

# A quantitative analysis of two scale characters in snakes

Kevin Moore, Kate Jackson\*

**Abstract.** We quantified the effectiveness of two scale characters commonly used to identify snakes: smooth versus keeled dorsal scales and straight versus oblique dorsal scale rows. We examined 169 species of African snakes from close-up photographs of the dorsal scales. We calculated the prominence of keels (if present) along the dorsal scales and the degree of straightness or obliqueness of the dorsal scale rows. We compared our measurements to species descriptions from the literature and looked for overlap of the character states with each other. Our results show a distinct difference between keel prominence for species described as having keeled dorsal scales versus species described as having smooth dorsal scales. Our results also show considerable overlap of straightness or obliqueness between species described as having straight dorsal scale rows versus those described as having oblique dorsal scale rows. Revision of this character would be beneficial.

*Keywords:* description, identification, scales, Serpentes, taxonomy.

## Introduction

Snake identification is contingent upon physical observations of a variety of characters. These can range from size and shape of the body, to more-detailed scale characters (e.g., Boulenger, 1888; Meirte, 1992; Chippaux, 2006). Many of these scale descriptions, which are still widely used today, have been in practice since before the advent of Darwinian theory (e.g., Smith, 1831) and there has been no real, critical analysis performed to ascertain the usefulness, or even the accuracy, of these characters. Scale descriptions have been used primarily for the identification of species; but also to determine phylogenetic relationships (Bogert, 1940; Dowling, 1969) and even to examine relationships between morphology and fitness (Arnold, 1983). However, none of these studies ask the question of whether we ought to simply continue relying upon these previously-established means of identification, or if reconsidering the usefulness of some of these characters is necessary. In this study, we investigated two commonly used scale characters by quantitatively assessing their effectiveness at differentiating one character state from the other.

We quantified two particular characters: keeled versus smooth dorsal scales, and straight versus oblique dorsal scale rows. We hypothesized, based on personal observations, that the character of smooth versus keeled was a reliable character to use, and that our data would support this hypothesis that species described in the literature as being keeled would demonstrate a significant difference from species described in the literature as being smooth. Our second hypothesis concerned the character of straight versus oblique dorsal scale rows. The subjectivity of this particular character oftentimes makes it difficult to distinguish one character state from the other. We hypothesized that there would be no significant difference between the data for species described in the literature as being straight versus those described as being oblique; and, as a result, this particular character would be unreliable as a distinguishing character in further studies or species identification.

## Materials and methods

Data were collected from fluid-preserved specimens held at the Royal Museum of Central Africa in Tervuren, Belgium. 169 species of central and western African snakes were examined. The choice of species was based on availability of specimens in the collection. A specimen of each species was photographed mid-body, to clearly show the dorsal scales.

---

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

\*Corresponding author; e-mail: jacksok@whitman.edu

Photographs were taken remotely using a 10.0 megapixel Olympus Digital Camera mounted on a copy stand. The camera was equipped with a 50 mm 1 : 2 Macro ED Lens as well as an Olympus Ring Flash and its corresponding Macro Flash Controller. Measurements were made using Image J 1.41 software (©Wayne Rasband).

For measurements of keeled versus smooth scales, three scales dorsal scales were measured from the photographs. If a keel was at all discernible, then measurements were made of the length of the keel and the length of the entire scale for each scale. A ratio was calculated of keel length to scale length to quantify the percent of the scale that the keel covered (fig. 1a and b).

In order to compare straight versus oblique scale rows, the same images of the dorsal scale rows were used. The lengths of the two posteriorly angled edges of each of three scales were measured and a ratio was obtained for each scale by dividing the measurement of the longer edge by the measurement of the shorter edge (fig. 1c and d). The mean of the three ratios was used to quantify the degree of straightness or obliqueness of the dorsal scale rows.

The ratios calculated from the measurements were then compared to data obtained from the literature (Chippaux 2006) in which species were described in detail, including information about whether the dorsal scales were smooth or keeled and whether dorsal scale rows were straight or oblique.

## Results

The results of comparison of species described as having keeled dorsal scales versus species described as having smooth dorsal scales showed a clear difference between these two taxonomic characters. Every species described as having smooth dorsal scales possessed no keel of any form on its dorsal scales, and only 6 species which the literature described as having keeled scales were found in fact to have smooth scales (fig. 2a).

By contrast, the results for species described as having straight dorsal scale rows versus those described as having oblique dorsal scale rows showed considerable overlap between the two character states (fig. 2b). The results for the species described as having straight dorsal scale rows show a distinct, right-skewed trend while the results for the species described as having oblique scale rows show no such trend. A total of 36 species of snakes described in the literature as having oblique dorsal scale rows fall

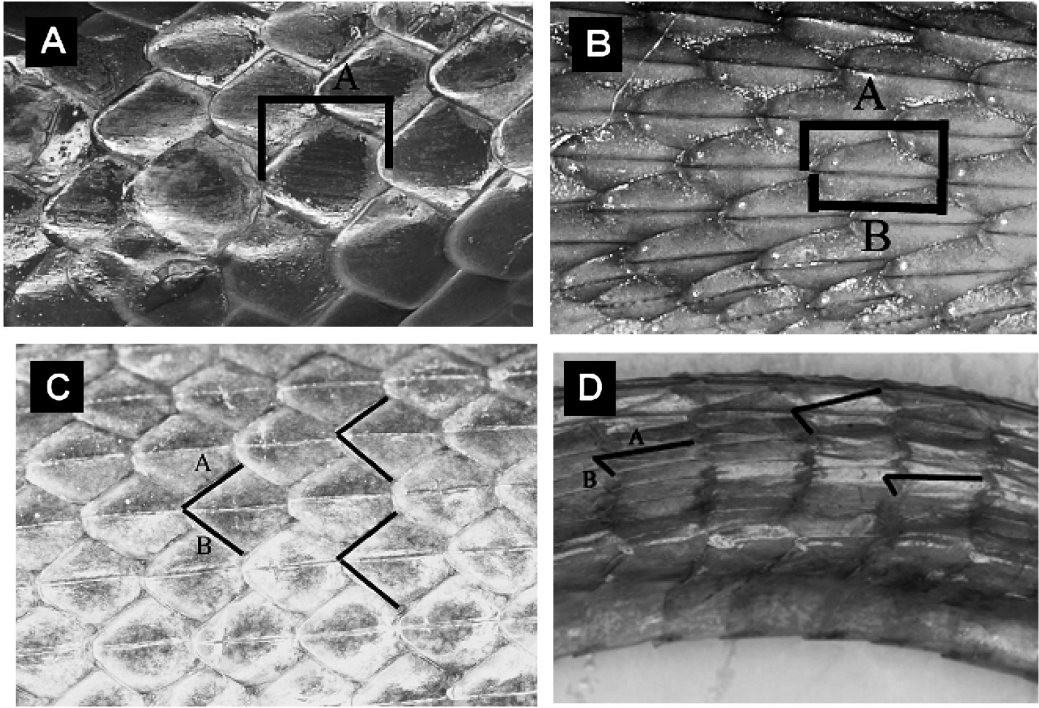
into the range of the species described as having straight dorsal scale rows. A list of specimens examined, the ratios calculated for them, and their character state as described in the literature is provided in Appendix 1.

## Discussion

Based on the comparison of measurements made in this study with descriptions of species in the literature (Chippaux, 2006) as having keeled dorsal scales versus those described as having smooth dorsal scales, this appears to be a reliable character to use when identifying or describing species. While there were six species described as having keeled scales which yielded ratios indicating no such keel, there are a few possible explanations for these anomalies. The literature which contains species descriptions is oftentimes based on small sample sizes (e.g., Witte, 1930), and this might lead to species accounts which do not account for proper variation. It is also possible that the data collection techniques (measurements made on photographic images) may have contributed to this complication. Despite these six outliers however, there was still a marked difference between the measurements of species described in the literature as having smooth dorsal scales versus those described as having keeled dorsal scales. This is a viable character to use in identification of snake species.

The character of straight versus oblique dorsal scale rows proves to be as complicated as anticipated. The data show substantial overlap between what should be two, separate character traits. This leads us to propose a revision of this particular character.

One potential solution would be to quantify exactly how oblique dorsal scale rows must be before they can be considered oblique (as is done with eye size in snakes). For example, it could be stipulated that the longer, posteriorly-angled edge of the scale must be at least three times longer than the shorter, posteriorly-angled edge. One drawback to this system is that it

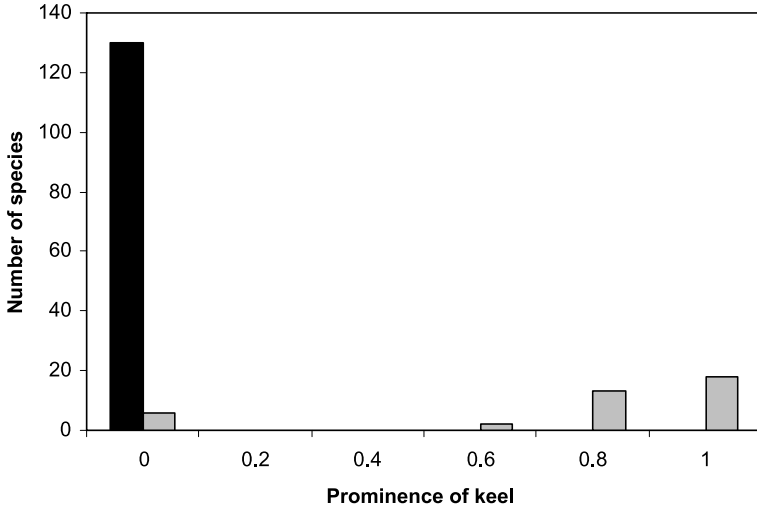


**Figure 1.** (a) *Aparallactus capensis*: example of measurements made of a species with smooth dorsal scales. Ratio = 0.000. (b) *Dasypletis atra*: example of measurements made of a species with keeled dorsal scales. Ratio = 0.923. (c) *Hydraethiops melanogaster*: example of measurements made of a species with straight dorsal scale rows. Ratio = 1.065. (d) *Dispholidus typus*: example of measurements made of a species with oblique dorsal scale rows. Ratio = 3.559.

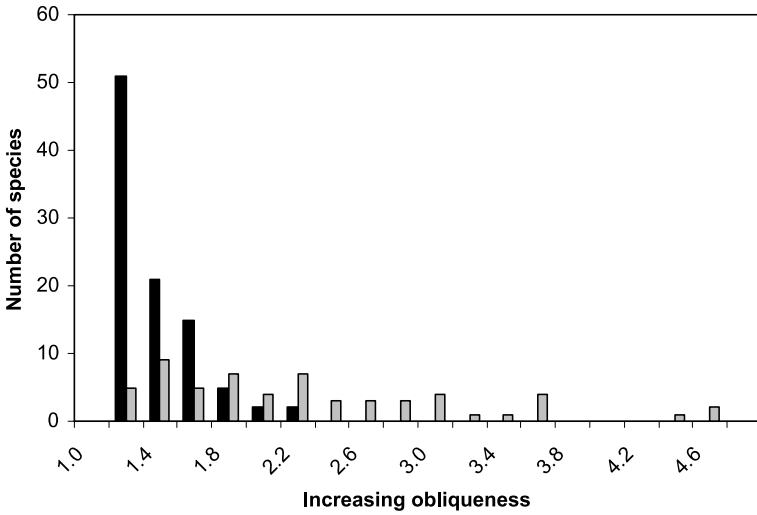
would be impractical to make such measurements in the field, or even the museum without image-analysing software. A better solution would be to discontinue using this particular character in dichotomous keys or other systems of identification. It would still be acceptable to keep information regarding the degree of straightness or obliqueness of the dorsal scale rows in species descriptions; but researchers should be aware of the subjectivity and variation inherent in this character.

It has been noted that there is an enormous amount of variation in scale characters in snakes (Marx and Rabb, 1972); but, to date, there are no previous published studies which quantitatively assess the effectiveness of these scale characters as we use them today. The preliminary study presented here, studied two such characters. Future related projects could investigate aspects of quantification of scale characters from additional perspectives. For exam-

ple, future studies could examine both other scale characters and additional specimens from more diverse localities. A total of 169 separate species of snakes were examined here, but they were all from central and western Africa, for the practical reason that the data collected here were collected in the course of a larger study of African snakes. It would be useful to know if these results can be generalised for species from other continents as well, particularly Europe and North America where the taxonomy of the snakes is better-known. A failing we have noted in the literature as the possible source of erroneous information about character states is the small sample size on which original descriptions are typically based. Here too we examined only one specimen of each species, constrained by availability of materials working with rare taxa, and focusing on comparing taxa, whereas an alternate project would be to look at many individuals of a single species in order to de-



(a)



(b)

**Figure 2.** (a) Prominence of keel in species described in the literature as having keeled dorsal scales (indicated by the gray data bars) versus those described in the literature as having smooth dorsal scales (indicated by the black data bar). The value along the x-axis represents the percentage of the dorsal scale that is covered by a keel for each individual species. (b) Degree of straightness or obliqueness for species described in the literature as having straight dorsal scale rows (indicated by the black data bars) versus species described in the literature as having oblique dorsal scale rows (indicated by the gray data bars). The value along the x-axis demonstrates the ratio of the length of the longer, posteriorly-angled edge of a dorsal scale over its shorter, posteriorly-angled edge.

termine the extent of intraspecific variation in these characters. Such an approach has the potential to reveal variation related to sexual dimorphism and ontogeny. Another issue to consider is that of variation of scales in a single individual. We measured three scales from each specimen, but in some cases there is variation

in these characters in a single specimen (e.g., Scales may be keeled on one part of the body but smooth on another; An otherwise smooth-scaled snake may have a few scales that could be considered “weakly-keeled”).

For situations where quick, accurate identifications of species are necessary (e.g., Wozniak,

Wisser and Schwartz, 2006) it is imperative that our understanding of scale characters include detailed knowledge of their inherent subjectivity, if any. The field of herpetology would also benefit from a critical analysis of the traditional system of species identification based on morphological characters. The results of such studies would make possible a long overdue revision of the use of scale characters.

**Acknowledgements.** We thank D. Meirte and G. Cael for access to the collection of the Royal Museum of Central Africa. J.-P. Chippaux provided helpful insights into this project in its early stages. H. Greene provided suggestions during the preparation of the manuscript. W. Kunkel and K. Moyer assisted with the collection of data. This project was funded in part by a Perry Award from Whitman College. We thank two anonymous reviewers for helpful comments.

## References

- Arnold, S.J. (1983): Morphology, performance and fitness. *American Zoologist*. **23**: 347-361.
- Bogert, C.M. (1940): Herpetological results of the Vernay Angola expedition, with notes on African reptiles in other collections. Part I. Snakes, including an arrangement of African Colubridae. *Bull. Am. Mus. Nat. Hist.* **23**: 1-107.
- Boulenger, G. (1888): On new or little-known South African reptiles. *Mag. Nat. Hist.* **2**: 136-141.
- Chippaux, J.-P. (2006): *Les Serpents d'Afrique Occidentale et Centrale*, 3rd Edition. Institut de Recherche pour le Developpement, Paris.
- Dowling, H.G. (1969): Relations of some African colubrid snakes. *Copeia* **2**: 234-242.
- Marx, H., Rabb, G.B. (1972): Phyletic analysis of fifty characters of advanced snakes. *Fieldiana: Zoology* **63**: 1-321.
- Meirte, D. (1992): Clés de détermination des serpents d'Afrique. *Annls. Mus. Roy. Afr. Centr., Sci. Zool.* **276**: 1-152.
- Smith, A. (1831): Contributions to the natural history of South Africa. *South African Quart. J.* **1**: 9-24.
- Witte, G.F. (1930): Un serpent nouveau du Congo Belge (*Rhinocalamus rodhaini* sp. n.). *Rev. Zool. Bot. Afr.* **19**: 1-3.
- Wozniak, E.J., Wisser, J., Schwartz, M. (2006): Venomous adversaries: a reference to snake identification, field safety, and bite-victim first aid for disaster-response personnel deploying into the hurricane-prone regions of North America. *Wilderness and Environmental Medicine*. **17**: 246-266.

Received: May 11, 2009. Accepted: September 23, 2009.

**Appendix 1.** List of individual specimens of species included in the study. The columns "smooth versus keeled" and "straight versus oblique" refer to the way they are described in Chippaux (2006). The remaining columns show the ratio calculated for each specimen.

Species	RMCA number	Keeled or smooth	Keel/smooth data	Straight or oblique	Str/obl data
<i>Afronatrix anascopus</i>	29 566	Keeled	0.862	Straight	1.108
<i>Amblyodipsas katagensis</i>	9322	Smooth	0.000	Straight	1.085
<i>Aparallactus capensis</i>	15 144	Smooth	0.000	Straight	1.090
<i>Aparallactus lunulatus</i>	3862	Smooth	0.000	Straight	1.066
<i>Aparallactus modestus</i>	A7-003-R-0032	Smooth	0.000	Straight	1.084
<i>Aparallactus moeruensis</i>	240	Smooth	0.000	Straight	1.092
<i>Apsidelaps lubricus</i>	10 668	Smooth	0.000	Oblique	2.014
<i>Atheris chlorechis</i>	30 949	Keeled	0.714	Straight	1.070
<i>Atheris hispida</i>	15 841	Keeled	0.838	Straight	1.084
<i>Atheris nitschei</i>	29 760	Keeled	0.862	Straight	1.109
<i>Atheris squamigera</i>	A7-028-R-0070	Keeled	0.860	Straight	1.119
<i>Atractaspis aterrima</i>	29 590	Smooth	0.000	Straight	1.514
<i>Atractaspis battersbyi</i>	21 056	Smooth	0.000	Straight	1.516
<i>Atractaspis bibronii</i>	1587	Smooth	0.000	Straight	1.290
<i>Atractaspis boulengeri</i>	109	Smooth	0.000	Straight	1.476
<i>Atractaspis congica</i>	18 701	Smooth	0.000	Straight	1.392
<i>Atractaspis corpulenta</i>	901	Smooth	0.000	Straight	1.248
<i>Atractaspis dahomeyensis</i>	29 742	Smooth	0.000	Straight	1.261
<i>Atractaspis irregularis</i>	8757	Smooth	0.000	Straight	1.221

## Appendix 1. (Continued).

Species	RMCA number	Keeled or smooth	Keel/smooth data	Straight or oblique	Str/obl data
<i>Atractaspis microlepidota</i>	73-15-R-236	Smooth	0.000	Straight	1.228
<i>Atractaspis reticulate</i>	A7-003-R-0029	Smooth	0.000	Straight	1.083
<i>Bitis arietans</i>	A7-0028-R-0090	Keeled	0.870	Oblique	1.298
<i>Bitis gabonica</i>	78-16-R-59	Keeled	0.822	Oblique	1.373
<i>Bitis nasicornis</i>	29 335	Keeled	0.798	Oblique	1.196
<i>Boiga blandingii</i>	28 408	Smooth	0.000	Oblique	2.049
<i>Boiga pulverulenta</i>	20.271	Smooth	0.000	Oblique	2.476
<i>Bothrolycus ater</i>	9276	Smooth	0.000	Straight	1.312
<i>Bothrophthalmus lineatus</i>	75-28-R-40	Keeled	0.876	Straight	1.018
<i>Buroma depressiceps</i>	18 091	Keeled	0.599	Straight	1.097
<i>Calabaria reinhardtii</i>	29 853	Smooth	0.000	Straight	1.086
<i>Causus lichtensteinii</i>	11 237	Smooth	0.000	Straight	2.121
<i>Causus maculatus</i>	15 885	Smooth	0.000	Straight	1.580
<i>Causus resimus</i>	14 383	Smooth	0.000	Straight	1.418
<i>Cerastes cerastes</i>	28 580	Keeled	0.650	Straight	1.280
<i>Cerastes vipera</i>	8496	Keeled	0.660	Straight	1.055
<i>Chamaelycus christyi</i>	1802	Smooth	0.000	Straight	1.011
<i>Chamaelycus fasciatus</i>	87-43-R-23	Smooth	0.000	Straight	1.805
<i>Chamaelycus parkerii</i>	15 423	Smooth	0.000	Straight	1.775
<i>Chilorhinophis gerardi</i>	748	Smooth	0.000	Straight	1.107
<i>Crotaphopeltis degeni</i>	76-003-R-0146	Smooth	0.000	Straight	1.475
<i>Crotaphopeltis hippocrepis</i>	73-014-R-0045	Smooth	0.000	Straight	1.097
<i>Crotaphopeltis hotamboeia</i>	27 163	Weakly Keeled	0.000	Straight	1.149
<i>Dasypeltis atra</i>	76-3-R-423	Keeled	0.923	Oblique	1.453
<i>Dasypeltis fasciata</i>	28 097	Keeled	0.905	Oblique	1.626
<i>Dasypeltis palmarum</i>	A7-028-R-0107	Keeled	0.878	Oblique	1.283
<i>Dasypeltis scabra</i>	11 824	Keeled	0.789	Oblique	1.045
<i>Dendroaspis augusticeps</i>	11 184	Smooth	0.000	Oblique	2.243
<i>Dendroaspis jamesoni</i>	A7-028-R-0085	Smooth	0.000	Oblique	1.935
<i>Dendroaspis polylepis</i>	74-13-R-28	Smooth	0.000	Oblique	2.379
<i>Dendroaspis viridis</i>	28 289	Smooth	0.000	Oblique	3.005
<i>Dipsadoboa duchesni</i>	476	Smooth	0.000	Oblique	1.240
<i>Dipsadoboa elongate</i>	18 537	Smooth	0.000	Oblique	1.063
<i>Dipsadoboa shrevei</i>	8257	Smooth	0.000	Oblique	1.321
<i>Dipsadoboa unicolor</i>	16 888	Smooth	0.000	Oblique	1.156
<i>Dipsadoboa viridis</i>	A1-102-R-0001	Smooth	0.000	Oblique	1.183
<i>Dipsadoboa weileri</i>	2488	Smooth	0.000	Oblique	1.396
<i>Dispholidus typus</i>	73-17-R-149	Keeled	0.556	Oblique	3.559
<i>Dromophis lineatus</i>	14 861	Smooth	0.000	Straight	1.412
<i>Dromophis preornatus</i>	29 464	Smooth	0.000	Straight	1.478
<i>Duberria lutrix curry linolahli</i>	21 634	Smooth	0.000	Straight	1.321
<i>Duberria lutrix shirana</i>	77-46-R-3	Smooth	0.000	Straight	1.411
<i>Elapsoidea guntherii</i>	1482	Smooth	0.000	Straight	1.588
<i>Elapsoidea laticincta</i>	30 846	Smooth	0.000	Straight	1.462
<i>Elapsoidea loveridgei</i>	78-29-R-44	Smooth	0.000	Straight	1.859
<i>Elapsoidea semiannulata</i>	A7-003-R-0014	Smooth	0.000	Straight	1.892
<i>Gonglyophis muelleri</i>	73-15-R-261	Smooth	0.000	Straight	1.387
<i>Gonionotophis brussaui</i>	89-20-R-79	Keeled	0.835	Straight	1.069
<i>Gonionotophis klingi</i>	29 670	Keeled	0.896	Straight	1.133
<i>Grayia Caesar</i>	1663	Smooth	0.000	Straight	1.245
<i>Grayia ornate</i>	A4-046-R-0003	Smooth	0.000	Straight	1.093
<i>Grayia Smythii</i>	R 1667	Smooth	0.000	Straight	1.224
<i>Grayia tholloni</i>	A6-007-R-0007	Smooth	0.000	Straight	1.194
<i>Haemorrhhois dorri</i>	29 513	Smooth	0.000	Straight	1.260

## Appendix 1. (Continued).

Species	RMCA number	Keeled or smooth	Keel/smooth data	Straight or oblique	Str/obl data
<i>Hapsidophrys lineatus</i>	9781	Keeled	0.848	Oblique	1.271
<i>Hapsidophrys smaragdina</i>	1158	Keeled	0.914	Oblique	1.206
<i>Helophis schoutedeni</i>	85-21-R-20	Weakly Keeled	0.000	Straight	1.117
<i>Hemirhagerrhis notataenia</i>	1901	Smooth	0.000	Straight	1.483
<i>Hormonotus modestus</i>	21 564	Keeled	0.000	Straight	1.440
	76-14-R-121				
<i>Hydraethiops melanogaster</i>	2.768	Keeled	0.854	Straight	1.065
<i>Hyoptophis wilsoni</i>	74-13-R-128	Smooth	0.722	Straight	1.101
<i>Lamprophis fuliginosus</i>	78-29-R-1	Smooth	0.000	Straight	1.718
<i>Lamprophis lineatus</i>	81-25-R-71	Smooth	0.000	Straight	1.419
<i>Lamprophis olivaceus</i>	87-37-R-1	Smooth	0.000	Straight	1.087
<i>Lamprophis virgatus</i>	77-9-R-2	Smooth	0.000	Straight	1.365
<i>Limnophis bicolor</i>	80-32-R-72	Smooth	0.000	Straight	1.315
<i>Lycodonomorphus bicolor</i>	78-11-R-16	Smooth	0.000	Straight	1.350
<i>Lycodonomorphus leleupi</i>	17 637	Smooth	0.000	Straight	1.147
<i>Lycodonomorphus subtaeniatus</i>	14 864	Smooth	0.000	Straight	1.116
<i>Lycophidion capense</i>	86-01-R-51	Smooth	0.000	Straight	1.317
<i>Lycophidion irroratum</i>	29 707	Smooth	0.000	Straight	1.424
<i>Lycophidion laterale</i>	87-42-R-6	Smooth	0.000	Straight	1.436
<i>Lycophidion meleagre</i>	97-021-R-0101	Smooth	0.000	Straight	1.846
<i>Lycophidion nigromaculatum</i>	A7-036-R-0027	Smooth	0.000	Straight	1.343
<i>Lycophidion ornatum</i>	79-15-R-16	Smooth	0.000	Straight	2.111
<i>Lycophidion polylepis</i>	1743	Smooth	0.000	Straight	1.417
<i>Lycophidion semicinctum</i>	29 489	Smooth	0.000	Straight	1.722
<i>Lytorhynchus diadema</i>	28 572	Smooth	0.000	Straight	1.246
<i>Macrelaps microlepidotus</i>	81-6-R-185	Smooth	0.000	Straight	1.084
<i>Malpolon moilensis</i>	28 589	Smooth	0.000	Straight	1.110
<i>Mehelya capensis</i>	29 931	Keeled	0.777	Straight	1.515
<i>Mehelya crossi</i>	28 061	Keeled	0.854	Straight	1.009
<i>Mehelya guirali</i>	97-021-R-0103	Keeled	0.830	Straight	1.053
<i>Mehelya laurenti</i>	21 026	Keeled	0.647	Straight	1.729
<i>Mehelya nyassae</i>	30 641	Keeled	0.690	Straight	1.321
<i>Mehelya poensis</i>	83-24-R-53	Keeled	0.914	Straight	1.457
<i>Mehelya stenophthalmus</i>	87-43-R-36	Keeled	0.753	Straight	1.669
<i>Meizodon coronatus</i>	29 718	Smooth	0.000	Straight	1.070
<i>Meizodon regularis</i>	29 826	Smooth	0.000	Straight	1.105
<i>Meizodon semiornatus</i>	1867	Smooth	0.000	Straight	1.200
<i>Naja anchietae</i>	4497	Smooth	0.000	Oblique	2.066
<i>Naja annulata</i>	A7-31	Smooth	0.000	Straight	1.190
<i>Naja christyi</i>	11 559	Smooth	0.000	Straight	1.244
<i>Naja haje</i>	28 509	Smooth	0.000	Oblique	1.754
<i>Naja katiensis</i>	29 286	Smooth	0.000	Oblique	2.327
<i>Naja melanoleuca</i>	21 432	Smooth	0.000	Oblique	2.949
<i>Naja nigricollis</i>	8303	Smooth	0.000	Oblique	2.924
<i>Natriciteres fuliginoides</i>	89-20-R-99	Smooth	0.000	Straight	1.135
<i>Natriciteres olivacea</i>	6576	Smooth	0.000	Straight	1.236
<i>Natriciteres variegata</i>	29 881	Smooth	0.000	Straight	1.306
<i>Paranaja multifasciata</i>	76-1-R-3	Smooth	0.000	Oblique	3.426
<i>Philothamnus bequaerti</i>	3346	Smooth	0.000	Oblique	2.648
<i>Philothamnus carinatus</i>	15 105	Smooth	0.000	Oblique	1.555
<i>Philothamnus dorsalis</i>	90-60-R-5	Smooth	0.000	Oblique	2.127
<i>Philothamnus heterodermus</i>	1910	Smooth	0.000	Oblique	2.008
<i>Philothamnus heterolepidotus</i>	5141	Smooth	0.000	Oblique	2.813

## Appendix 1. (Continued).

Species	RMCA number	Keeled or smooth	Keel/smooth data	Straight or oblique	Str/obl data
<i>Philothamnus hoplogaster</i>	78-17-R-36	Smooth	0.000	Oblique	1.737
<i>Philothamnus irregularis</i>	5834	Smooth	0.000	Oblique	2.573
<i>Philothamnus nitidus</i>	R.G. 19 054	Smooth	0.000	Oblique	2.601
<i>Philothamnus ornatus</i>	30 673	Smooth	0.000	Oblique	2.793
<i>Philothamnus semivariiegatus</i>	85-30-R-186	Smooth	0.000	Oblique	2.006
<i>Polemon acanthias</i>	29 550	Smooth	0.000	Straight	1.314
<i>Polemon bocourti</i>	9388	Smooth	0.000	Straight	1.103
<i>Polemon christyi</i>	8256	Smooth	0.000	Straight	1.113
<i>Polemon collaris</i>	87-43-R-48	Smooth	0.000	Straight	1.132
<i>Polemon fulvicollis</i>	1558	Smooth	0.000	Straight	1.130
<i>Polemon gabonensis</i>	10 545	Smooth	0.000	Straight	1.137
<i>Polemon notatus</i>	A7-003-R-0035	Smooth	0.000	Straight	1.055
<i>Polemon robustus</i>	8761	Smooth	0.000	Straight	1.021
<i>Prosymna ambigua</i>	2177	Smooth	0.000	Straight	1.081
<i>Prosymna meleagris</i>	29 591	Smooth	0.000	Straight	1.123
<i>Psammophis angolensis</i>	A7-028-R-0088	Smooth	0.000	Oblique	1.782
<i>Psammophis elegans</i>	29 572	Smooth	0.000	Oblique	1.365
<i>Psammophis phillipsii</i>	30 816	Smooth	0.000	Oblique	1.746
<i>Psammophis schokari</i>	2203	Smooth	0.000	Oblique	1.692
<i>Psammophis sibilans</i>	21 200	Smooth	0.000	Oblique	1.954
<i>Psammophis subtaeniatus</i>	76-3-R-252	Smooth	0.000	Oblique	1.695
<i>Psammophylax tritaeniatus</i>	11 180	Smooth	0.000	Straight	1.148
<i>Pseudaspis cana</i>	18 208	Smooth	0.000	Straight	1.105
<i>Pseudohaje goldii</i>	15 464	Smooth	0.000	Oblique	2.597
<i>Python natalensis</i>	15 386	Smooth	0.000	Straight	1.069
<i>Python regius</i>	A7-036-R-0010	Smooth	0.000	Straight	1.116
<i>Python sebae</i>	3	Smooth	0.000	Straight	1.128
<i>Ramphiphis acutus</i>	30 787	Smooth	0.000	Straight	1.107
<i>Ramphiphis oxyrhynchus</i>	29 650	Smooth	0.000	Straight	1.336
<i>Scaphiophis albopunctatus</i>	97-021-R-106- TOT 110	Smooth	0.000	Straight	1.084
<i>Spalerosophis diadema</i>	R.G. 2232	Weakly Keeled	0.000	Straight	1.106
<i>Telescopus obtusus</i>	2235	Smooth	0.000	Oblique	1.435
<i>Telescopus semiannulatus</i>	28 046	Smooth	0.000	Oblique	2.071
<i>Thelotomis capensis</i>	78-9-R-9	Keeled	0.767	Oblique	3.394
<i>Thelotomis kirtlandii</i>	11 243	Keeled	0.790	Oblique	4.201
<i>Thrasops aethiopissa</i>	14 669	Smooth	0.000	Oblique	3.435
<i>Thrasops batesii</i>	19 070	Smooth	0.000	Oblique	2.993
<i>Thrasops flavigularis</i>	R.S. 1448	Keeled	0.000	Oblique	3.471
<i>Thrasops jacksoni</i>	76-3-R-125	Keeled*	0.000	Oblique	4.416
<i>Thrasops occidentalis</i>	28 236	Keeled	0.751	Oblique	4.418
<i>Xenocalamus bicolor</i>	7965	Smooth	0.000	Straight	1.040
<i>Xenocalamus mechowii</i>	11 763	Smooth	0.000	Straight	1.147
<i>Xenocalamus michellii</i>	18 247	Smooth	0.000	Straight	1.151

\* Keels only present on paravertebral rows which were not included in measurements for any specimens.