not necessarily indicate that it is the sister group of the former. However, Nagy et al. (2005) and Vidal et al. (2008) each included six atractaspid genera, including *Macrelaps*, in their analysis which found *Homoroselaps* to be the sister group to *Atractaspis*. We therefore decided to perform two analyses of relationships within *Atractaspis* for comparison using two different outgroups: *Macrelaps microlepidotus* and *Homoroselaps lacteus*.

### MATERIALS AND METHODS

Data were collected at the Royal Museum of Central Africa in Tervuren, Belgium using the museum’s collection of specimens preserved in 70% ethanol. Seventy specimens representing *Macrelaps microlepidotus* and 10 different species of *Atractaspis* (Appendix 1) were examined, and 32 external morphological character states were recorded. The head of each specimen was photographed in lateral, dorsal, and ventral views. These photographs were later used as a reference for characters not initially recorded and also to make the measurements necessary to quantify certain morphological characteristics of head scales. Four additional species were added to the study (*A. engdahli*, *A. leucomelas*, *A. microphilis*, and *A. microlepidota*) using data from the primary literature (Laurent 1950; Trape et al. 2006). Specimens of *Homoroselaps lacteus* were examined in the collection of the Field Museum of Natural History.
Of the 32 characters initially recorded, only the following were found to be informative: (1) anal plate single or divided; (2) fusion of sublinguals to infralabials (Fig. 1); (3) division of the nasal scale; (4) presence of preocular scale; (5) number of dorsal scale rows; (6) number of infralabials; (7) number of infralabials in contact with the sublinguals; (8) number of pairs of sublinguals; (9) subcaudals single or divided; (10) temporal formula; (11) number of supralabials; (12) number of ventrals and subcaudals; and (13) presence of postocular scales.

Laurent (1950), Trape et al. (2006), and others have recorded the number of gulars in contact with the sublinguals (Fig. 1) and the frontal length/interparietal suture length ratio (Fig. 2) as useful characters for distinguishing different *Atractaspis* species, and examination of these characters in our photographs proved them to be useful phylogenetically. This brought our total count of useful traits up to 15. Definitions of scale characters can be found in Chippaux (2006).

Character Analysis: *Macrelaps microlepidotus* as the Outgroup

Table 1 lists the characters used to construct the tree with *Macrelaps* as the outgroup. Of the 15 traits analysed, 13 were found to be useful. The presence of postocular scales was not found to be an informative characteristic. Similarly, the number of pairs of sublinguals was not used in the construction of this tree, as this count did not differ between *Macrelaps* and *Atractaspis*.

Scoring characters.—Plesiomorphic and derived character states are listed in Table 1. Anal plate division, fusion of sublinguals to infralabials, nasal scale division, presence of a precocular scale, number of dorsal scale rows, number of infralabials, and number of infralabials in contact with the sublinguals were all recorded as two

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**Figure 1.** Ventral view of *Atractaspis corpulenta* (left) and ventral view of *Atractaspis irregularis* (right). A, a gular scale; B, sublinguals fused to 2nd infralabials; C, sublinguals not fused to infralabials; 1–5; gulars in contact with sublinguals.
character states. The first four of these characters were found to have binary states (e.g. single vs. divided, fused vs. not fused). Dorsal scale row counts were taken from midbody, with the recorded division based on a natural break in dorsal scale row ranges. Infralabials were observed to be either in the plesiomorphic range of 4–6 scales or the derived state of 7–8 scales. Similarly, the presence of three infralabials in contact with the sublinguals was found to be plesiomorphic, while the occurrence of four was viewed as the derived state in the construction of this tree.

The remaining characters had more than two states. The partial division of subcaudals found in one species (*A. dahomeyensis*) was treated as an intermediate state, while the total division of all subcaudals was viewed as derived. Both temporal formula and the number of gulars in contact with the sublinguals displayed a trend towards an increasing number of scales, creating the three states listed in Table 1. In contrast, the number of supralabials had a plesiomorphic count of seven (as found on *M. microlepidotus*), an intermediate count of six, or the most derived state of five supralabials.

The number of ventral scales was added to the number of subcaudal scales to minimise artefacts resulting from sexual dimorphism (males usually have more subcaudals than females, while females have more ventrals than males). The combined count was split into three different ordered character states, also based on natural breaks in the data (Fig. 3). The LF/LP character states were also based on natural breaks found in the ranges of all species (Fig. 4). *Macrelaps* had the lowest LF/LP (length of frontal to length of interparietal suture), so all LF/LPs below 1.25 were treated as plesiomorphic, while LF/LPs between 1.25 and 2.75 were treated as intermediate, and LF/LPs above 2.75 were treated as the most derived state.

**Character Analysis: Homoroselaps lacteus as the Outgroup**

Of the 15 traits, 12 were found to be useful for the construction of the tree using *Homoroselaps* as the outgroup. The presence of preocular scales, nasal scale division and number of infralabials in contact with the sublinguals were not used in tree construction.

**Scoring characters.**—Table 2 lists plesiomorphic and derived character states. As in the analysis using *Macrelaps*, two character states were found for anal plate division,
Table 1. Summary of data collected for tree with *Macrelaps* as outgroup. Character states: Subcaudals: 0 = single; 1 = partially divided; 2 = divided. Anal plate: 0 = single; 1 = divided. Temporal formula: 0 = 1 + 2; 1 = 1 + 3/4; 2 = 2/3 + 4 + 5. Number of infralabials: 0 = 7–8; 1 = 4–6. Number of dorsal scale rows: 0 = x < 25; 1 = x > 25. Number of ventrals + subcaudals: 0 = x < 275; 1 = 275 < x > 325; 2 = x > 325. Sublingual fusion to 2nd infralabials: 0 = not fused; 1 = fused. Gulars in contact with sublinguals: 0 = 3; 1 = 5; 2 = 7. LF/LP: 0 = x < 1.25; 1 = 1.25 < x > 2.75; 2 = 2.75 < x. Number of supralabials: 0 = 7; 1 = 6; 2 = 5. Preocular scale: 0 = present; 1 = absent. Number of infralabials touching sublinguals: 0 = 1–4 touching; 1 = 1–3 touching. Nasal scale: 0 = nasal semi-divided; 1 = nasal divided.

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fusion of sublinguals to infralabials, number of dorsal scale rows, number of infralabials, number of supralabials, and number of pairs of sublinguals. Dorsal scale rows were again counted at midbody, and divided using a natural break in the scale row ranges.

Six characters were found to have more than two states. The partial division of subcaudals seen in *A. dahomeyensis* was again treated as an intermediate state, while a divided subcaudal was plesiomorphic and an undivided scale treated as derived. Temporal formula and the number of gulars in contact with the first pair of sublinguals both showed trends towards an increasing number of scales. Three states were recorded for temporal formula, while the number of gulars had two

![Figure 3](image-url)

**Figure 3.** Ventral + subcaudal ranges from RMCA specimens. Data below 275 (the dashed line) fall in the pleisiomorphic range. Data above 325 (the solid line) fall in the most highly derived range.

![Figure 4](image-url)

**Figure 4.** LF/LP (length of frontal to length of interparietal suture ratio) ranges from RMCA specimens photographed. Species marked with * indicate data taken from the literature (see Materials and Methods). LF/LP ranges below 1.25 (the dashed line) were counted as pleisiomorphic. LF/LP ranges above 2.75 (the solid line) were counted as the most highly derived. Values falling between 1.25 and 2.75 were counted as intermediates.
Table 2. Summary of data collected for tree with *Homoroselaps* as outgroup. Character states: Subcaudals: 0 = divided; 1 = partially divided; 2 = single. Anal plate: 0 = divided; 1 = single. Temporal formula: 0 = 0 + 1; 1 = 1 + 2; 2 = 1 + 3/4; 3 = 2/3 + 4 + 5. Number of infralabials: 0 = 4–6; 1 = 7–8. Number of dorsal scale rows: 0 = x < 25; 1 = 25 < x. Number of ventrals and subcaudals: 0 = x < 275; 1 = 275 < x > 325; 2 = 325 < x. Sublingual fusion: 0 = not fused; 1 = fused. Gulars in contact with 1st pair of sublinguals: 0 = none; 1 = 3; 2 = 5; 3 = 7. LF/LP (length of frontal to length of interparietal suture ratio): 0 = x < 1.25; 1 = 1.25 < x < 2.75; 2 = 2.75 < x. Number of postoculares: 0 = absent; 1 = present; 2 = 1 or 2 postoculares. Number of supralabials: 0 = 6; 1 = 5. Number of pairs of sublinguals: 0 = 2 pairs; 1 = 1 pair.

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intermediate counts, in addition to the plesiomorphic and derived character states. The absence of a postocular scale was plesiomorphic, while the presence of one postocular was an intermediate step. The occasional presence of two postoculars (found only in *A. watsoni*), was treated as the most derived state.

Ventral scales were again added to the number of subcaudals, and the combined count split into three states, based on natural breaks in the data. The three character states created from the LF/LP ratios were similarly based on natural breaks found in the ranges of all species, and matched the divisions found in the *Macrelaps* analysis.

**Data obtained from published sources.**—Scale counts were checked against Chippaux (2006), for all species of *Atractaspis* used in this study except *A. leucomelas* and *A. engdahli*, which are not native to the geographical range covered by that book. Data for *A. engdahli* and *A. leucomelas* were taken from Laurent (1950), including LF/LP ratios, which were measured from line drawings included in the paper. Data for *A. micropholis* and *A. microlepidota* were taken from Trape *et al.* (2006) and Chippaux (2006). Number of gulars in contact with sublinguals data for *A. microlepidota*, *A. dahomeyensis*, and *A. watsoni* were taken from Trape & Mané (2006). The number of gulars in contact with the sublinguals for *A. battersbyi* was taken from de Witte (1959), as the museum specimen photographed was too badly damaged to be useable for this character. Scale counts for both *Macrelaps* and *Homoroselaps* were checked against Marais (2004).

**Generating a phylogeny.**—A single maximum parsimony, strict consensus tree was generated using PAUP 4.0 (Swofford 2003). Trees were then manipulated using MacClade 4.08 (Maddison & Maddison 1992) to determine where certain character states evolved.

**RESULTS**

The strict consensus tree generated in PAUP with *Macrelaps* as the outgroup is illustrated in Figure 5, with changes in characters mapped onto the tree itself. Using 13 informative characters, the treelength is 19 steps. Figure 6 shows the strict consensus tree constructed with *Homoroselaps* as the outgroup. Treelength is 20 steps, based on 12 informative characters. Clade support for our trees was assessed with the nonparametric bootstrap (1,000 pseudoreplicates) and was weak (<70%) throughout the trees. Detailed descriptions of changes to character states can be found in Appendix 2.

While the branching order overall was quite different, a few similarities can be observed in both of the trees constructed. *Atractaspis aterrima* and *A. bibronii* form a clade in both analyses, determined by a return to plesiomorphic character states—an undivided subcaudal scale when *Macrelaps* was used as the outgroup, and a reduced temporal formula with *Homoroselaps* as the outgroup.

*Atractaspis battersbyi*, *A. reticulata* and *A. congica* formed a clade in both analyses as well, with *A. congica* serving as sister group to the other two. In both cases, the total number of ventrals and subcaudals separated these species, with *A. battersbyi* and *A. reticulata* having the most derived character state. Interestingly, when *Macrelaps* was used as the outgroup, this clade was most closely related to
A. *aterrima* and *A. bibronii*, but appeared more distantly related in the *Homoroselaps* tree.

One further clade composed of *A. leucomelas*, *A. watsoni*, *A. microlepidota* and *A. micropholis* was almost consistent between the two analyses (*A. leucomelas* is not included in the clade in the *Macrelaps* tree) and were united by a count of six supralabials in both of the trees constructed. In the *Macrelaps* tree the clade was further distinguished by a dorsal scale count of over 25 and a temporal formula of 2/3 + 4 + 5, while in the *Homoroselaps* tree the clade was further distinguished by an infralabial count of 7–8.

**DISCUSSION**

The results of this study yielded several surprises – some thought to accurately represent the evolutionary history of *Atractaspis*, while others were possibly the
result of the small number of specimens available for the study, the limitations of being forced to rely on external morphology, and the choice of outgroups. It was surprising, for example, that *A. corpulenta* and *A. reticulata*, the only species in this study in which the sublinguals are fused to the second pair of infralabials, were not closely related in either of our phylogenies. While this may be due to the low number of characters used, it may also accurately indicate convergence in this character.

Underwood & Kochva (1993) recognised two groups within *Atractaspis*: (1) the ‘bibronii’ group (represented in our study by *A. aterrima*, *A. boulengeri*, *A. congica*, *A. corpulenta*, *A. dahomeyensis*, *A. irregularis* and *A. reticulata*), characterised by normal-sized venom glands and a sub-Saharan distribution, and (2) the ‘microlepidota’ group (represented in our study by *A. engdahli*, *A. leucomelas* and *A. micropholis*), characterised by highly elongate venom glands and a North African/Middle-Eastern distribution. Neither of the phylogenies constructed in this study separated into two clades corresponding to the *bibronii* and *microlepidota* groups, nor did their groupings correspond to the geographic distributions of the species in any other way.

Figure 6. Maximum Parsimony, strict consensus tree of *Atractaspis* species obtained using *Homoroselaps* as outgroup. 1, *Atractaspis*, LF/LP greater than 1.25; postocular present; one pair of sublinguals and three gulars (rather than two pairs of sublinguals); increase in temporal formula to 1 + 3/4. 2, Increase to five gulars. 3, Decrease to five supralabials. 4, Increase to more than 25 dorsal scale rows. 5, Decrease in temporal formula to 1 + 2. 6, Increase in number of ventrals and subcaudals to over 275. 7, Sublingual fused to 2nd pair of infralabials. 8, Anal plate single rather than divided. 9, Subcaudals single rather than divided. 10, Increase to five gulars. 11, Decrease in dorsal scale rows to less than 25. 12, Sublingual fused to 2nd pair of infralabials. 13, Subcaudals partially divided. 14, Increase to 7–8 infralabials; increase in temporal formula to 2/3 + 4 + 5. 15, Increase to seven gulars. 16, Supralabials increase to six; increase in LF/LP to over 2.75. 17, Decrease in temporal formula to 1 + 3/4; increase in gulars to seven; decrease in dorsal scale rows to less than 25. 18, 1–2 postoculars. 19, Decrease in temporal formula to 1 + 2. 20, Increase in number of ventrals and subcaudals to 275–325.
A trend toward adaptations for fossoriality might be expected to represent the derived condition in *Atractaspis* species. Such adaptations include the fusion or loss of head scales (Inger & Marx 1965; Savitzky 1983), an absence of keels and pits on dorsal scales, lack of change in dorsal scale row counts along the body, a shortening of the tail, a reduction of the size of the head, rounded rostral, loss of loreal, loss of preocular, loss of anterior temporals, and a reduced distinction between the head and neck (Inger & Marx 1965; Savitzky 1983).

As explained in the introduction, the lack of agreement about the phylogenetic placement of *Atractaspis* within the Colubroidea made the choice of a suitable outgroup difficult. *Macrelaps* was selected on the basis of its phylogenetic position as determined by Underwood & Kochva (1993) and *Homoroselaps* was chosen on the basis of the molecular study by Nagy et al. (2005). However, the sister group (assumed following the results of Nagy et al. to be *Homoroselaps*) is not necessarily the best choice as an outgroup. *Homoroselaps*, like *Atractaspis*, are fossorial in their habits, while *Macrelaps* are semi-aquatic (Fitzsimons 1974). The possibility therefore exists that characters scored as pleisomorphy based on outgroup comparison with *Homoroselaps* actually represent convergent adaptations to a fossorial lifestyle.

For example, while there is a significant reduction in the number of subcaudals in *Atractaspis* as compared to *Macrelaps* (suggesting a trend towards fossoriality), other characters used in this study (e.g. a trend towards gaining head scales rather than their loss, increase in the number of gulars in contact with the sublinguals, increase in the number of temporal scales, increase in the number of infralabials) suggested the opposite. Similarly, while *Homoroselaps* has more supralabials than most species of *Atractaspis*, in most of the other characters studied more scales are added (dorsal scale row increases over 25, number of infralabials increases to 7–8, etc.). Despite this, some of these character state changes underwent subsequent reversals in certain lineages in both the *Macrelaps* and *Homoroselaps* trees. If future studies of the placement of the taxonomic affiliations of *Atractaspis* lead to consistent results, it may be possible to select a more informative outgroup. However, given the current state of knowledge, we favour the shorter tree, using *Macrelaps* as the outgroup, as a better reflection of the evolutionary history of the genus.

This study was limited by factors inherent in studying a rare group of snakes. The low sample sizes may have introduced artefacts. For example, 10 or more individuals were available for *A. aterrima*, whereas for *A. battersbyi*, only two specimens were available. *A. leucomelas* is one of the species included in this study, though all information comes from Laurent’s (1950) description of just three specimens.

It is hoped that this preliminary study will serve as a starting point for future phylogenetic analyses/character evolution studies of *Atractaspis*. Relationships recovered from our analyses are tentative because of the weak bootstrap support. Information about internal morphology and molecular data (if tissues could be obtained), have the potential to increase the robustness of our proposed phylogenies. In addition, further morphological studies such as that of Laurent (1950) and Trape et al. (2006) are needed to discern specific relationships between the various species and subspecies of *Atractaspis* in order to confidently reconstruct the evolutionary history of snakes of the genus *Atractaspis*. 
ACKNOWLEDGEMENTS

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REFERENCES


APPENDIX 1. MATERIALS EXAMINED


*Specimens photographed, from which data for LF/LP and data for number of gulars in contact with sublinguals were taken. Four additional specimens of A. irregularis (RMCA 444, RMCA 829, RMCA 1364, and RMCA 1367) were photographed, but not used in data collection for the rest of the characters in this study. No gular data were taken from A. battersbyi RMCA 20567 due to a badly damaged lower jaw. Only LF/LP data was taken from the photo of RMCA 1946.1.18.7 (A. micropholis).

**APPENDIX 2. CHANGES IN CHARACTER STATES**

**Phylogenetic analysis of characters: Macrelaps as outgroup.**—Anal plate: The anal plate pleisiomorphic condition is undivided. At points 10 (A. engdahli and A. irregularis) and 14 it becomes divided. Dorsal scale rows: The pleisiomorphic condition for dorsal scale rows is a count of less than 25. At points 2 (A. microlepidota, A. micropholis, A. watsoni), and at point 12, scale counts increase to over 25. Gulars in contact with sublinguals: It appears that the number of gulars in contact with the sublinguals increases at 1 from 3 to 5, and increases even further to 7 in A. leucomelas and A. micropholis at points 5 and 4. Gulars in contact decrease from 5 to 3 again at point 12, but return to 5 at 16 for A. battersbyi. A. irregularis has a variable number of gulars in contact with sublinguals. Number of infralabials: The number of infralabials decreases from 7–8 to 4–6 at point 6 in the largest main Atractaspis clade. LF/LP: The most parsimonious explanation for variation in the ratio of length of frontal to length of interparietal suture (LF/LP) is an increase at the base of the Atractaspis clade, point 1, and a further increase at point 5 and 3,
A. leucomelas and then A. microlepidota and A. watsoni respectively. Subcaudals: Subcaudals change from undivided to partially divided at point 8, and become fully-divided at point 9. At point 18 it reverts back to undivided for A. aterrima and A. bibronii. Sublingual fusion: Fusion of sublinguals to 2nd pair of infralabials occurs separately in 2 different species, A. reticulata and A. corpulenta (points 17 and 7, respectively). Temporal formula: The temporal formula increases to 1 + 3/4 at point 1 and increases further to 2/3 + 4 + 5 at point 2 for A. microlepidota, A. micropholis, and A. watsoni. It reduces back to 1 + 2 at point 13 for A. aterrima, A. bibronii, A. battersbyi, A. reticulata, and A. congica. Sum of ventrals and subcaudals: Sum of ventrals and subcaudals increases to an average of over 275 separately in A. aterrima and A. leucomelas (points 19 and 5, respectively). Ventral + subcaudals increase to over 325 in A. battersbyi and A. reticulata at point 15 (see Fig. 3). Supralabials: Decreases from 7 to 6 supralabials at 5 and 2, and up to 5 supralabials at 4 (A. micropholis). Also decreases to 5 supralabials at 6, but increases to 6 supralabials again at 11 for A. engdahli. Preocular: Macrelaps has no preocular, while the presence of the preocular is a synapomorphy of Atractaspis (point 1). Number of infralabials in contact with the sublinguals: Macrelaps has 3 infralabials in contact with the sublinguals, while Atractaspis is characterised by having 4 infralabials in contact with the sublinguals (point 1). Nasal division: Atractaspis is characterised by having a fully-divided nasal scale (point 1), while Macrelaps has a semi-divided nasal scale.

Phylogenetic analysis of characters: Homoroselaps as outgroup.—Anal plate: The pleisiomorphic state of the anal plate is divided. It becomes single at point 8. Dorsal scale rows: A dorsal scale count of less that 25 is the pleisiomorphic state. At point 4 the dorsal scale count increases to over 25. Dorsal scale count decreases below 25 again at point 11 for A. corpulenta and A. dahomeyensis, and at point 17 for A. leucomelas. Pairs of sublinguals: The outgroup Homoroselaps has 2 pairs of sublinguals, while as the Atractaspis clade starting at point 1 has only one pair of sublinguals. Gulars in contact with 1st pair of sublinguals: Sublinguals in contact with 1st pair of sublinguals has only one pair of sublinguals, and was counted as having 0 gulars in contact with the 1st pair of sublinguals. At point 1 (Atractaspis) it increases to 3 gulars, and increases to 5 gulars for A. engdahli at point 2. An increase to 5 gulars is also seen at point 10, and an increase to 7 gulars is seen at points 17 and 15 for A. leucomelas and A. micropholis, respectively. Number of infralabials: A count of 4–6 infralabials is the pleisiomorphic state. There is an increase to 7–8 infralabials at point 14 for the A. leucomelas, A. micropholis, A. microlepidota, and A. watsoni clade. LF/LP: Homoroselaps has an LF/LP of less than 1.25. This increases to over 1.25 at point 1 for Atractaspis. LF/LP increase further to over 2.75 at point 14 for the A. leucomelas, A. micropholis, A. microlepidota, and A. watsoni clade. Subcaudals: The pleisiomorphic state for subcaudals is divided. The subcaudals are single from point 9 on, and are partially divided for A. dahomeyensis at point 13. Sublingual fusion: The pleisiomorphic state for sublinguals is that they are not fused to the second pair of infralabials. At points 7 and 12, A. reticulata and A. corpulenta, respectively, the sublinguals are found to be fused to the 2nd pair of infralabials. Temporal formula: Homoroselaps has a temporal formula of 0 + 1. At point 1, Atractaspis, temporal formula increases to 1 + 3/4. It decreases to 1 + 2 at point 5 for the A. battersbyi, A. reticulata, and A. congica clade, and at point 19 for A. aterrima and A. bibronii. Temporal formula...
increases to $2/3 + 4 + 5$ at point 14 and decreases to $1 + 3/4$ again at point 17 for 
*A. leucomelas* (though one could also interpret it such that a temporal formula of $2/3 + 4 + 5$ arose separately in *A. micropholis*, *A. microlepidota*, and *A. watsoni*). Sum of ventrals and subcaudals: The pleisiomorphic state for ventrals and subcaudals is a count of less than 275. The count increases to over 325 at point 6 for *A. battersbyi* and *A. reticulata*. The count increases to over 275 but less than 325 at points 20 (*A. aterrima*) and 17 (*A. leucomelas*). Supralabials: The pleisiomorphic state for supralabials is a count of 6. This decreases to 5 at point 3, for the largest part of the *Atractaspis* clade. At point 16 it increases back to 6 supralabials for *A. leucomelas*, *A. microlepidota*, and *A. watsoni*. Postocular: *Homoroselaps* has no postoculars, while the presence of a postocular begins at point 1 at the *Atractaspis* clade. *A. watsoni*, at point 18, can have 1 or 2 postoculars.