Body elongation and decreased reproductive output within a restricted clade of lizards (Reptilia: Scincidae)

HUGH GRIFFITH*

Department of Integrative Biology, University of California, Berkeley, California 94720, USA

(Accepted 4 August 1993)

(With 3 figures in the text)

Relationships between body shape and relative abdominal size were compared among differentially elongate species within the scincid lizard genus *Brachymeles*, to investigate how morphological evolution affects the proportion of body volume available to hold eggs and offspring. Relative abdominal size is inversely related to elongation, suggesting that relative clutch mass decreases with addition of abdominal body segments. Shape–volume relationships contradict trends seen in comparisons among distantly related limbed and limbless squamates (lizards and snakes), in which snakes have relatively more abdominal volume. Comparison within a phylogenetically restricted group allows the identification of functional and ontogenetic factors potentially limiting reproductive output. In *Brachymeles*, constraining factors include retention of anterior body segments bearing parasternal ribs, which prevents extension of the clutch anteriorly within the body, and reduction of allometry of abdominal segments, which provides extended series of uniformly-sized vertebrae for limbless locomotion, but reduces the relative size of the abdomen. The latter trait is associated with overall size reduction, which affects relative egg-size and packing. Factors constraining abdominal volume in this genus are probably common to other elongate lizards, a morphological group that has been rarely represented in comparative studies of life history.

Contents

	Page
Introduction	541
Materials and methods	542
Results	543
Elongation and correlated morphological variation	543
Elongation and reproductive output	546
Discussion	547
References	549
Appendix 1	550

Introduction

Interspecific variation in reproductive output within lizards and snakes has received substantial attention (e.g. Tinkle, 1969; Tinkle, Wilbur & Tilley, 1970; Vitt & Congdon, 1978; Vitt & Price, 1982; Ballinger, 1983; Stearns, 1984; Dunham & Miles, 1985; Dunham, Miles & Reznick, 1988; Shine & Greer, 1991; Shine, 1992). A common measure of reproductive output is relative clutch mass (RCM), a ratio of mass of the clutch relative to maternal mass (including or excluding clutch

* Present address: 14127 64th Ave., Surrey, British Columbia, V3W 1Y9, Canada

mass). Vitt & Congdon (1978) found that differences in body shape among lizards with different foraging modes accounted for much of the observed variation in RCM, and suggested that RCM could be predicted for given body shapes. In a recent quantitative study, Shine (1992) determined that differences in body morphology, expressed as a ratio of trunk volume:total mass, could account for the higher RCMs in snakes than in limbed lizards, and thus regarded body shape as having a role in constraining or explaining RCM. Relationships among lizards (from several families) were less clear, but there was some statistical correlation between shape and RCM.

Both of these studies, and others (e.g. Ballinger, 1983; Stearns, 1984; Dunham & Miles, 1985; Dunham, Miles & Reznick, 1988) have compared 'typical' species from different genera, families or suborders. Perhaps because of unavailability of live animals or published data, comparative studies of life history have rarely exploited broad ranges of morphologies within more restricted groups (within families or genera). In particular, comparative studies of reproductive output have neglected elongate, limb-reduced lizards, which offer an extreme body form to investigate further relationships between shape and RCM, without making a phylogenetic leap to snakes.

Elongation has evolved in a multitude of clades (Gans, 1975), and it is not known if this recurrent general morphology is correlated with high RCMs in any lizard taxon, as it is in snakes (Seigel & Fitch, 1984; Shine, 1992). Snakes are different from limbless lizards in several respects which may influence the amount of the trunk available to retain the clutch, including numbers of abdominal segments, and morphology and arrangement of internal organs. An elongate body, plus lack of limbs may lead to a high relative abdomen size in snakes (compared to 'typical' lizards), but it is unclear whether that same relationship would be obtained from a phylogenetically restricted comparison within lizards only. Limb-reduced lizards retain elements of saurian anatomy and morphology that are absent in snakes, and the degree to which ancestral traits are present varies among members of different families and genera. Depending on how elongation occurs (by increasing the number of abdominal segments, or their relative sizes), limb-reduced lizards may not have a relatively large available abdominal volume, despite overall elongation of the body.

In this paper, relative abdominal size for several species within the genus *Brachymeles*, a clade of lizards in which there is considerable variation in morphology, is estimated. Also tested is if relatively serpentine body forms correlate with higher abdominal volume:body mass ratios, and therefore potentially to higher RCM values, as has been determined for snakes. This result should provide a first relative estimate of RCM in limbless lizards, a phylogenetically diverse group that shows uniformity in numerous features (Gans, 1975). In addition, through interspecific comparisons of anatomy and allometric growth within *Brachymeles*, ancestral features are identified in elongate species which influence abdominal size, and it is suggested that elongate lizards have constraints to body volume that have been overcome in the evolution of snakes.

Materials and methods

Brachymeles contains approximately 14 species, and is endemic to the Philippines and part of Sarawak, Malaysia (Brown & Alcalá, 1980; Hikida, 1982). It is a monophyletic group, as evidenced by several features, which are believed to be synapomorphies for the genus because of their uniqueness to *Brachymeles* relative to the remaining Scincidae plus its sister group, the Cordylidae (Estes, de Queiroz & Gauthier, 1988). All species possess a depressed triangular head with a broad, bluntly-rounded snout, bearing thickened rostral and anterior labial scales. The first labial scale is much longer than subsequent scales, and may be fused with the postnasal scale (see Brown & Alcalá, 1980). Fore- and hindlimbs, if present, are short with very short digits.

A series of comparisons was made to assess interspecific variation in elongation and other aspects of morphology. Seven species representing the range of elongation within the group were examined in detail. *Brachymeles boulengeri*, *B. gracilis*, *B. talinus* and *B. schadenbergi* are relatively large, and have short, pentadactyl limbs. *Brachymeles tridactylus* and *B. bonitae* are small, and have tiny limbs with three or fewer minute digits. *Brachymeles vermis* is small, and has no external limb elements. Mensural and anatomical data were collected from specimens in the herpetology collection of the California Academy of Sciences (**Appendix 1**). Digital callipers were used to measure head length (snout-tip to posterior margin of interparietal scale), body width at mid-body, body depth at mid-body, snout-vent length (SVL), and axilla-groin length. For the limbless species *B. vermis* axilla-groin length was estimated from radiographs, using the distance between limb girdles. This provided an accurate approximation, as determined by comparison of values obtained similarly from radiographs of specimens of limbed species with their external measurements.

Counts of presacral vertebrae (PSV) and parasternal ribs (PSR) (*sensu* Camp, 1923) were obtained from radiographs. In order to assess relative size of vertebrae along the length of the trunk, centrum lengths of all presacral vertebrae from juveniles and adults of each species were measured to the nearest 0.1 mm from radiographs using an EP01 microscope mounted with a digital calliper.

Sex determination, reproductive status, numbers, state, position, and orientation of eggs and embryos relative to internal organs and the longitudinal maternal body axis were determined by dissection and X-radiography.

Because there is no unambiguous anatomical differentiation of the trunk into 'thorax' and 'abdomen', I defined it in functional terms. Abdominal length was designated as the length of that portion of the trunk in which the clutch mass is contained, as measured from radiographs of females containing well-formed embryos. All species are viviparous. For Group 1, the anterior limit of the abdomen was found to be at the level of the 15th vertebra. For Group 2 species except *B. vermis*, it was at the 24th vertebra, and for *B. vermis* it was at the 30th vertebra. The pubis was designated as the posterior limit to the abdomen in all species. For non-gravid adult females, which were included to increase sample sizes, the anatomically equivalent length was measured, by reference to homologous vertebrae. Sample sizes varied among species, with a minimum of 4 in *B. vermis*, and a maximum of 18 in *B. tridactylus*.

The ratio of abdominal volume to body mass was calculated for at least 4 adult females of each species. Abdominal volume was modelled as an elliptical cylinder, with major and minor axes being half of mid-body width, and half of mid-body depth, respectively, and abdominal length being cylinder height. Individuals were weighed after being drained of excess preserving fluid, and dried externally with paper towels. As in Shine (1992), I assumed that there is little variation in body distension, or relative 'fullness' of the abdomens of females of different species. This is a relatively strong assumption because of the restricted phylogenetic level of the present study.

A more simple comparison of relative size of the abdomen involved dividing the length of the trunk used to retain eggs for each species by body (axilla-groin) length. This comparison assumes that longitudinal variation in the cross-sectional shape of the adult trunk does not differ significantly among species, which seems likely, because of the generally cylindrical form of all species. The ratio is analogous to comparisons using estimates of volume and mass, but avoids the error resulting from relatively inaccurate measurements of body width and depth, and high variability in body mass in preserved specimens.

Results

Elongation and correlated morphological variation

The species examined fall within two principal size-shape groups (Fig. 1). The first (Group 1) consists of large, pentadactyl species with 30–32 PSV. Most species in this group are almost an order of magnitude more massive than species from the second group (Group 2), which contains slender species with reduced limbs and elevated numbers of PSV (Table I). Within Group 2, *B. bonitae* and *B. tridactylus* (with tiny, 2–3-digitated limbs) have 48–50 PSV, and *B. vermis* (lacking

FIG. 1. Plot of axilla-groin length versus size, represented by head length, for seven species of *Brachymeles*, showing the distinct separation in body form between 'Group 1' (*B. boulengeri*, (□); *B. gracilis*, (■); *B. schadenbergi*, (△); *B. talinus*, (▲)), and 'Group 2' (*B. bonitae*, (○); *B. tridactylus*, (●); *B. vermis*, (⊙)).

TABLE I

Measures of elongation and size for adults of seven species of *Brachymeles*. See text for definition of groups. PSV = presacral vertebrae; PSR = parasternal ribs. Modal values are in parentheses. Linear measures are in mm, with standard deviation

Species	Sex	n	No. PSV	No. PSR	Head length (mm)	Snout-vent	
						length (mm)	mass (g)
Group 1							
<i>boulengeri</i>	M	2	30-32	4-5	9.9±0.2	86.0±0.0	9.5±0.1
	F	11	30-(32)	(4)-5	9.1±0.6	85.0±7.5	9.7±0.9
<i>gracilis</i>	M	23	(30)-32	(4)-5	8.0±1.4	75.6±1.1	6.2±0.5
	F	18	(30)-32	(4)-5	8.0±1.0	77.1±10.8	6.5±0.6
<i>schadenbergi</i>	M	10	31-(32)	3-(5)	11.4±0.6	100.1±6.7	17.4±2.6
	F	9	31-(32)	3-(5)	11.0±0.8	106.1±10.1	17.5±4.9
<i>talinus</i>	M	9	31-(32)	3-(5)	11.2±0.9	107.9±8.9	18.2±5.1
	F	11	30-(32)	3-(5)	10.8±0.9	108.1±9.3	18.7±4.7
Group 2							
<i>bonitae</i>	M	2	50	15	5.4±0.2	65.5±2.1	1.6±0.3
	F	11	(48)-50	(14)-15	5.1±0.4	71.2±5.1	1.5±0.2
<i>tridactylus</i>	M	8	(48)-50	13-15 (14)	5.8±0.4	74.4±5.8	2.5±0.5
	F	26	(48)-51	13-15 (14)	5.5±0.5	71.3±7.7	2.4±0.8
<i>vermis</i>	F	6	59-(60)	16-17	4.3±0.5	63.8±9.9	0.8±0.1

TABLE II

Least-squares regression of axilla-groin length vs. head length for five species of *Brachymeles*. Data $\log_{10}$ -transformed. a = intercept; b = allometric coefficient $\pm$ standard error; r^2 = coefficient of determination

Species	Sex	a	b	r^2	P	n
<i>boulengeri</i>	F	0.20	1.62 ± 0.34	0.74	0.0013	10
<i>gracilis</i>	M	0.67	1.10 ± 0.25	0.62	0.0009	13
	F	0.60	1.21 ± 0.31	0.58	0.0025	13
<i>schadenbergi</i>	M	0.50	1.25 ± 0.23	0.79	0.0006	10
	F	0.05	1.74 ± 0.57	0.61	0.0217	8
<i>talinus</i>	M	0.57	1.23 ± 0.15	0.86	0.0001	13
	F	0.22	1.59 ± 0.19	0.80	0.0001	20
<i>tridactylus</i>	M	0.94	1.07 ± 0.03	0.55	0.155	5
	F	0.93	1.11 ± 0.00	0.54	0.178	22

external limbs) has 58–60. Intraspecific variation in numbers of PSV was low in both groups, and did not appear to be sexually dimorphic in any species (Table I). In all species, there were the same numbers of cervical vertebrae (10), and vertebrae associated with the sternal ribs (three) and xiphisternal ribs (two). Numbers of PSR increased with numbers of PSV (Table I).

Interspecific variation in adult size was found within both groups (Table I). In Group 1, *B. talinus* and *B. schadenbergi* are approximately 20 to 30 mm longer than *B. gracilis* and *B. boulengeri*. Size variation was lower within Group 2, but based on the small sample of adult *B. vermis* ($n=4$), this species seems to be shorter than *B. bonitae* and *B. tridactylus*. Statistically significant sexual dimorphism in sizes of head and body were not found in any species.

FIG. 2. Lengths of vertebrae within the presacral series for adults and juveniles of Group 1 species *B. schadenbergi* (■), and Group 2 species *B. tridactylus* (○), and for an adult of Group 2 species *B. vermis* (▲). Plot shows that variation in vertebral lengths increases with ontogeny in both groups, and among species is inversely related to numbers of presacral vertebrae.

Allometric growth of the body is evident in all species except *B. bonitae* and *B. vermis* (Table II). In *B. bonitae*, a significant allometric regression was not obtained for either sex. This may be due to small sample sizes and variation in vertebral counts among specimens, which would cause deviations from a single linear relationship. In *B. vermis*, the sample was too small to show a relationship. Positive allometry of the trunk is correlated with differentiation of vertebral lengths along the presacral series that accompanies maturation. Differentiation is more prominent in species from Group 1 than from Group 2 (Fig. 2). Adults from Group 2 show relatively low levels of differentiation in the abdominal vertebral series, comparable to that in juveniles from Group 1. Differentiation in vertebral lengths decreases with increasing numbers of vertebrae, and is especially low in the most elongate species, *B. vermis*, in which the abdominal vertebrae comprise a long series of almost uniform length.

Elongation and reproductive output

All species have relatively small clutches ($n < 7$) (Table III). Clutches in Group 1 tend to be larger and more variable than in Group 2, although clutches as low as two were found in the former group, most frequently in the smaller species, *B. boulengeri* and *B. gracilis*. Species from Group 2 have consistently small clutches and relatively little variance in clutch size; a mode and maximum of two offspring was observed in all species.

In all species, egg masses were tightly packed within the abdominal cavity. Because eggs are unshelled, yolk masses tend to spread and fill all available space. In species from Group 1, embryos at late stages of development form discoidal coils around their yolk masses, which are about twice as broad as high. Eggs may be arranged in slightly staggered pairs if clutch sizes are greater than two. In Group 2 species, late-stage embryos are folded rather than coiled, and with their yolk from cylindrical masses that are approximately three times longer than wide, with diameters equivalent to that of the distended maternal abdomen. They lie lengthwise in single file. In individuals from Group 1 with large clutches, there was significant intrusion of the clutch mass into the region bounded by parasternal ribs (Fig. 3a), to the level of the 14th or 15th vertebra. In species from Group 2, the clutch is limited to the region posterior to the last pair of parasternal ribs (Fig. 3b). It seems to be restricted from more anterior positioning, either by the presence of the viscera (lungs, liver and stomach), or the restriction to lateral distension caused by the parasternal ribs.

TABLE III

Clutch sizes and estimates of abdominal size potentially analogous to relative clutch mass for seven species of Brachymeles. Ratios calculated from four (B. boulengeri, B. vermis) or five (remaining species) adult females

Species	Group	Clutch size (mode)	Number of clutches	Volume: mass (mm ³ /g)	Abdomen: axg
<i>boulengeri</i>	1	1-3 (2)	6	377.5 ± 87.9	0.70 ± 0.02
<i>gracilis</i>	1	2-3 (2)	8	320.8 ± 30.2	0.75 ± 0.03
<i>schadenbergi</i>	1	2-5 (3)	4	368.0 ± 51.8	0.82 ± 0.05
<i>talinus</i>	1	3-6 (4)	11	451.2 ± 111.1	0.78 ± 0.02
<i>bonitae</i>	2	2	1	316.0 ± 63.1	0.65 ± 0.02
<i>tridactylus</i>	2	1-2 (2)	13	248.6 ± 58.4	0.67 ± 0.04
<i>vermis</i>	2	2	1	261.3 ± 69.2	0.60 ± 0.03

FIG. 3. Schematic drawing of gravid females (drawn to scale, from real individuals) of (a) *B. schadenbergi* (Group 1) and (b) *B. tridactylus* (Group 2), showing position, size and shape of eggs, and position of posteriormost parasternal rib (PSR). Scale bar = 20 mm.

Both estimates of relative sizes of abdomens indicated that the 'usable' volume decreases with body elongation (Table III). Significant differences in the ratios of abdominal volume:body mass were found among representative species of varying vertebral counts (ANOVA $F = 16.94$, $d.f. = 2, 28$, $P < 0.00001$), and in relative lengths of usable abdomen (ANOVA $F = 65.18$, $d.f. = 2, 28$, $P < 0.00001$). There is some overlap in the relative lengths of usable abdomen between groups, but on average, abdominal length decreases with increasing numbers of presacral vertebrae.

Discussion

Although the present study is not an exhaustive survey of *Brachymeles*, examination of a few individuals of several additional species (see **Appendix 1** for all material examined), and detailed descriptions of remaining species (Brown & Alcalá, 1980; Hikida, 1982), suggest that all species can unambiguously be assigned to either Group 1 or Group 2 as recognized herein, which are equivalent to the 'pentadactyl' and 'non-pentadactyl' groups of Brown & Alcalá (1980).

Two groups were recognized to simplify discussion, although there is variation in size or degree of elongation within each of potential functional significance. The groups are considered as grades, rather than monophyletic groups, because there is no interspecific phylogenetic hypothesis available to suggest otherwise. Small size (as shown by Group 2) and elevated numbers of presacral vertebrae are expected to be apomorphic, because relatively low vertebral counts and moderate body size are primitive for the Scincidae (based on outgroup comparison with the Cordylidae). Thus, the hypothetical common ancestor of *Brachymeles* was most likely morphologically more similar (in size and general shape) to members of Group 1 than to members of Group 2, although at least some, and probably all Group 1 species have diverged from it in some respects.

Morphological variation in *Brachymeles* is accompanied by variation in reproductive output. Elongation is correlated with decrease in numbers of offspring and decreases in the relative amount of abdominal volume available to contain the clutch. Within Group 1, the largest clutches occur in the largest species, in accordance with the commonly observed inverse allometric trend between species size and egg size (Dunham & Miles, 1985; Tinkle & Dunham, 1986; Shine & Greer, 1991). In Group 2, clutches tend to be invariant (two eggs), and are restricted to a smaller, more posterior portion of the maternal abdomen than in Group 1. This appears to be due to the limited confines of a more slender body, and an increase in the relative size of eggs, whose minimum dimensions presumably are limited by functional and ontogenetic factors.

Through comparison between plesiomorphic (Group 1) and Group 2 allometries and morphologies, it is possible to identify ontogenetic differences associated with elongation, which account for differences in relative abdominal size. Instead of strong positive allometry of the posterior abdominal segments, as occurs in Group 1, there is little differentiation in relative lengths of abdominal segments in Group 2. This trend is illustrated further by differences within Group 2 between *B. vermis* and other species (Fig. 2). Although elongation includes addition of abdominal segments, which plausibly could enhance abdominal volume, the number of anterior, rib-bearing somites also increases, so that in relative terms there is little or no increase in abdominal size, and abdominal volume:mass ratios decrease despite the reduction of limbs.

I did not determine by direct measurements that relative abdominal size (volume or length) is strongly correlated with RCM in *Brachymeles*. However, given that the usable abdominal size is lower relative to mass in species with elevated numbers of PSV, the only ways that RCM would not be lower in Group 2 than in Group 1 would be if the available portions of abdomens in small species distend more, or are more densely packed with eggs, than in larger species. Neither appears to be the case, and either would seem to be unlikely, because axial flexibility and a small body diameter are needed for limbless, burrowing locomotion.

Some aspects of morphology of elongate *Brachymeles* related to clutch retention also occur in other elongate lizards, suggesting similar low reproductive output. Most or all limb-reduced lizards have elevated numbers of uniformly-sized vertebrae (Hoffstetter & Gasc, 1969; Leonard, 1981). This morphology most likely facilitates limbless locomotion, but it may have a reproductive cost due to reduction of relative size of abdominal segments, which restricts abdominal volume. Small adult masses and body diameters, which complicate functional considerations of abdominal size because of female-egg allometry, and which are characteristic of members of many clades of lizards (e.g. *Anniella*, dibamids, some pygopodids, some anguids, and skinks from several major lineages), seem to be associated with retention of the juvenile condition of having relatively little variation in vertebral lengths. Perhaps the only 'means' of achieving uniformity in vertebral size is by reducing allometry among segments by limiting somatic growth, which results in small adult

size. A general pattern of paedomorphic (progenetic) evolution may be involved in the derivation of elongate forms, which also is suggested by their relatively juvenile cranial morphologies (Rieppel, 1984; Griffith, 1990).

The apparent difference in RCMs between Group 2 *Brachymeles* and snakes (see Shine, 1992), despite coincident elongation, should not be surprising given the antiquity of the divergence between snakes and lizards, and subsequent radiation in snake size, morphology and anatomy. The morphology of snakes shows dissociation from traits that limit abdominal volume in elongate lizards, such as small body diameter and retention of limb girdles. Other morphological differences which could affect relative volume include differential development of lungs, asymmetrical arrangement of internal organs, and further variation in numbers of body segments. Relative abdominal volumes in snakes may be higher than those in typical lizards, explaining higher RCMs but differences from values in elongate lizards may be greater still because of anatomical differences between suborders that are not apparent externally.

Because few elongate lizards have near relatives which retain moderate size and a relatively plesiomorphic (lacertiform) body, it is rarely possible to determine if evolutionary elongation is correlated with decreased body volume to mass relationships. Patterns in *Brachymeles* may provide a general model explaining or predicting low reproductive output in elongate members of other clades, but variation in ancestral traits and in evolutionary novelties in those groups may result in significantly different mass-volume relationships, and potentially, significant differences in RCM. As yet, few comparative ecological or morphological data have been collected for elongate lizards. Further comparative studies, including evaluation of size and anatomy of relatively closely related, short-bodied taxa, and body form and function in elongate species from other clades, are needed to assess implications of body elongation to life history in lizards.

I am grateful to the staff of the Herpetology Department of the California Academy of Sciences, especially Jens Vindum, who provided workspace and easy access to the collection. Dave Catania (CAS) helped produce radiographs. I thank M. Koo and M. H. Wake for critically reading the manuscript. This work was funded by NSF Grant DEB92-07555 (to M. H. Wake), and an NSERC postdoctoral fellowship.

REFERENCES

- Ballinger, R. E. (1983). Life-history variations. In *Lizard ecology: studies of a model organism*: 241–260. Huey, R. B., Pianka, E. R. & Schoener, T. W. (Eds). Cambridge, Massachusetts: Harvard University Press.
- Brown, W. C. & Alcalá, A. C. (1980). *Philippine lizards of the family Scincidae*. (Silliman University Nat. Sci. Monogr. Ser. 2). Dumaguete City, Philippines: Silliman University Press.
- Camp, C. L. (1923). Classification of the lizards. *Bull. Am. Mus. nat. Hist.* **48**: 289–461.
- Dunham, A. E. & Miles, D. B. (1985). Patterns of covariation of life history traits of squamate reptiles: the effects of size and phylogeny reconsidered. *Am. Nat.* **126**: 231–257.
- Dunham, A. E., Miles, D. B. & Reznick, D. N. (1988). Life history patterns in squamate reptiles. In *Biology of the Reptilia* **16**: 441–551. Gans, C. & Huey, R. B. (Eds). New York: Alan R. Liss Inc.
- Estes, R., de Queiroz, K. & Gauthier, J. (1988). Phylogenetic relationships within the Squamata. In *Phylogenetic relationships of the lizard families. Essays Commemorating Charles L. Camp*: 119–228. Estes, R. & Pregill, G. (Eds). Stanford, California: Stanford University Press.
- Gans, C. (1975). Tetrapod limblessness: evolution and functional corollaries. *Am. Zool.* **15**: 455–467.
- Griffith, H. (1990). Miniaturization and elongation in the genus *Eumeces* (Sauria: Scincidae). *Copeia* **1990**: 751–758.
- Hikida, T. (1982). A new limbless *Brachymeles* (Sauria: Scincidae) from Mt. Kinabalu, North Borneo. *Copeia* **1982**: 840–844.
- Hoffstetter, R. & Gasc, J.-P. (1969). Vertebrae and ribs of modern reptiles. In *Biology of the Reptilia* **1**: 201–310. Gans, C., Bellairs, A. d'A. & Parsons, T. S. (Eds). New York: Academic Press.
- Leonard, C. J. (1981). Evolution of limblessness among scincid lizards of South Africa. *S. Afr. J. Sci.* **77**: 94.

- Rieppel, O. (1984). Miniaturization of the lizard skull: its functional and evolutionary implications. *Symp. zool. Soc. Lond.* No. 52: 503–520.
- Seigel, R. A. & Fitch, H. S. (1984). Ecological patterns of relative clutch mass in snakes. *Oecologia* **61**: 293–301.
- Shine, R. (1992). Relative clutch mass and body shape in lizards and snakes: is reproductive investment constrained or optimized? *Evolution* **46**: 828–833.
- Shine, R. & Greer, A. E. (1991). Why are clutch sizes more variable in some species than in others? *Evolution* **45**: 1696–1706.
- Stearns, S. C. (1984). The effects of size and phylogeny on patterns of covariation in the life-history traits of lizards and snakes. *Am. Nat.* **123**: 56–72.
- Tinkle, D. W. (1969). The concept of reproductive effort and its relation to the evolution of life histories of lizards. *Am. Nat.* **103**: 501–516.
- Tinkle, D. W. & Dunham, A. E. (1986). Comparative life histories of two syntopic sceloporine lizards. *Copeia* **1986**: 1–18.
- Tinkle, D. W., Wilbur, H. M. & Tilley, S. G. (1970). Evolutionary strategies in lizard reproduction. *Evolution* **24**: 55–74.
- Vitt, L. J. & Congdon, J. D. (1978). Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *Am. Nat.* **112**: 595–608.
- Vitt, L. J. & Price, H. J. (1982). Ecological and evolutionary determinants of relative clutch mass in lizards. *Herpetologica* **38**: 237–255.

Appendix 1

Material examined (catalogue numbers from California Academy of Sciences)

Brachymeles apus: 142488, 142489 (embryos); *B. bicolor*: 54613; *B. bonitae*: 25710, 25724, 25725, 25782, 25783, 25880–25882, 25884, 25889, 25891, 25893–25898, 25901, 61376, 61377, 62578, 137053, 144233, 144270, 152024–152026; *B. boulengeri*: 24834, 24837, 24838, 24842, 24843, 24853, 24857, 24860, 24863, 24864, 24868–24871, 24875, 24881; *B. cebuensis*: 24401, 24403, 27537; *B. elerae*: 61499, 61500; *B. gracilis*: 24158, 24160, 24165, 24171, 27401, 27426, 27477, 27479, 27480, 27536, 27541–27544, 28992–28995, 28972–28976, 92852–92858, 92860–92863, 124707, 137603, 139306–139311; *B. samarensis*: 152024–152026; *B. schadenbergi*: 26272–26281, 26283–26287, 124917–124928, 153227–153231; *B. talinus*: 12225, 18359, 28969, 28970, 28977, 28978, 89813, 114229, 114230, 124148, 127663–127668, 127584–127587, 127870–127975, 127962, 128158, 133870, 133871, 144341, 144342, 128159, 133944, 154689, 154692; *B. tridactylus*: 18354, 18355, 153817–153826, 27152, 27154, 27159, 27160, 27162, 27164, 27166, 27170, 27172, 27175, 27177, 27179, 128160, 128161, 1278786, 127877, 127915, 131701, 137566, 137602; *B. vermis*: 60720–60722, 60857, 60858, 62489.